INFOMATION FLOW ON INTERACTION NETWORKS

SIMON LEBLANC

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ADVISERS: IAIN COUZIN AND SIMON LEVIN

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Abstract

Living in groups provides many benefits to individuals, like improved survival in the
face of predators, increased ability to find food, or mates. In addition, group living an-
imals, by pooling knowledge, can make better decisions than individuals in isolation.
To gain such former benefits from being in a group, information has to be exchanged
among group members, and how this is achieved when individuals are uncertain, have
competing interests, exhibit individual differences, and must make decisions within
complex habitats is not completely understood. While some animals communicate
by exchanging signals, the majority of schooling fish predominantly use cues. They
leak information through their actions: where, when and how they move. Fish have
access to a lot of visual information, and yet how they use this has not been examined
in depth. From recent knowledge of how fish employ visual information, interaction
networks can be reconstructed revealing hidden pathways of communication (how
the behavior of individuals influences others). In this thesis, I provide the tools and
models necessary to generalize experimental techniques of visual field reconstruction
to computer generated groups of individuals in arbitrary configurations. Then, I use
the flexibility afforded by these methods to study multiple problems related to the
anti-predatory behaviors of fish schools. A group has many eyes to keep watch of its
surroundings, but how many? I show that the answer depends on multiple factors,
like the global state of the group, its density, and the peripheral vision of the fish.
Once a threat is detected, an effective response requires an alarm wave to spread. Al-
though the capacity to detect predators can vary depending on their position around
the group, alarms tend to spread equally well in all directions by virtue of the topol-
yogy of the interaction network, itself a consequence of the embeddedness of the fish
bodies in their environment. By studying how groups may adapt to perceived danger,
I find that alarms spread best when individuals adjust their rules of motion, and their
sensitivity to the movements of others, simultaneously. Finally, using a dynamical
model, I show that predators can benefit from coordinating while hunting.
Acknowledgements

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To Imène, Lila, and Malik
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Chapter 1

Introduction

Throughout their lives, animals must make decisions, and the results of their decisions directly affect their reproductive fitness. Even for the simplest organisms, these decisions are rarely random, but based on a context, which can be local, such as the immediate surroundings of the organism (contact sensing), but can also span much larger areas and include other organisms like predators or conspecifics. Individuals within groups often contribute to decentralized collective decisions despite the selfish interests of their members. However, the distribution of information in a group can be unequal so information must also be transferred between group members. In my thesis, I study the flow of information as it enters and percolates, via contagious behavioral change, within a group of social animals—principally schools of fish—on a short time scale and under various environmental conditions. In addition, I explore the role of embeddedness, the interaction between the body and the world, versus explicit decisions in the information transfer capabilities of individuals within a group, and the consequences these have on collective dynamics.

Although multiple sensory modalities, including audition, olfaction and the lateral-line, are thought to play a role in fish schooling [1, 2], vision appears to be the principal modality for many species [3–5]. The golden shiner (Notemigonus crysoleucas), a
widespread freshwater species, has recently been used as a model organism for the study of collective behavior. It swims close to the water surface [6], and the lateral line is thought to contribute minimally to schooling [7, 8]. These fish, like many other, exhibit fast-start behavior [9] mediated by a reflex circuit involving Mauthner cells [10] which sometimes triggers in the absence of any external stimuli. Rosenthal et al. [11] have used this species in experiments and were able to reconstruct the visual fields of every individual in schools of \( \approx 150 \) fish using a ray-casting method, and used these visual fields to infer the interaction networks underlying the transfer of information during spontaneous startle events. While the visual field reconstruction methods developed in this paper are very powerful, they are only suitable for the analysis of experimental data. Analyzing experimental data is extremely valuable, but the study of collective behavior can also greatly benefit from the use of simulations, and it would be very useful to be able to compute the interaction network of a simulated school of fish. To this end, I develop in chapter 2 a model where a group is composed of elliptical individuals in the plane for which it is possible to mathematically reconstruct their field of views. A method to handle the multitude of occlusions that inevitably occur in such groups is also presented. Lastly the validity of the method is assessed by reproducing the analysis of [11] using the same dataset of fish positions and orientations as they used but mapping the positions and orientations of the fictive elliptical individuals on the positions and orientations of the actual fish. Despite the inherent simplifications of my model, both methods are found to be in good agreement.

It is thought that many animals live in groups to decrease their risk of predation [12–14]. One common mechanism potentially used to achieve this goal is known as the “many eyes” principle [13, 15] whereby many individuals simultaneously watch their surroundings increasing the overall vigilance of the group. Clearly, access to external visual information must depend on one’s position within the group. For instance, it seems intuitive that individuals located near the core of the group should
not be able to see as much of the outside world as individuals located near the edge of the group. However, except briefly in [11] for schools of golden shiners, the actual access to external visual information has never been studied and measured precisely. Furthermore, fish schools often dynamically change among different states, characterized by order parameters, such as swarming (low polarization, low rotation), schooling (high polarization, low rotation), and milling (low polarization, high rotation) [16], which can give them very different internal structures further influencing who has access to external information. Besides the predator detection problem comes the problem of acquiring pertinent social information about a potential threat, which is also likely influenced by the configuration of the group at the time of detection. In what is known as the “Trafalgar effect”, information (behavioral change) typically propagates similarly to a wave at a speed much faster than the speed of the individual group members [17]. But describing precisely this propagation requires us to know both the location of the first responders as well as the interaction network of the prey school and has never been achieved at a sufficient level of detail. In chapter 3, I use the tools developed in chapter 2 to analyze both the detection and the acquisition of social information capabilities of schools of golden shiners. The question of the active positioning of the fish in order to enhance (or weaken) these capabilities is also addressed by running a comparative analysis on artificial schools of elliptical particles. I find that the embeddedness of the individuals in their environment—their elongated body shape and the visual occlusions that they provide—is sufficient to explain most of the observations made in this chapter and it is found that fish do not need to maintain strict fixed relative positions to efficiently detect and react to predators.

As stated before, the reduction of the predation risk is considered one important reason for living in groups [12–14]. Multiple cues, mostly visual and olfactory, can give away the presence of a predator to a fish school [18]. Once it is suspected that a predator is nearby, the individual, and collective, behavior of the fish can change
noticeably. At the individual level fish sometimes dash, freeze, reduce their foraging behavior [19], reduce their speed, and move more predictably [20]. At the group level most species tend to form tighter schools [21, 22]. Minnows move closer to other fish and position themselves so as to be surrounded by near neighbors on all sides [22]. It is reasonable to assume that individuals would want to increase their collective vigilance if the environment is perceived as risky. One fairly obvious way to achieve this is for individuals to increase their own sensitivity to alarm cues by responding more easily to the alarm behaviors exhibited by their conspecifics. But other less explicit changes in individual behavior, combined (or not) with modifications of the sensitivity, might also lead to the emergence of a heightened vigilance at the group level. For instance, changes in how individuals position themselves relative to their neighbors will affect the structure of the network which in turn affects how information is transferred. In general, individual vigilance tends to decline as group size increases [23–25] but without lowering collective vigilance thanks to an increased probability of detecting predators (many eyes) combined with a reduction in individual risk (dilution effect) [26, 27]. It has been shown that some social prey increase individual vigilance in the presence of predators [28]. Many species of fish have in their skin a chemical compound that can only be released when the skin is damaged, for instance by the teeth of a predator, which serves as an olfactory alarm cue to warn of the presence of a predator [29–31]. This alarm substance known as schreckstoff can be extracted and used to make the environment appear risky to schooling fish during experiments. Preliminary experiments conducted by Matt Grobis and myself show that golden shiners, the species after which the visual framework used throughout this thesis is modeled, reduce their inter-individual distances and form tighter schools when exposed to schreckstoff. In chapter 4, I study the effect of adjusting inter-individual distances and sensitivity to social cues on the ability of fish to detect threats in their surroundings and to propagate information relative to a potential danger. I show that increasing both
the density of the group and the sensitivity of individuals simultaneously is much more effective at optimizing information transfer than increasing each one of these individually.

Although predator-prey interactions are fundamental and shape a lot of collective behaviors, their fine scale dynamics and their effect on how groups process information have not been well studied. In addition, obtaining data from the field has always been a challenge [32]. Krause and Godin [33] ran experiments on the interactions between cichlid predator (*Aequidens pulcher*) and guppies (*Poecilia reticulata*) and concluded that despite the over-proportionately high attack risk for individuals in large shoals, per capita predation risk is lower than in small shoals. Major [34] studied the predator-prey interactions between the predatory jack (*Caranx ignobilis*) and the Hawaiian anchovy (*Stolephorus purpureus*) and observed that single predators were the most successful at capturing isolated prey, and relatively unsuccessful at capturing individuals in schools, whereas grouped predators were the most successful at capturing schooling prey. Furthermore, larger predator groups were able to break up schools of prey more quickly, resulting in increased numbers of prey becoming isolated which facilitated capture. In [35], we used a high-resolution imaging sonar to record “acoustic videos” of the highly dynamic interactions between the spotted sea trout (*Cynoscion nebulosus*), and its schooling prey, the juvenile Gulf menhaden (*Brevoortia patronus*) in their natural environment. We show that the fragmentation of prey schools increased their per capita risk and that predators often form coordinated hunting groups, with up to five individuals in a line formation, despite the prey being abundant and the predators being unrelated to each other. We hypothesize that coordinated hunting groups may facilitate fragmentation to disrupt the ability of prey to communicate and increase the predators’ chances of catching prey from much smaller schools than they would encounter if hunting alone. But such a strategy appears evolutionary unstable as a predator could benefit from the coordination of other predators without paying
the cost of contributing, or in other words be a successful cheater. In chapter 5, I build a simple dynamical model of the coarse grain interactions between a group of prey and a group of predators, and show that mixed strategies in which predators invest some of their time in coordination (how much time depends on the fission-fusion dynamics of the prey) can not only be beneficial but can maximize the net collective benefits for predators.
Chapter 2

An Approach to Visual Field Reconstruction in Groups

Abstract  Like many species of schooling fish, golden shiners (Notemigonus crysoleucas) rely primarily on vision for schooling [7, 8, 36, 37]. Rosenthal et al. [11] have developed a powerful method for inferring the interaction networks of fish schools which requires the knowledge of the visual fields of every individual. They reconstructed the visual fields of every individual in schools of \( \approx 150 \) golden shiners using a ray-casting method. While powerful, this method of reconstructing visual fields relies on knowing the full body shapes of the fish which are rarely included in simulations of fish schools. In this chapter, we model fish schools as a collection of identical elliptical objects and solve the problem of reconstructing their visual fields in the plane while taking occlusions into account. This model can be used as a basis to compute interaction networks in both static and dynamic simulations and enables rapid and flexible virtual experimentation. To test the validity of this approach, we map the position and orientation of the objects in the model to those of the actual fish in [11] and reproduce their results. Despite the simplification of the model, both methods are found to be in good agreement.
2.1 Motivation

In the study of collective animal behavior, pathways of communication are typically not directly observable. Animal groups sometimes appear to move as if orchestrated by a single operator yet no messages of any sort appear to be exchanged between individuals. It was even considered, until the first half of the 20th century, that transference of thoughts could explain the stunning coherence of motion within large flocks of birds [38]. But we now know that birds in flocks and fish in schools can see, hear, smell and sometimes feel each other and use this information to act coherently [39].

Many species of fish in particular appear to primarily rely on vision for schooling [3–5]. The golden shiner (Notemigonus crysoleucas), an obligate schooling freshwater species frequently used as a model organism for the study of collective behavior, is one of them [36, 37]. In this species, the lateral line has been shown to contribute minimally to schooling [7, 8].

To be able to reveal the hidden networks of interaction of animal groups, Rosenthal et al. [11] have developed a powerful method by observing rapid waves of behavioral changes in schools of golden shiners, which relies on the knowledge of what each fish can see. Golden shiners, like many other, exhibit fast-start behavior [9] mediated by a reflex circuit involving Mauthner cells [10] which sometimes triggers in the absence of any external stimuli, and sometimes causes other fish in the school to react as well. Rosenthal et al. were able to track the positions and body postures of all individuals in schools of around 150 fish and reconstructed their complete visual fields using ray casting. Golden shiners swim close to the water surface in schools that are essentially flat [6, 40] thus a planar representation of their visual fields captures the most relevant part of their sensory during these critical waves of behavioral changes. Thanks to the findings in [11], interaction networks can be computed directly from the visual fields of all individuals in the school at any given time, without having to know their dynamics.
One advantage offered by their method of reconstructing visual fields is that it is very accurate since the full body posture of the individuals is taken into account. One important drawback is that it is constrained to the analysis of experimental data (videos of fish schools swimming). While manipulating schools of fish in experiments is possible to a certain degree, it can be very challenging and time consuming. Firstly, there may be ethical concerns restricting the realm of what is possible to do. Secondly, while it has recently become possible to control the sensory input of live animals in isolation [41, 42], controlling a large number of interacting animals simultaneously is currently out of reach.

On the other hand, models and computer simulations offer quasi-infinite flexibility, at the cost of not being a perfect representation of nature, and have provided and still provide tremendous insights in the field of collective behavior [43–48]. Interaction networks are key to understanding the exchange of information within fish in schools, and to have the flexibility of being able to compute the interaction network of any school with arbitrary fish positions and orientations is very valuable.

In this chapter we describe a model where our fish have idealized body shapes resembling those of golden shiners—ellipses with a large aspect ratio—whose geometrical properties allow us to precisely reconstruct their visual fields. There are two main challenges while developing such a model. The first one is to reconstruct the visual extent of one individual as seen by a focal individual independently of the locations of both individuals. The second one is dealing with occlusions, which is more complex and more expensive in terms of computational cost. In this chapter, we describe the model and validate it using data from [11]. Many other chapters in this thesis then build upon this model to address specific scientific questions.
2.2 Model

In the following, we refer to our pseudo-fish as *individuals* in the hope that this model be applied widely to other species whose typical body shape can be approximated by an ellipse and for which vision is an important modality.

2.2.1 Description of an individual

Each individual has the shape of an ellipse of length 1 and width $w$ (Figure 3.1). Conveniently, this implies that all distance measurements can be read directly in body lengths. We define the *center of mass* of an individual as a point located along the main axis of the individual at a distance $\ell/2$ from the center of the ellipse. Thus $\ell = 0$ means that there is no offset between the center of mass and the center of the ellipse while $\ell = 1$ means that the center of mass is at the tip of the ellipse. We use the center of mass both as the position of the individual in evaluating distances, its center of rotation and the location of its unique eye.

![Figure 2.1: An elliptical individual facing right with its center of mass shown in red.](image)

The *state* of an individual is the combination of its position and its orientation in the plane. For dynamic models, the orientation can be replaced by the velocity.

2.2.2 Reconstructing visual fields

We define the *visual field* of an individual as the union of the triangles joining its eye to the extremal visible points of every other individual.
Thanks to their elliptical shape, it is possible to reconstruct analytically the field of view of each individual. This is done in two steps. The first step consists of finding the location on each observed individual of the two extremal points that intercept a ray cast by the observer. Such a pair of points defines a segment which represents the full section of an individual. The second step consists of splitting these segments and removing the portions which are occluded by other individuals. An illustration is shown in Figure 2.2.

![Figure 2.2: Visible (solid green) and invisible (dotted red) sections of two individuals as seen from a focal individual (bottom left). The individual in the middle occludes part of the individual on the top right.](image)

We now derive the analytic formula for the position of the two points delimiting a visible section (without occlusions).

![Figure 2.3: Position and orientation of a target ellipse relative to an observer in O.](image)

Let the observer be at the origin of a polar coordinate system, and the target individual be at location \((r, \theta)\) with orientation \(\phi\) (Figure 2.3). As previously mentioned, the target individual has length 1, width \(w\), and an offset of \(\frac{\ell}{2}\) between the center of the ellipse and the center of mass of the individual. The center of the ellipse is thus
located at \((r_e, \theta_e)\) where:

\[
\begin{align*}
    r_e \cos \theta_e &= r \cos \theta - \frac{\ell}{2} \cos \phi, \\
    r_e \sin \theta_e &= r \sin \theta - \frac{\ell}{2} \sin \phi.
\end{align*}
\]  

(2.1)

We are looking for the points of intersection of the ellipse with its two tangents passing through the origin.

We can write the parametric equation for the ellipse as:

\[
\begin{align*}
    r_e \cos \theta_e + \frac{1}{2} \cos \phi \cos \psi + \frac{w}{2} \sin \phi \sin \psi \\
    r_e \sin \theta_e + \frac{1}{2} \sin \phi \cos \psi - \frac{w}{2} \cos \phi \sin \psi
\end{align*}
\]  

\[\psi \in [0, 2\pi).\]  

(2.2)

To find the equation of the tangent at \(\psi\), we take the derivative of (2.2) with respect to \(\psi\) to get:

\[
\begin{align*}
    -\frac{1}{2} \cos \phi \sin \psi + \frac{w}{2} \sin \phi \cos \psi \\
    -\frac{1}{2} \sin \phi \sin \psi - \frac{w}{2} \cos \phi \cos \psi
\end{align*}
\]  

\[\psi \in [0, 2\pi).\]  

(2.3)

We can now find the two points on the ellipse at which the tangent is parallel to the line going through the point and the origin:

\[
\begin{vmatrix}
    r_e \cos \theta_e + \frac{1}{2} \cos \phi \cos \psi + \frac{w}{2} \sin \phi \sin \psi & -\frac{1}{2} \cos \phi \sin \psi + \frac{w}{2} \sin \phi \cos \psi \\
    r_e \sin \theta_e + \frac{1}{2} \sin \phi \cos \psi - \frac{w}{2} \cos \phi \sin \psi & -\frac{1}{2} \sin \phi \sin \psi - \frac{w}{2} \cos \phi \cos \psi
\end{vmatrix} = 0
\]  

(2.4)

Solving for \(\psi\), we find the two solutions:

\[
\begin{align*}
    \psi_1 &= 2 \arctan \frac{\alpha - r \sin (\theta - \phi)}{(2r \cos (\theta - \phi) - 1)w} \\
    \psi_2 &= -2 \arctan \frac{\alpha + r \sin (\theta - \phi)}{(2r \cos (\theta - \phi) - 1)w}
\end{align*}
\]  

(2.5) (2.6)
where
\[ \alpha = \sqrt{-w^2 + \frac{w^2 + 1}{2} r^2 + \frac{w^2 - 1}{2} r^2 \cos(2(\theta - \phi))} \] (2.7)

The two points defining the section are therefore, in cartesian coordinates:

\[
\begin{pmatrix}
  r \cos \theta - \ell \cos \phi + \frac{1}{2} \cos \phi \cos \psi_1 + \frac{w}{2} \sin \phi \sin \psi_1 \\
  r \sin \theta - \ell \sin \phi + \frac{1}{2} \sin \phi \cos \psi_1 - \frac{w}{2} \cos \phi \sin \psi_1
\end{pmatrix}
\] (2.8)

and

\[
\begin{pmatrix}
  r \cos \theta - \ell \cos \phi + \frac{1}{2} \cos \phi \cos \psi_2 + \frac{w}{2} \sin \phi \sin \psi_2 \\
  r \sin \theta - \ell \sin \phi + \frac{1}{2} \sin \phi \cos \psi_2 - \frac{w}{2} \cos \phi \sin \psi_2
\end{pmatrix}
\] (2.9)

Figure 2.4: While visible segments are often almost perpendicular to the observer (like for the top left ellipse), they can also be more surprising for some orientations of the target (like for the bottom right ellipse).

Note that the shape of the observer is irrelevant. Each individual may have unique \(w\) and \(\ell\) values. In practice, we often assume that all individuals are identical.

When the eye of the observer is located inside the body of the target individual, the problem becomes ill-posed so the target individual is ignored and no visual field is defined.

In subsection 2.2.4, we will see that chunks of the segment defined by the two points given in (2.8) and (2.9) may have to be removed due to occlusion. Examples of complete segments are shown in Figure 2.4.
2.2.3 Dealing with occlusions

Occlusions occur when objects are *shadowing* a target from the point of view of an observer. While total occlusion is easy to handle, partial occlusions are subtler. In this case we are concerned about individuals either located in between an observer and a target individual or intersecting with a target individual. Given an observer, a target individual and another individual (the *obstacle*), there are four possible occlusion patterns: none, total, lateral and splitting; they are obtained from six distinct configurations because lateral and splitting occlusions can also occur from intersections between the target individual and the occluding individual. These patterns are summarized in Figure 2.5.

Figure 2.5: Six distinct configurations yield four patterns of occlusion: no occlusion (a), total occlusion (b), lateral occlusion (c) and (d), and splitting (e) and (f).

Given a point of observation, a target segment and the segment of another po-
entially occluding individual, the occlusion pattern of the target individual by the other individual can be computed by testing if the two segments intersect and if the ends of each segment are located in specific areas relative to the segment of the other individual and the point of observation. These areas are the \textit{cone} which is the zone delimited by the two half-lines going from the observer to each extremity of the segment of the target (Figure 2.6a), and the \textit{back} which is the half-plane away from the observer delimited by the line going through both extremities of the segment of the target (Figure 2.6b).

![Diagram](https://via.placeholder.com/150)

(a) The \textit{cone}  
(b) The \textit{back}

Figure 2.6: The classification of occlusions requires for each pair of segments to identify in which area(s) each end of a segment lies relative to the other one. (a) shows the \textit{cone} and (b) shows the \textit{back}.

For instance, if the two segments do not intersect and both ends of the target segment are in the cone and in the back of the other segment, then the target is fully occluded (first line of Table 2.1).

For completeness, one must handle the fact that segments have no particular orientation, their ends are interchangeable, so matching rules often have to be duplicated. The full list of matching rules for classifying occlusion patterns is given in Table 2.1.
Table 2.1: Patterns of occlusion of the target segment by another segment (obstacle). A checkmark (✓) in Target ▷ First end ▷ Cone means that the first end of the target is inside the cone defined by the observer and the obstacle. A cross (×) means the opposite (not inside the cone). A dot (·) means that whether or not the point is inside the cone is irrelevant. The first line to match gives the pattern of occlusion.

<table>
<thead>
<tr>
<th>Target</th>
<th>Obstacle</th>
<th>Pattern of occlusion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intersect</td>
<td>Cone</td>
<td>Back</td>
</tr>
<tr>
<td>.</td>
<td>✓</td>
<td>✓</td>
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<tr>
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</table>
2.2.4 Scaling up

We have seen methods for reconstructing visual fields and detecting occlusions for a single observer, a single target and a single obstacle, we can now scale this up to a full group of individuals.

Let $N$ be the number of individuals in the group. There is no constraint on the position and orientation of the individuals except that overlays where the eye of one individual is inside the body of another are to be avoided as much as possible (because the visual field is not well defined in this case). There are three common ways to set the position and orientation of individuals: random generation, using existing fish data or using a model. The choice does not matter at this point but all three are used at some point in this thesis.

The algorithm to find the full visual field of all individuals proceeds as follows: First, from the point of view of each individual, the segment corresponding to every other individual is computed. This part is computed in linear time for the number of individuals. Then, for each segment, every other segment is tested for occlusions. If a segment is found to be partially occluded, the segment is split and the occluded chunks are discarded. This part is the most expensive, it is computed in polynomial time. However, it can be sped up if limitations in detection capabilities are introduced (maximum range, minimum subtended angle...), in which case individuals might be discarded quickly based on their distance to the observer and orientation. The result is a list of visible chunks for each individual in the group. An example representation of the complete visual field of one individual in a group is shown in Figure 2.7.

2.3 Validation

In order to validate our model, we reproduce some of the results of Rosenthal et al. [11] using the same dataset of fish positions and orientations but replacing actual body
Figure 2.7: Reconstructed visual field of one individual in a school.
shapes by ellipses whose shape closely matches the typical body size of the fish. We use a body length of 5 cm, which was the typical length of the fish in this dataset [11].

2.3.1 Position within the group

It is often useful to be able to look at individual level properties at an intermediate level, where variables are combined over a domain that encompasses multiple individuals, but that is still much smaller than the full group. To this end we need to characterize the position of individuals within the group independently of its shape or position. In particular, we would like to know if individuals are close to the edge, or, for polarized groups, where the orientation of the group can easily be defined, if individuals are close to the front or to the back.

Since typical groups have irregular shapes, we use $\alpha$-shapes [49] to find the edges. Following [11], we use a radius of 5 body lengths. We can then, for each individual, compute their distance to the edge. As in [11], individuals who are in a degenerate position (either out of the main $\alpha$-shape or connected to the main $\alpha$-shape but not part of its volume) are excluded from the analysis as they do not directly take part in the collective behaviors.

To determine if a group is polarized, we compute its polarization and angular momentum and follow the classification defined in [16]. For polarized groups only, the orientation of the group is defined as the average orientation of all individuals, and the distance from back to front of each individual is obtained by measuring the position of the center of each individual along the longitudinal axis and normalizing such that the rearmost individual is at distance 0 and the frontmost individual is at distance 1.

2.3.2 External visual field

The first element of comparison is the external visual field, that is for each individual the cumulated angle of all portions of their visual field that extend outside the group.
An example is shown in Figure 2.8. Since this is an individual measure, we can summarize it by plotting the distribution of external visual fields as a function of the binned distance from the back to the front of the group (in the case of polarized groups, Figure 2.9a) and the binned distance from the edge to the center of the group (Figure 2.9b).

![Figure 2.8](image)

Figure 2.8: External visual field of all individuals in a group. A value of 1 means 360° of external visual field.

### 2.3.3 Social influence

The second element of comparison is the social influence. It is defined in [11] for each individual as the local weighted directed clustering coefficient of the corresponding node in the interaction network. This definition was chosen to take into account not only the influence of an individual on its direct neighbors but also the indirect influence it has on others via the influence it has on its direct neighbors. The interaction network
Figure 2.9: Distribution of external visual field as a function of (a) distance from back (polarized groups only), and (b) distance from edge. The black line shows the median.
is computed using two characteristics of the visual fields: the log of the metric distance (LMD) between individuals $i$ and $j$, and the ranked angular area (AR) of individual $j$ subtended on the eye of individual $i$. The weight $w_{ij}$ of edge $(i, j)$ is given by the following equation from [11]:

$$w_{ij} = (1 + \exp(-\beta_1 - \beta_2 \text{LMD} - \beta_3 \text{AR}))^{-1}$$

(2.10)

where $\beta_1 = -1.985$, $\beta_2 = -1.421$ and $\beta_3 = -0.126$. Note that the value of $\beta_1$ is different than in [11] to account for the different unit system (body lengths versus centimeters). More details can be found in [11].

![Figure 2.10: Social influence of all individuals in a group (log scale).](image)

An example of the spatial distribution of social influence within a group is shown in Figure 2.10. The distribution of social influence as a function of the binned distance from the back to the front of the group (in the case of polarized groups) is shown in Figure 2.9a, and as a function of the binned distance from the edge to the center of
the group in Figure 2.9b.

2.3.4 Direct comparison

We can see that despite the fact that the shape of real fish is not perfectly matched by ellipses, we still find that properties such that external visual field and social influence as a function of position within the group are easily reproduced (Figure 2.12). The most notable difference is the relatively lower social influence very close to the edge of the group in Figure 2.12b compared to Figure 5F of [11]. This is a side effect of approximating true fish bodies of varying size with fixed size ellipses. This particular data point is very sensitive to the radius of the $\alpha$-shape because it includes the individuals that are exactly on or very close to the edge, as defined by the $\alpha$-shape. In [11], a radius of 25 cm was used for fish of length 4-5 cm. For simplicity, we assumed that all fish were 5 cm long which mandates a radius of 5 body lengths.

2.4 Discussion

We have shown that it is possible to reconstruct the complete visual fields with full occlusions for all individuals in a group assuming they all have an elliptical body shape. The knowledge of these visual fields provides information about the sensory inputs of each individual with high granularity (how much angular area does each neighbor cover on the retina of a focal individual, how much angular area does the outside of the group cover) as well as a very detailed weighted directed network of interaction which can be constructed and used for analyzing social behavior. We have also shown that this model can be used in conjunction with real data from experiments on live animals, and that it is a sufficiently good approximation for reconstructing visual fields that yield valid networks of interaction and individual properties. But the main contribution of this model is the great flexibility it affords for exploring configurations
Figure 2.11: Distribution of social influence as a function of (a) distance from back (polarized groups only), and (b) distance from edge. The black line shows the median.
Figure 2.12: External visual field and social influence as a function of (a) distance from back (polarized groups only), and (b) distance from edge. Units are standardized such that the mean is 0 and SD is 1. Data from Figure 3E and 3F of [11] is reproduced with permission.
that could not be attained with live animals, as well as the possibility to explore how visual properties of the environment can affect schooling, as will be demonstrated in the next chapters.
Chapter 3

Predator Detection and Network Structure

Abstract  One function of schooling is to provide increased detection, and response, to predators. A well-known proposed mechanism is the “many eyes” principle \[13, 15\] whereby the multitude of fish composing the school can collectively watch their surroundings with increased coverage and redundancy. Although this mechanism has been observed qualitatively for a variety of fish species, it has never been studied quantitatively. A quantitative description can provide insight into the trade-offs faced by fish within schools when balancing predator defense and other goals. In this chapter we use reconstructed visual fields to predict, quantitatively, the predator detection capabilities of schools of golden shiners. We show that schools in different configurations have different predator detection capabilities but that this does not necessarily mean that they are at an increased risk. In addition, using the same analysis on artificial schools with randomized fish positioning, we show that these properties result for the most part from the body characteristics of the fish and how they interact visually with each other, and not from active positioning of the individuals within a school.
3.1 Motivation

Predation is widely believed to be a major evolutionary driving force in fish schooling [12, 13, 21, 50, 51]. Multiple anti-predator mechanisms have been proposed to explain how individual fish benefit from schooling.

The passive mechanisms include the dilution of risk [15, 52] by which the chance of a single prey being captured by a predator is much lower if it is surrounded by many other similar individuals. This mechanism works very well as long as the group is larger than the number of prey a satiable predator can eat during an attack, such that the risk keeps decreasing as the group becomes larger.

Being in a school can also reduce the probability of being detected by predators [52] by combining the visual footprint of each individual into a single visual sphere of comparable size. This effect which might seem small to us terrestrial creatures takes a lot of importance in water where visible ranges are shorter and where turbidity often restricts visible ranges further still.

![Figure 3.1: Schooling can help fish reduce their global visual footprint.](image)

Another particularly robust mechanism which could be considered both passive and active (depending on how a particular prey species reacts to predators) is the confusion effect [53, 54] by which a predator’s sensory system is distracted by a large number of moving prey, preventing it from focusing on and effectively hunting a single target. The effect is further enhanced in homogeneous fish schools where prey all look very similar, as it has been shown that in this context, the oddity of a prey greatly
increases its chance of being captured [55, 56].

A more active approach consists of employing social cues to increase individual vigilance in order to detect predators earlier and react faster. The “many eyes” principle [17] is the pooling of the predator detection efforts of many individuals. This provides for a better coverage of the space since one individual can watch an area that another individual cannot see, for instance because its own field of view is limited, either by occlusion or simply because it does not extend to 360°. This also provides for redundancy since a single point in space might be seen by multiple individuals simultaneously.

But while the general principle is well accepted and understood, little is known about the specifics of how vigilance is distributed among the members of the group nor how this relates to the effectiveness of the collective response. As seen in chapter 2, individuals at the edge of the group tend to have better access to external information than those inside the group and are thus more likely to be the first to detect a threat. But individuals inside the group can also sometimes have good access to external information, depending on the alignment of their neighbors with respect to their own body orientation, and individuals at the back of a polarized school (thus near the edge) might not have very good detection capabilities if they have overlapping blind zones behind them. Hence the number of “eyes” watching a certain area might fluctuate depending on the spatial configuration of the school, and the first responders to a threat might be in unexpected locations. This might also have implications as to how individuals can and choose to balance their time between predator vigilance and other tasks.

Furthermore, detecting a predator is not enough. When a threat is detected, information about the threat has to propagate for an efficient collective response to take place. This rapid propagation, known as the “Trafalgar effect”, is typically much faster than the maximum swim speed of the fish themselves [17]. It is not
known if in order to reap the benefits of the many eyes, the fish must play an active role by maintaining themselves in specific positions relative to their neighbors or if these benefits tend to be robust to the internal configurations of schools. Active positioning exists in other contexts, for instance, it is known that in some species of birds [57–59] and some schooling fish [51, 59–61] individuals may tend to prefer specific positions relative to their neighbors that allow them to save energy by taking advantage of turbulent vortices, although evidence for this is not conclusive. Or more simply individuals in schools or flocks tend to keep a buffer zone around themselves to avoid collisions with their conspecifics. The reason this might be important is that the positioning of the individuals within the group determines the occlusion patterns in the visual fields of everyone and thus the information pathways. The important point is that the mere embedding of the bodies in their environment can affect the group in different ways. While at the individual level, the brain of the animals processes most information, at the group level the internal structure of the school and the anatomy of the fish might also play important roles.

3.2 Overview

In the following section, we examine different properties of either the interaction network or the collective visual capabilities of schooling fish modeled as elliptical individuals. The position and orientation of all individuals are taken from the golden shiner dataset of [11] with a fixed body length of 5 cm and an aspect ratio of 8:1 which is close to that of real fish based on empirical fitting to fish images. This dataset is labelled C for Control. To measure the influence of the positioning of the fish relative to each other on the predator detection and information transfer capabilities of the schools, we also generate several transformed versions of the original dataset where some properties of the first dataset are altered but other properties are conserved.
Running the same analysis on all of these datasets unveils which of these properties (if any) are required or important to facilitate the acquisition and/or transfer of information within these groups.

To ensure that all the datasets are comparable, the shape of each school and the number of fish are held constant across all the transformed datasets and match the original one. The properties being altered are, at the individual level, the position and orientation of each fish, and at the macroscopic level the density (or rather its homogeneity), and the polarization of the whole group.

The following procedure is used to randomize individual fish positions while conserving the shape and the number of fish of each school: First, the boundaries of all schools in the original dataset are computed using $\alpha$-shapes with a radius of 5 body lengths. Then, for each school in the original dataset, a number of points equal to the corresponding number of fish in the school are chosen randomly (more details in the next paragraph). Rejection sampling is used to ensure that all selected points are within the bounds of the $\alpha$-shape of the original fish school.

One of the main questions asked in this chapter is whether or not, and to what extent, golden shiners are positioning themselves relative to each other to increase their collective information processing capabilities. The first transformed dataset, labelled PD for random Position+Density, is one where the position of individuals is uniformly random within the bounds of the original schools. In this dataset the density is much more heterogeneous than in the original dataset since nothing prevents two random uniform points from being very close to each other.

Density might play an important role on vision by clearing or occluding fields of view. Furthermore, we observe that golden shiners like to keep a buffer zone around themselves, both to avoid collisions and perhaps to conserve a reasonable field of view, so they rarely end up very close to each other. We thus generate a second transformed dataset, labelled P for random Position, where we control for density. In
this dataset, positions are randomized using Mitchell’s best-candidate algorithm [62] (using 3 candidates) instead of sampling uniformly to keep density fluctuation under control. The algorithm consists of, for each point that needs to be sampled, sampling $k$ points from a uniform distribution, keeping only the one that is the furthest apart from all previously sampled points, and discarding the $k - 1$ other points. The effect is to increase the minimum inter-individual distance which mimics the natural short-range repulsive tendency of real schooling fish. A small number of candidates ($k = 3$) is used so as not to completely remove density fluctuations.

The orientation of individuals is also likely to be an important factor in the resulting pattern of field of views. Both of the aforementioned transformed datasets come in two flavors: the polarization is either conserved or the individual orientations are uniformly randomized. The procedure for conserving the polarization is as follows: for each selected point, the orientation is copied from the orientation of the nearest point in the first dataset and a small angular perturbation of standard deviation $\sigma = 10^\circ$ from a wrapped normal distribution is subsequently added to it so as to conserve both local orientations and global angular momentum. The result is a randomized school with approximately the same state (polarized, milling, swarming, or transitioning) as in the original dataset. The two corresponding transformed datasets are labelled POD for Position+Orientation+Density, and PO for Position+Orientation.

For completeness, a fifth transformed dataset, labeled O for Orientation, is also included in which only the orientations are uniformly randomized (the positions are identical to those in the original dataset). Figure 3.2 shows the same example fish school in each dataset.

We then analyze several group-level properties of fish schools, both real and randomized, to find out the extent to which precise positioning, orientation, density control, or a combination thereof play a role in enabling them, and reflect on the role of the elongated shape of the fish bodies on their visual capabilities.
Figure 3.2: A real fish school (a) and its randomly generated counterparts (b) to (f). The shape of the original school as well as the number of individuals is conserved across all datasets.
3.3 Analysis

3.3.1 Orientation of strongly connected components

We start by analyzing some properties of the interaction networks reconstructed from the visual fields. Remember that these networks are both weighted and directed since the weight \( w_{ij} \) corresponds to the empirical probability of individual \( i \) to startle if individual \( j \) has startled. We are particularly interested in features of the network that can influence the transfer of information within the schools. A casual observation of the networks seems to reveal an interesting internal structure where the strongest connections lie transversally relative to the local direction of motion of the fish. This is especially apparent in highly polarized schools (for instance, see Figure 3.3).

To get to these small groups of highly connected fish, we can start pruning the networks of their weakest links. To do so, we start by removing all edges whose weight is below a set threshold, then we compute the strongly connected components of the pruned networks. All nodes in a strongly connected component are connected to every other and, most importantly, the connections are reciprocal, which can facilitate information flow. Once we have the strongly connected components, their size distribution tells us if we successfully partitioned the network into small disconnected clusters containing highly connected individuals (which can be seen as the state of the network \textit{before percolation}) or if the threshold was too low and weak links are still holding the network into one large component (\textit{after percolation}).

Figure 3.4 shows what happens when we increase the threshold for pruning the weakest links. Initially, there is just one strongly connected component composed of all the fish (minus some outliers). As the threshold increases, the school breaks down into multiple strongly connected components. The change occurs abruptly when the weakest link becomes larger than approximately \( 10^{-1.25} \). We are mostly interested in the small components regime (\textit{before percolation}), that is when the weakest link
Figure 3.3: Reconstructed visual interaction network for a polarized school (a). Showing only the strongest connections (b). Opacity indicates strength of connection. Color indicates directedness. The strongest connections tend to be transversal.

Based on the positions of the fish inside each component, we can compute the orientation of the component by fitting an ellipse. If the aspect ratio of the ellipse is above a certain threshold ($1/\sqrt{2}$), then the orientation of the component is well defined: it is the orientation of its major axis (here the direction is irrelevant). Figure 3.5 shows the distribution of the relative angle between the orientation of each component and the orientation of the whole school. Note that non-polarized schools are excluded from this analysis since the orientation of these schools is not well defined. In the
Figure 3.4: Distribution of the size of strongly connected components as weaker links are removed. The median is shown in black. The inner structure is revealed after all links weaker than around $10^{-1.25}$ are removed (percolation limit).

domain of small strongly connected components (right part of the plot), they tend to be oriented transversally relative to the orientation of the school. The peaks occur around $80^\circ$ while the median is slightly lower at around $65^\circ$ and there are no clear signs of handedness since the plots appear to be symmetric around the $0^\circ$ axis.

Thus we can confirm our intuition that the strongest connections lie transversally relative to the direction of motion of the fish. It is pretty clear why this happens when you look at how the weights are defined in relation to the geometry of the problem. When fish are aligned and side by side, they can easily get closer than one body length apart without risking a collision due to the elongated shape of their body. Furthermore, in this configuration, their neighbors can subtend a very large angle on their retina. Hence it is not surprising that the weights, which are based on the log of the metric distance and the ranked angular area of their neighbors, are the highest in
Figure 3.5: Distribution of the orientation of the first principal component of positions within strongly connected components relative to the orientation of the whole school as weaker links are removed. The medians for positive and negative values are shown in black. Before percolation (right side), small components are oriented transversally. There seems to be no difference between left and right (no handedness).

But are the fish positioning themselves in a particular way to either increase or decrease this natural geometric effect? To answer this question, we perform the same analysis on the P and PD datasets, where the positions are random. Note that this analysis requires polarized schools so it cannot be applied on any dataset where the orientations are randomized (O, PO, and POD). Figure 3.6 shows that when positions are randomized, more links must be pruned for the size of strongly connected components to drop (in other words, the percolation threshold has been lowered), but the differences are relatively small. Random positions, especially when the density fluctuations are not controlled, lead to stronger links overall because many individuals end up closer to each other and this has the additional effect of creating very large...
Figure 3.6: Median size of strongly connected components as weaker links are removed for each dataset. Randomness in the fish positions facilitates percolation which means that strongly connected components are more connected to the rest of the group than in real schools. But the differences are relatively small.

The correlation between ranked visual angle and shorter distances gets stronger which causes an increase in the average weights of the network. This might explain some of the differences between the datasets. However once in the domain of small components, Figure 3.7 shows that randomizing positions does not affect their orientation relative to the orientation of the school. This confirms that these strong transversal connections are a principally consequence of body shapes and that the positioning of the real fish nor the uniformity of the density do not influence the orientation of the most strongly connected clusters.
3.3.2 Relative position of neighbors

It is also interesting to look at the relative position of strongly connected neighbors from the point of view of the fish. We can compute the relative angular position of fish within the strongly connected components (Figure 3.8). We find that when considering the full network (left part of Figure 3.8), neighbors are often found in front, rarely directly in front (0°) but rather offset by around 20°, and in the back with the same slight offset. Once in the domain of small strongly connected components (right part of Figure 3.8) however, strongly connected neighbors are rarely in front or in back of each other and often on the side but on a wide range of side positions (90°±45°). Again there are no clear signs of handedness since the plots appear to be symmetric around the 0° axis.
Figure 3.8: Distribution of the relative angular position of direct neighbors within strongly connected components as weaker links are removed (dataset C). Before percolation (right side), neighbors tend to be located at $90^\circ \pm 45^\circ$ (on the side). After percolation (left side), neighbors tend to be located around $20^\circ$ and $160^\circ$ (slightly off the front and back). There seems to be no difference between left and right (no handedness).

The same analysis on datasets P and PD reveals similar patterns as those seen on Figure 3.8 with the following notable differences. For dataset P (random positions), the main difference is that more strongly connected neighbors tend to be located further to the back at up to $170^\circ$. The increased asymmetry (around $90^\circ$) could be reflective of the larger variety of angles between edges of the strongly connected components obtained by randomizing positions (e.g. in triangle or star shaped sub-components). When we control for density (dataset PD), there is much more variability in the location of neighbors for any weakest link threshold, including many more strongly connected neighbors directly in front of each other, but the underlying patterns are still similar to dataset P. The greater variability is likely due to Mitchell’s algorithm:
attempting to maintain a constant density leads to very more even angular positioning of neighbors.

There are also notable similitudes between the random and non-random cases. One would think that the low number of fish located directly in front of each other could be an active attempt of the fish to reduce the risk of frontal collision by keeping a clear space ahead of them. While it cannot be ruled out, we do observe the same pattern with the datasets P and PD where the positions are randomized (but local orientations are not). Note that this only applies when considering the full network. Once in the domain of strongly connected components, it is most likely due to the intrinsically lower subtended angle produced by a neighbor on the retina of a focal fish when it is in front of it and has a similar orientation.

### 3.3.3 Predator detection

For most prey animals, the most important piece of information often is the presence and/or location of predators. Schooling fish and other social species that live in groups have the advantage that they can share information among themselves. But inevitably, information has to come from somewhere and when a threat presents itself to the group, some individuals have to be the first responders. Of course, the power of decentralization found in swarms comes from the fact that even if individual members are imperfect, the group can do better by pooling resources and capabilities. In the case of predator detection, not only the individual capabilities but also the quantity and positioning of potential first responders are very important.

Given the visual fields of all individuals in a group and any point in space, we can determine the number of individuals able to detect this point as well as their identities. A point of interest could be the location of a nearby predator for instance. Since we need to make general statistics of the detection capabilities of a group of individuals, we will use a dense grid of points much larger than a typical group size.
Figure 3.9: Heatmap of the number of fish able to detect any point around sample fish schools ($N \approx 150$) in different states: milling ((a), (b)), polarized (c), swarming (d). Detection appears much sparser on the sides of polarized schools. For all other states, detection appears to be more uniform all around the schools. In most cases, a higher density leads to lower overall detection counts.
For each of our dataset, we reconstruct the visual fields of all individuals as described in chapter 2 and compute the interaction network of each school. In addition, we classify the state of each school using the method described in [16]. Then we compute for each point of a 100x100 grid of points covering the domain $[-50, 50] \times [-50, 50]$ (body lengths) around the center of mass of each school the list of individuals whose visual fields contain the point. The length of the list gives the number of individuals that can detect the point. Typical heatmaps of the detection counts for schools in different states are shown in Figure 3.9. While in general the coverage is quite uniform over every angle around the school, for polarized schools the number of detections is much higher at the front and back than on the sides. This is further reinforced by the fact that fish schools are dynamic. In the milling and swarming states, the motion of the school increases the fluctuations of the detection counts at all angles, hence

\begin{figure}
\centering
\includegraphics[width=\textwidth]{heatmap}
\caption{Mean detection counts as a function of distance to the edge of the school by state. Some states facilitate detection. Overall, a point outside the school is detected by more individuals the further it is from the school.}
\end{figure}
the time-averaged detection counts are very uniform at all angles around the swarm. In the polarized state however, the motion of the school does not affect much the configuration so the spatial distribution of time-averaged detection counts is similar to the spatial distribution in any instantaneous snapshot.

When plotted against distance to the edge of the school (Figure 3.10), the mean detection counts are highest in the milling state. The second highest mean detection counts correspond to polarized schools despite the observed anisotropy of detections when schools are highly polarized. The lowest detection counts occur in the swarming state, where they are around 20% lower than in the milling state. For completeness, the transitioning state is also included in Figure 3.10 and it shows than in terms of the ability to watch their surroundings, fish schools are not particularly at risk while transitioning from one state to another.

As described in chapter 2, we detect the boundaries of the groups using $\alpha$-shapes and we use them to compute the distance of each point of the grid to the edge of the group. For polarized groups, where the heading of the school is well defined, we compute the angle of each point of the grid to the heading of the school relative to the center of mass of the school. We can then compute for points outside the schools the average detection counts as a function of distance to the edge of the school and the angular position relative to the school’s orientation (Figure 3.11). Note that other factors, like the ability to resolve an object at a distance, also come into play when evaluating the capacity of a school to detect predators, but the detection counts are interesting as a measure of the redundancy of the information that can be garnered by the fish. We observe that the detection counts are generally lower for locations in space near the edge of the school. Individuals on the edge cast a *shadow* that gets progressively filled by the fields of view of other individuals as the distance from the edge of the group increases. This has interesting implications for predation in low visibility environments: a predator approaching the school could stay undetected.
Figure 3.11: Average detection counts as a function of both the distance from the edge of the school and the angular position relative to the school’s orientation (polarized schools only). (a) Without blind zone. (b) With 25° blind zone. The detection counts are generally lower near the edge of the school and on the sides.
for a while and only become visible in the close vicinity of a school where it can subsequently only be detected by a small number of fish. Similarly, a sit-and-wait predator could stay undetected until the school gets very close to it. We also see that when you go further from the edge, the detection counts are lower on the sides of the school. Lastly, further away from the edge of the group, the detection counts tend to be higher at the back than at the front of the group.

Figure 3.12 shows the distribution of the detection counts as a function of the angle relative to the school’s orientation. This confirms very clearly that the detection counts are much sparser on the sides of polarized schools.

The same analysis on the random datasets P and PD reveals that the average detection counts as a function of both the distance from the edge of the school and the angular position relative to the school’s orientation are similar to that of dataset C. As seen on Figure 3.13, the principal difference is that the overall detection counts are lower for randomized schools and that the asymmetry between front and back is less pronounced. Controlling for density brings the detection counts back up on the edges, and this is also true at the front to a lesser extent, but not at the back. When the density is uniform, individuals that are not on the edge of the group are more likely to be able to see the exterior and contribute to the detection counts.

In reality, golden shiners do not have full peripheral vision. They have a rear blind area of approximately 25° in their vision [63]. If we take this blind zone into account and remove the corresponding detections, we find that it makes little difference in the milling and swarming states for which the detection counts are almost isotropic, but it makes a huge difference in the polarized state where the detection counts at the back of the group become even lower than on the sides (see Figure 3.14 for an example).
Figure 3.12: Distribution of detection counts as a function of the angular position relative to the school’s orientation (polarized schools only). (a) Without blind zone. (b) With 25° blind zone. The detection counts are much lower on the sides of the school.
Figure 3.13: Average detection counts as a function of the angular position relative to the school’s orientation (polarized schools only, no blind zone) for datasets C, P, and PD.

Figure 3.14: detection counts around a polarized school (pointing right). (a) Without blind zone, the detection counts at the front and at the back are comparable. (b) With a 25° blind zone, the detection counts at the back drop dramatically.
3.3.4 Spread of cascades

In the previous sections, we have seen possible pathways of information in the structure of the interaction networks, and possible sources of information in the collective detection capabilities of fish schools. In this section, we explore information transfer as a function of the location of the source.

In a fish school, when a threat is detected, information tends to propagate quickly. It has been shown on multiple occasions, and for different species, that information in groups propagates faster than the speed of the individuals [11, 17, 64–66]. While not exactly true in practice, we will assume in this model that the propagation of information happens on a much faster time scale than the motion of the fish such that the schools are completely static during propagation events (as in Rosenthal et al. [11]). We will simulate startle response, the typical cascading alarm response of a school, as if initiated by the presence of a predator at a specific location around the school. By characterizing the cascades as a function of the stimulus position, we can infer the efficiency of the network for propagating information and once again compare real fish school to randomized ones to discern the effect of body shapes from active positioning of the individuals.

To simulate a startle response, we use the following algorithm: Given a set of first responders $S_0$ among all individuals in the network, let $S = S_0$. We collect in a set $E$ all edges pointing from any individual $i$ not in $S$ to any individual $j$ in $S$. Then for each edge in $E$ by decreasing order of weight, we draw a number from a uniform distribution between 0 and 1. If that number is less than the weight of the edge (recall that weight $w_{ij}$ is the empirical probability that $i$ startles if $j$ does), then individual $i$ is added to the set $S'$, otherwise the edge is removed (to ensure that edges are never considered more than once so as not to inflate the probability of response). Then we set $S = S \cup S'$ and $E = \emptyset$ and we iterate until there are no more edges to consider. We end up with a set $S$ containing the list of individuals who startled, while $S_0$ contains
Figure 3.15: Expected cascade size as a function of distance to the edge of the school by state. Following the detection counts, cascades tend to be larger when their origin is further from the school. No blind zone.

One interesting measure of a simulated startled response is the relative spread that we define as $\rho = \frac{|S|-|S_0|}{|S_0|}$. $\rho$ can be seen as the amplification factor of the startle response. Large values of $\rho$ indicate that a startle propagated well beyond the set of initial responders.

The swarming state tends to correspond to the least social influence. As we have seen in Figure 3.10, the detection counts are lowest in the swarming state. It is interesting to see that despite these relatively low detection counts, cascades spread well (Figure 3.15) and the relative spread is the highest (Figure 3.16).

We observe that the relative spread is approximately isotropic for milling schools. This is expected since these schools are for the most part symmetric around their center of mass. Relative spread is typically anisotropic for swarming schools, however these schools are highly dynamic hence it is isotropic when you take a time-average.
Figure 3.16: Relative spread of cascades as a function of distance to the edge of the school by state. Although detection counts tend to increase with distance, the relative spread is almost independent of distance.

For polarized schools, without including a blind zone, it turns out that despite the anisotropic detection counts (more detections at the front and back than on the sides, see Figure 3.12), relative spread is isotropic (Figure 3.17a). But if you include a blind zone as in the previous section, the relative spread becomes anisotropic: it is 30% higher at the back of the school (Figure 3.17b).

Across all datasets, relative spread is higher in average when a blind zone is included (Figure 3.18). This is consistent with the previous observation that relative spread is as high or slightly higher near the edge than further away from the school even though the expected cascade sizes are lower (Figure 3.15 and 3.16).

Figure 3.18 also shows that randomizing the orientation of the individuals does not decrease the average relative spread despite strongly altering the structure of the network. However, controlling for density (increasing homogeneity) yields a
Figure 3.17: Distribution of expected relative spread as a function of the angular position relative to the school’s orientation (polarized schools only). The median is shown in black. (a) Without blind zone, the distribution is isotropic ($\bar{\rho} \approx 0.35$). (b) With blind zone, the relative spread is 30% higher at the back of the school.
Figure 3.18: Average relative spread of cascades for all datasets with and without a blind zone.

significantly higher average relative spread, even compared to dataset C. This seems to be a consequence of the greater variability of relative location of neighbors around a focal individual described in subsection 3.3.2.

3.4 Discussion

In schools of golden shiners, response to the presence of a predator follows a complex contagion pattern, where detection by multiple fish can be necessary to engage a collective response [11]. Thus polarized schools could be at an increased risk of incurring successful attacks from the sides where the detection counts are lower than at the front, and also from the back which has even lower detection counts if you take into account the blind zone in the visual fields of the fish. However, we observe that when a startle is initiated from the back of the school, although the detection counts
might be the lowest, the relative spread of the startle response is the highest. If we choose to ignore the blind zone and assume full peripheral vision for every fish in the school, we still find that despite lower detection counts on the sides, the relative spread of the startle response is isotropic, meaning that in terms of diffusion of information about a potential danger, the school is not particularly at risk for being polarized. In other words, at the school level, anisotropy in the number of fish able to detect a threat does not imply anisotropy in the spreading power of the alarm response. The strong transversal connections observed in the interaction network could be a viable mechanism to compensate for the lower detection on the sides by lowering the number of direct detections required for a startle to propagate. Indeed, when multiple individuals that are strongly connected can all see the same stimulus, they do not gain as much social information as if they were weakly connected or if only some of them were able to see the stimulus because the information they get is highly redundant. When the stimulus is on a side of a polarized school, the individuals on the edge who are best located to detect it tend to be weakly connected together, thus offering to individuals inside the school to which they are strongly connected multiple sensors with little redundancy which provides a lot of information.

Throughout this chapter, we found that most of the properties of fish schools that we investigated were conserved when the position of individuals was randomized within the bounds of the original schools. Controlling for density only had a small effect, sometimes bringing more realism into the generated schools. This indicates that these properties arise principally from the geometry of the individuals, their elongated body shape, more so than from the internal structure of the school. This is both desirable and unsurprising because fish schools are highly dynamic thus the internal structure changes all the time and the collective predator detection capabilities should not be affected by these reorganizations. In other words, these features are robust to change happening inside the schools and this robustness comes from the fact that the
structure of the interaction network is maintained passively and effortlessly thanks to the elongated bodies of the fish and how they affect visual fields in a planar situation.
Chapter 4

Information Flow in Risky Environments

Abstract  For schooling fish to increase their chances of survival, early detection of predators and effective propagation of alarms are critical. Multiple types of cues can indicate the presence of a predator and put nearby prey in a state of alert. It is also possible to induce this perception of risk experimentally using an alarm substance found in the skin of many fish. When risk is perceived, fish can change their behavior, for instance by adjusting their sensitivity to social cues or by restructuring themselves, to attempt to increase their collective alertness. In particular, the literature (as well as preliminary experiments on Golden shiners) suggest that the density of schools of many fish species will change in environments perceived as risky. In this chapter, we study the effect of adjusting inter-individual distances and sensitivity to social cues on the ability of fish schools to detect threats in their surroundings and to propagate information relative to a potential danger. We show that forming tighter schools and being individually more sensitive to social cues both facilitate the propagation of alarm cues, but that the effect of doing both at the same time provides even greater benefits.
4.1 Motivation

One of the essential motivation for fish to form schools is to improve their chances of survival from predation [12–14, 52]. Multiple mechanisms decreasing the per capita risk have already been discussed in chapter 3. Here we focus on the effect of the perceived riskiness of the environment on the behavior of the fish and their schools. Prey fish can be alerted of the proximity of a predator by multiple types of cues, mostly visual and olfactory [18, 67], after which their behavior, both at the group and the individual levels, can change noticeably [21]. These changes in behavior can be seen as the fish school entering a temporary state of alert.

The point of being in a state of alert is to increase the chance that actual threats are detected promptly and that alarm cues propagate efficiently while simultaneously avoiding propagation of false alarms (which waste energy and time). The mechanisms in place to achieve this collective behavior are unknown but we would expect natural selection to have exerted strong selection on them, and thus we can formulate hypotheses that we can test using our visual interaction framework. Since it is the subject of this thesis, we will focus on the social mechanisms rather than on the direct detection of predators although it is likely that both would be at play in this situation.

The first possible mechanism that comes to mind is that each individual would adjust their own alarm response thresholds to be more sensitive to the alarm response behaviors of their conspecifics. There is a cost associated with this change (or the fish would be more sensitive to begin with) and part of it probably due to the increased frequency of false alarms.

Another possible mechanism is for each individual to adjust slightly their rules of motion so as to swim closer or farther from each other. The cost associated with this change might be related to the increased difficulty of avoiding collisions (when the density is higher than usual) or maintaining cohesion (when the density is lower than usual). These two mechanisms are not mutually exclusive and the reality might well
be a combination of both.

Numerous studies show that animals respond quickly and adaptively to changes in the risk of predation [67–70]. Among many animal groups, it has been observed that individual vigilance declines as group size increases [23–25, 71]. This effect is likely a consequence of the overall increase in vigilance, as well as the reduction in individual risk, resulting from being surrounded by many conspecifics [26, 27]. It has also been shown that some social prey increase individual vigilance in the presence of predators [28] but we have no data on vigilance in fish. Some schooling fish also respond to risk by reducing their inter-individual distances to form more compact groups [72].

The response of fish schools to risk can be studied in the lab without having to introduce real predators, as many aquatic organisms show anti-predator behavior in response to chemical cues, from predators themselves but also from injured prey [20, 67, 73]. *Schreckstoff* is a substance present in the skin of some fish which gets released when they get injured, for instance when their skin is torn down by the teeth of a predator, and which can be used to induce fear [19, 22, 29–31, 74]. For instance, Hoare et al. [74] used skin extracts to manipulate the perception of risk in shoals of banded killfish (*Fundulus diaphanus*) and found that shoal size increased with perceived risk. Preliminary experiments conducted by Matt Grobis and myself show that golden shiners temporarily form tighter schools after being exposed to schreckstoff. Figure 4.1 shows the result of one such experiment where the treatment group becomes significantly denser than the control group after being exposed to schreckstoff (as opposed to water for the control group). All of these experiments give weight to the hypothesis that fish adjust their rules of motion in risky environments but do not rule out the possibility that individuals would also adjust their sensitivity to social cues or change their behavior in additional ways [20].

In this chapter, we explore the consequences of varying inter-individual distances
Figure 4.1: Effect of schreckstoff (alarm pheromone) on a school of golden shiners. The plot shows the surface area (cm$^2$) occupied by two schools of golden shiners over time. Both of them were pre-exposed to the substance two days before. The black area represents the minute during which schreckstoff (red curve) and water (blue curve) was sprayed over the tank. Immediately after being exposed and for a relatively long period of time, the surface occupied by the school gets 60% smaller in average for the treatment group than for the control group. Courtesy of Matt Grobis.

within fish schools on the structure of their interaction networks and, when combined with varying their sensitivity to social cues, on their collective capacity to respond to threats from predators.

4.2 Analysis

We use the method described in chapter 2 to reconstruct the visual fields and interaction networks of all schools in the dataset from [11].

In order to simulate density variations, such as the compaction of a group in a risky environment, we analyze rescaled versions of each school in the dataset. To rescale a group by a factor $\alpha$, we simply multiply all components of all position vectors by $\alpha$, leaving the orientation vectors untouched. Thus when $\alpha < 1$ the group is compacted,
whereas when $\alpha > 1$ the group is expanded.

We make the assumption that rescaling does not affect how the weights of the interaction network are calculated. In other words, we use in Equation (2.10) the parameters from [11] at all scales. This allows us to isolate the effect of varying the density from individual-level changes in behavior.

From the interaction network, we calculate the external visual field and social influence and study their spatial distributions as in chapter 2. In addition, we compute the capacity of every individual to detect any point outside of the swarm and simulate the spread of alarm cues as if initiated from any of these points as in chapter 3.

While rescaling addresses the global effect of restructuring interaction networks, we also need to address the effect of changing the sensitivity of individuals to see how those two strategies compare to each other and what happens when they are combined.

To do this we introduce a sensitivity factor $\beta \in \mathbb{R}$ which modifies the weights of the network edges to simulate individual variations of social sensitivity. Remember that the weights are estimated probabilities that an individual will exhibit a startle response upon seeing another individual doing so. Thus we introduce $\beta$ in the following way: let $p$ be the original (unaltered) weight of one edge of the network, then the modified weight is

$$q = \text{logit}^{-1}(\text{logit}(p) + \beta)$$

(4.1)

where

$$\text{logit}(x) = \log \left( \frac{x}{1-x} \right)$$

(4.2)

and

$$\text{logit}^{-1}(x) = \frac{1}{1 + \exp(-x)}.$$  

(4.3)

The logit transform is necessary to ensure that the altered weights remain valid probabilities at all times and to suppress the potential bias towards zero that oc-
curs when the simulations are implemented using floating point numbers (uneven distribution of discrete values on the \([0, 1]\) interval).

## 4.3 Results

### 4.3.1 Rescaling

Access to external visual information decreases when density increases (Figure 4.2 and 4.3) since as density increases, only individuals very close to the edge of the group retain access to external visual information (Figure 4.3).

![Figure 4.2: External visual field as a function of the front-back position within the group for different scaling factors. Access to external visual information decreases when density increases.](image)

Social influence increases with density independently of the front-back position (Figure 4.4) and almost independently of the normalized distance from the edge of the group (Figure 4.5). This means that the relative weights of the edges of the
Figure 4.3: External visual field as a function of the distance from the edge of the group for different scaling factors. The main plot uses normalized units (body length × scaling factor) while the inset uses absolute units (body length). As density increases, only individuals very close to the edge of the group retain access to external visual information.

interaction network are almost insensitive to the change of density. By definition, the weights of the edges of the interaction network which depend for the most part on the log of the metric distance between individuals should be uniformly affected by the rescaling, so on this account, we expect the social influence to vary uniformly during rescaling. However, since body shapes are not rescaled, the visual fields do change during rescaling. In particular, the number and size of occlusions increase with density which modifies the second component on which the weights are based: the ranking of the angular area subtended by the neighbors of an individual. The probable reason why the variations of the social influence appear to be almost uniform is because the structure of polarized swarms is very predictable and amenable to keeping the ranks constant during rescaling.
Figure 4.4: Social influence as a function of the front-back position within the group for different scaling factors. Social influence increases with density independently of the front-back position.
Figure 4.5: Social influence as a function of the distance from the edge of the group for different scaling factors. The distance is in normalized units (body length $\times$ scaling factor). Social influence increases with density almost independently of the normalized distance from the edge of the group.
When we simulate behavioral cascades and we look at the expected cascade size as a function of the orientation of stimuli relative to the orientation of the school (Figure 4.6), we observe that cascade size is inversely proportional to density. This is surprising at first considering that social influence does increase with density. The reason is that access to external visual information is much lower at high density due to increased occlusions thus the sets of initiators are smaller and the overall cascade size is smaller too. Another interesting metric is the relative spread (Figure 4.7) and we observe that it increases with density and while it is isotropic at low density, it becomes anisotropic at high density, with the lowest values at the front of the schools and the largest on the sides.

Figure 4.6: Expected cascade size as a function of the orientation of stimuli relative to the orientation of polarized schools. Cascade size is inversely proportional to density.
Figure 4.7: Expected relative spread of cascades as a function of the orientation of stimuli relative to the orientation of polarized schools. Relative spread increases with density and becomes anisotropic at high density.

### 4.3.2 Sensitivity

Figure 4.8 shows that when the sensitivity to social cues of startle response of all individuals is decreased, cascades get slightly smaller, in particular at high densities, but the qualitative picture is the same: cascade size increases as density decreases. As explained in the previous section, the main reason is the large number of occlusions at higher densities which reduces the access to external information and lowers the number of initiators.

However, when the sensitivity is increased, the effect of density is reversed: cascades start getting larger at higher densities and the largest cascades are obtained when both the density and the sensitivity are highest. The reason is that despite the small set of initiators caused by the high level of occlusion at high densities, faint connections caused by partial occlusions become strong enough and the remaining strong connections ensure that spreading occurs with high probability.
Figure 4.8: Expected cascade size as a function of group scale and individual sensitivity. Reducing the density and increasing the individual sensitivity both lead to larger cascades but as the sensitivity gets larger, the effect of density is reversed.

Figure 4.9: Expected relative spread as a function of group scale and individual sensitivity. The largest relative spread is attained when density and sensitivity increase simultaneously.
Figure 4.9 shows very clearly that these very large cascades exhibit the highest relative spread meaning that the conditions of high density and high sensitivity produce the most efficient spreading of cascades: a small number of initiators can transfer information to most of their conspecifics.

4.4 Discussion

A possible response to an environment perceived as risky is for each individual in a group to change the way they interact with their neighbors. If every fish in a school starts swimming closer to its neighbors, the whole group gets denser which has consequences on each individual’s access to information: access to external visual information becomes exclusive to individuals on the edge of the group while access to social information is increased for everyone. But access to information is not the only factor governing an individual’s response to stimuli, it is the processing of this information that ultimately leads to actions and behavior.

Another way for a social individual to adapt to a risky situation is to change its sensitivity to social cues. An increased sensitivity for all individuals in a group might allow alarm cues to better propagate which would make it less likely not to notice a nearby predator, but might also mean a greater risk of spreading false alarms and incurring their associated costs (energy expenditure, stress, disruption of vigilance, etc.)

As we have seen in the previous section, when a school of fish is rescaled but individuals maintain their usual sensitivity to social cues, the effects of changing the density on the spread of alarm cues can be explained by the changes in individuals’ access to information.

When the group spreads and the density is low, individuals deep inside of the group are more likely to get a direct line of sight to the outside of the group allowing
them to obtain valuable information. When a threat presents itself to the group, the set of first responders is likely to be very large, enabling cascades to spread easily to the rest of the group.

On the other hand, when the group condenses and the density is high, visual occlusions abound and individuals on the edge of the group are the only ones who have good direct access to external information. Shorter inter-individual distances do increase the strength of the social connections which explains why the relative spread is highest in this case but since access to external information is limited, there tend to be fewer first responders which limits the size of the cascades.

However, if we gradually increase the sensitivity to social cues of each individual in a dense group, the weak connections caused by partial occlusions become strong enough to reinforce the social network up to the point where cascades spread very well despite being started by very few individuals. Interestingly, although increasing the sensitivity alone without rescaling the groups does have a positive effect on the spread of cascade, the effect is much stronger if combined with increasing the density. And while increasing the density without altering the sensitivity causes the relative spread to increase, it also leads to smaller cascades.

This demonstrates one of the trade-offs faced by these fish between access to information and processing of information: when the group condenses but individuals maintain their normal level of sensitivity to social cues, the reduced access to external visual information caused by the increased number of occlusions is overbearing compared to the increased likelihood of propagating alarm cues simultaneously obtained by reducing inter-individual distances. But slightly increasing the sensitivity of individuals is enough to make the propagation even more effective and overcome the detrimental effect of having a reduced number of first responders due to poor access to external information.

There are other considerations than the spreading power of alarm cues in how fish
schools adapt to risky environments. While the efficient transmission of legitimate alarms is beneficial to all individuals in the group, responding to false alarms is costly and detrimental. One way of simulating false alarms in the context of the present framework is by treating each node in the network as a Bayesian agent with prior information about the probability of legitimate and false alarms, which receives both direct external information and social information, and with a threshold on its posterior information used to determine whether or not it gets triggered and broadcasts its state to its neighboring nodes.

Lastly there are biological and environmental conditions that come into play when the density of a fish school or the sensitivity of its members change. Enlarging the group by decreasing the density reduces the cohesion and might cause splitting or scattering of individuals. This might be even more pronounced in turbid water when visibility is reduced. There are also limits to how dense a fish school can be and when in some situations fish swim extremely close to each other it might be impossible for them to rely much on vision. Similarly, fish might not be able to change their sensitivity to social cues very much or for prolonged periods of time, or it might impede other functions and counter-balance the benefits obtained.
Chapter 5

Coordinated Group Hunting and Risk among Schooling Prey

Abstract  Predator-prey interactions are a fundamental element in the life of fish schools but the behaviors involved are difficult to quantify precisely, both in the lab and in the field. That is why few studies have scrutinized how these interactions are mediated in realistic conditions. Using high-resolution sonar imaging [35], we have been able to record the tracks of predatory fish and their schooling prey during very dynamic hunting events in their natural environment without disturbing the fish. The analysis of the tracks reveals two important points: first that the fragmentation of the prey schools increases the per capita risk of the prey within those schools, and second that the predators form coordinated hunting groups, with up to five individuals in a line formation. We hypothesize that coordinated hunting groups may facilitate fragmentation to disrupt the ability of prey to communicate and subsequently increase capture rates. Using a simple dynamical model for this public goods problem, we show that this kind of coordinated attacks can be part of a strategy that maximizes the net collective benefits for predators.
5.1 Motivation

Predator-prey interactions are a fundamental element in the life of fish schools. They are recognized as a key driver in the evolution of schooling [13, 21, 50, 51] and can have important effects on the stability of ecosystems [75] but the behaviors involved are difficult to quantify precisely. The common dilemma is that it is very challenging to quantify behavior at the appropriate temporal and spatial scales in the animals’ natural environment, while it is also very challenging to represent appropriately the natural ecological conditions in the lab. An additional hindrance is the large number of animals involved. Tracking them manually would be too time-consuming and expensive so automated tracking software is necessary, but at this time such software is still incapable of tracking a large number of individuals in complex natural habitats, and for this reason few studies have attempted to track individuals within aggregations in the field [32].

As we have seen throughout this thesis, one of the functions of schooling is enhanced predator protection [12–14, 52]. If grouping is beneficial to prey, it is not very surprising that in some circumstances, it can be beneficial to predators as well. Collective hunting is in fact pretty common in the animal world but it is most commonly observed among groups of related individuals, for instance African wild dogs [76], lions [77], dolphins [78], or chimpanzees [79]. However, predatory fish hunting on a large prey school are unlikely to be closely related to their conspecifics. Yet coordinated hunting behavior might still evolve if the right environmental conditions are met [80].

Major [34] studied the predator-prey interactions between the predatory jack (Caranx ignobilis), a facultative schooling species, and its obligate schooling prey the Hawaiian anchovy (Stolephorus purpureus) and made the observation that single predators were the most successful at capturing isolated prey, and relatively unsuccessful at capturing individuals in schools, whereas grouped predators were the most
successful at capturing schooling prey. He also noted that the leading predator was the most successful member of a group at capturing isolated or schooling prey. Lastly, he observed that larger predator groups were able to break up schools of prey quickly, resulting in increased numbers of prey becoming isolated which facilitated capture.

In the first part of this chapter, we make similar observations and go further by first describing how highly dynamic predator-prey interaction data can be captured in the field with a very fine spatial and temporal resolution. We then proceed to analyze the data and find that these predators often form coordinated groups and that the prey’s risk per capita increases as the prey schools get smaller [35]. Based on these results, we formulate the hypothesis that predator coordination might be a mechanism causing the dislocation of large prey schools into smaller groups which disrupts the transmission of information among prey and facilitates their capture. In the second part of this chapter, we look at the problem of predator coordination through the lens of evolution. Using a simple dynamical model, we are able to show that under simple and reasonable assumptions, predator coordination can be part of a strategy that maximizes the net collective benefits against some of the defense mechanisms provided by schooling even if the predators are selfish.

5.2 Analysis of predator-prey interactions in the field

5.2.1 Methods

In Handegard et al. [35], we analyzed the dynamic interactions between a piscivorous predator, the spotted sea trout (*Cynoscion nebulosus*) and its schooling prey, the juvenile Gulf menhaden (*Brevoortia patronus*), a highly abundant and ecologically important species in the estuarine and near-shore ecosystems along the coast of the
Gulf of Mexico [81]. Menhadens form large and highly dynamic schools in these estuarine habitats which they use as nursery areas. To capture the motion of both predators and prey, we used a high-frequency imaging sonar (DIDSON, Sound Metrics, Lake Forest Park, WA) to record so-called “acoustic videos” with a spatial resolution of ≈ 2 cm and a temporal resolution of 125 ms (8 Hz) within a two-dimensional fan spanning an area of 24 m². Figure 5.1 shows an example of an acoustic image obtained from the sonar.

![Figure 5.1: An acoustic image (horizontal plane) showing schools of juvenile Gulf menhadens (light color) captured with a DIDSON sonar.](image)

After multiple steps of preprocessing (background subtraction, wavelet filtering and running mean), a single target detection algorithm [82] was used to detect the location of individual prey, as illustrated on Figure 5.2 (B–E).
Figure 5.2: Data collection and image processing steps. (A) An acoustic image from a vertically aligned DIDSON sonar, to illustrate the vertical dimension of the observation site (this is not the orientation used in the present study). Overlaid on the image is a line indicating the bottom substrate, the surface, the acoustic beam and vertical (-3 dB) opening angles of the horizontally aligned DIDSON beam. The image also shows an example of a vertical distribution of a fish school. (B) Raw image. (C) Image with background subtracted. (D) Wavelet filtered and running mean image. (E) Detected single preys shown as gray dots. (F) An example of a sonar image and velocity estimates presented in x-y domain, where the sonar image is shown in gray scale, the prey flow field estimates are given as green arrows, and the predators are presented as blue asterisks, with red arrows indicating their estimated velocities.
Because of the high noise present in the acoustic images and despite heavy filtering, the resulting detections could not easily be tracked from frame to frame so reconstructing the prey trajectories was not possible, but their velocity (speed and direction of motion) was estimated by extracting the optical flow between sequential images using Particle Image Velocimetry [83]. For every frame of the acoustic videos, the temporal derivative of pixel-wise luminosity was calculated by differentiating two successive frames, while the two spatial derivatives were calculated using 3 by 3 Sobel filters on each frame, and the products of these derivatives were convolved with a 3 by 3 Gaussian filter. This resulted in a velocity estimate for each pixel within each frame. The detections were used to mask the flow field data to regions where prey targets were present.

We used an alpha shape algorithm [49] with a radius of 20 cm to delineate individual fish schools. When two groups were connected by at least three detections (meaning each of the three detections was connected to both groups), they were treated as a single school. Groups with less than five detections were removed from the analysis. School area was used as a proxy for prey school size assuming constant density since constraints in the single echo detection algorithm makes valid density estimation difficult.

Full trajectories of the predators were obtained through manual tracking techniques using the ImageJ software (v1.42q, National Institute of Health, USA) with the MTrackJ plugin (v1.3.0, Erik Meijering, Erasmus MC-University Medical Center Rotterdam, Netherlands). The velocity of the predators was estimated by fitting second order splines to their trajectories.

Because of their size, predators often produce echoes on the acoustic images which can confuse the single detection procedure. Thus we used a 6-pixel disk around predators to remove predator targets being detected as prey. Despite this, it was observed that single pixels in close proximity to predators may still be classified as
prey targets, typically behind and at distances less than 20 cm to the predator. The sectors behind the predators are therefore removed from Figure 5.4 and 5.5.

Since the resolution and quality of the acoustic images do not allow us to observe capture events directly, we compute a risk proxy based on the assumption that risk increases when prey are sufficiently close to the predator. We use a threshold of 30 cm corresponding to twice the average body length of a predator which is slightly more than the typical nearest distance between predators and prey ($\approx 20$ cm). This allows us to determine a proxy for the per capita risk experienced by prey in different school sizes.

5.2.2 Results

The analysis of the speed and relative position of the fish reveals that the predators generally attack the prey from behind (Figure 5.3) at high speed: during attacks, the average speed of the predators was $0.249 \pm 0.002$ m/s (SEM) while the average speed of the prey in the half space in front the predator was $0.195 \pm 0.008$ m/s (SEM). The overall average speed of the prey was $0.117 \pm 0.001$ m/s (SEM) so they were swimming around 66% faster on average while trying to escape from predators.

Figure 5.4 and 5.5 shows that while prey are still in front of a predator, they tend to move directly away from it in what has been described as a flash expansion [51]. Once they find themselves behind a predator, they reorient so as to face it. This behavioral pattern has previously been described as a fountain effect [51, 84]. The initial escape followed by the regrouping of the prey once a predator has passed creates a sort of vacuole, a zone with a low prey density, that extends for about 50 cm behind the predator. In general, prey are rarely found closer than 20 cm from a predator.

The average direction of motion of the prey, indicated by the black arrows on Figure 5.4, reveals that even fish that are not immediate neighbors of the predator appear to be influenced by it. Since the environment is highly turbid (15 nephelometric
found that the correlation length increases linearly with the 
logarithmically mediated) interactions among the birds [“scale-free” behavior. In starlings, for example, local (topo-
rial, to be a singular unit, despite individual interactions 
that span the entire group [1]. Thus, flocks can effectively 
behave as a singular unit, despite individual interactions 
that span the entire group [2]. Similar phenomena have been observed in bird flocks 
of magnitude greater than the typical individual swim speed. For example, Makris et al. 
[18] demonstrate how compressional density waves can propagate over tens 
of kilometers in herring schools at a speed that is an order 
10 cm by 15° area. The color map represents the scaled number of predator detections 
in each bin, where 1 is equal to the maximum number of prey within a bin divided by 
the bin area. Predators tend to attack prey from behind. Adapted from [35, Fig. 1].

Figure 5.3: Distribution of the nearest predator around a representative focal prey. The prey is located in the center of the plot facing right (to scale). Each bin represents a 10 cm by 15° area. The color map represents the scaled number of predator detections in each bin, where 1 is equal to the maximum number of prey within a bin divided by the bin area. Predators tend to attack prey from behind. Adapted from [35, Fig. 1].

Figure 5.4: Distribution and average direction of prey around predators. The predator is located in the center of the plot facing right (to scale). The arrows show the average direction of all prey surrounding the predator. Each bin represents a 10 cm by 15° area. The color map shows the scaled number of prey detections in each bin, where 1 is equal to the maximum number of predators within a bin divided by the bin area. Note that the prey are rarely closer than 20 cm to the predator. Some predators can be detected as prey, and to ensure no interference, the data points (pixels) behind the predators were removed. Adapted from [35, Fig. 2].
Figure 5.5: Distribution and relative speed of prey around predators. The predator is located in the center of the plot facing right (to scale). The arrows show the average direction of all prey surrounding the predator. Each bin represents a 10 cm by 15° area. The color map shows the scaled number of prey detections in each bin, where 1 is equal to the maximum number of predators within a bin divided by the bin area. Note that the prey are rarely closer than 20 cm to the predator. Some predators can be detected as prey, and to ensure no interference, the data points (pixels) behind the predators were removed. Adapted from [35, Fig. S2a].

turbidity units), with an estimated visibility range of no more than 20 cm, this is likely the effect of social influence that extends through the school beyond the visible range of individuals and which might impair the hunting success of predators [85].

Figure 5.6 shows the relative position of nearest neighbor predators. Strikingly, the density is much higher four to five body length at the front and back of the focal predator, meaning that predatory sea trout exhibit highly coordinated behavior when hunting. In our study they were found forming coordinated groups of up to five individuals (but mostly hunted in pairs) and spent about one quarter of their time in such groups.

Figure 5.7 shows that the risk per capita, estimated from the time spent by prey schools of different sizes in close proximity to a predator, gets higher as the schools get smaller. This is consistent with the fact that most of the benefits of grouping
reaction determined reaction distances to be 20 cm in conditions similar to ours [17] for prey fish. Although we were not able to test the visual response of predators, it is highly likely that predator grouping may function to maintain incoherence between 50 and 100 cm behind a predator (can be seen from the vacuole (area devoid of prey) extending back). It is unclear whether this type of strategy is relevant to a situation where prey move in a dynamic and complex way. However, regardless of the sensory modalities involved, such as this where prey move in a dynamic and complex scale over which density is measured (see also [17]).

This brings forth the question of how predators influence prey schools. In low-visibility situations, like ours, sensory modalities like the lateral line are likely to be important for intra- and inter-specific interactions [34]. It is probable that predators influence prey behavior when hunting. The position of the nearest predator, which the predators can influence ("control") prey behavior. If true, this could impact the effectiveness of predators when hunting individuals in groups as indicated by our sonar image sequences ([34], Movie S1), vacuoles, and the color map shows the scaled number of predators detected in each bin. Each bin represents a 10 cm by 15° area. Adapted from [35, Fig. 4B].

Figure 5.6: Distribution of nearest neighbors among predators. Predators tend to attack in a line formation, suggesting coordination. The focal predator is located in the center of the figure facing right (to scale). The color map shows the scaled number of predators detected in each bin. Each bin represents a 10 cm by 15° area. Adapted from [35, Fig. 4B].

Figure 5.7: Risk proxy as a function of school area. Circles are individual data points, and the red line is the model fit. Adapted from [35, Fig. 4A].
initially increase with group size.

The above results show that spotted sea trout spend a significant amount of their hunting time in line formation. Such coordination in an environment when prey are abundant is initially surprising. However we know that for various reasons, schools are more resilient to predator attacks than isolated prey, so predator coordination might be an adaptation to counteract these effects. We also found that the size of the school plays an important role, as larger groups provide more protection than smaller ones, and risk of capture increases dramatically for schools of only a few individuals [35]. Finally, we saw that the juvenile Gulf menhaden perform some remarkable evasion maneuvers in which they split in front of the predator and regroup behind it at a safe distance. This results in a school that temporarily surrounds the predator but stays cohesive nonetheless after the predator has passed. Now if another predator was following the first one, the prey would only be able to regroup at a safe distance behind the trailing predator, meaning that the predators would have created a larger vacuole, further undermining the cohesion of the group and increasing the chance that the group might actually split, in particular if it was not very large to begin with. It is easy to see that an even longer chain of predators would amplify this effect and be able to break up even larger prey schools.

Another consequence of hunting in line formation is that the fragmentation of the prey schools might impair their capacity to exchange information. In our experiments, the visibility is so low due to the highly turbid environment that prey fish can only distinguish their immediate neighbors, yet the range of social influence seems to extend much further than that as can be seen by the effect that predators have on the orientation of distant prey. In fact, the data analysis reveals that like flocks of starlings, schools of juvenile menhaden exhibit a scale-free correlation of individual orientations, suggesting that the range of social influence might scale with group size [35, 86]. Fragmenting the schools might thus have the effect of reducing the range
of social influence among prey fish thereby undermining some of their social defense mechanisms.

Having to balance coordinated hunting, which benefits all predators whether they choose to coordinate or not, and solitary hunting, which benefits the hunter but only if enough others are coordinating, is a typical public goods problem. Predators can choose to contribute to the fragmentation effort by coordinating with others at the cost of not being able to catch prey immediately despite the energy spent but with the expectation that hunting will be much easier afterwards, or they can choose to hunt alone and use their energy to potentially catch a prey but with a probability of success that will gradually decrease as other predators choose to do the same and prey schools regroup, fuse back and become less fragmented.

The question of the evolutionary benefits of coordinated hunting was not directly addressed in [34] nor in [35], yet this is an important question as these predators are very likely unrelated to each other and can be considered selfish individuals with a priori no incentive to cooperate since there is no direct fitness benefit to do so. While it is clear that a cheater deciding to hunt individually in the vicinity of coordinated predators attacking a school would benefit from the presence of broken-up schools of fish without paying the cost of having to participate in coordinated maneuvers, it appears that some coordination is better than no coordination when attacking large fish schools. Therefore a mixed strategy between individualistic and coordinated hunting seems like a valid alternative that could explain the observed behaviors. However in this case we would like to propose a slightly different interpretation than the typical probabilistic description of mixed strategies. This interpretation is based on the dynamics of the hunting “game”. Initially, when predators approach a large school of fish, it is beneficial for them to coordinate their efforts to break the school apart into multiple smaller schools. At some point, depending on local conditions and opportunities (like the proximity of isolated preys), it becomes beneficial for some
predators to switch to a solitary hunting mode. As the prey regroup, it becomes beneficial for the predators to coordinate again, and the process repeats until satiation. At any time, the proportion of predators participating in coordinated attacks can represent the current state or *degree* of coordination among predators, which can be treated similarly to the probability of a group of predators choosing the coordinated versus the individualistic hunting strategy. A dynamical model based on this idea is presented in the rest of this chapter.

5.3 Dynamical model of predator coordination dynamics

In this section, a simple dynamical model of the interaction between predator coordination and prey fragmentation is developed and used to show that under some environmental conditions, a certain degree of coordination between predators is not only stable but beneficial to their hunting success.

The two relevant quantities are the prey fragmentation $x \in [0, 1]$ which is null when the prey school is whole and equals 1 when it is completely fragmented (isolated prey), and the predator coordination $y \in [0, 1]$ which is null when the predators are hunting individually and equals 1 when all the predators are participating in coordinated attacks.

The following assumptions are necessary to derive the rates of change of these two quantities:

- Prey fragmentation is assumed to increase in relation with the predator coordination but as the prey school becomes very fragmented, it becomes harder and harder for the predators to fragment it further. This is reflected in the first term on the right hand side of Equation (5.1). Parameter $a$ controls the propensity of prey schools to fragment under coordinated attacks ($a > 0$).
- It is assumed that the prey are constantly trying to regroup to bring fragmentation to zero. This is reflected in the second term on the right hand side of Equation (5.1). Parameter $b$ controls the prey’s regrouping rate ($b > 0$).

- Predator coordination is assumed to be necessary for the predators to be able to break-up the prey school until it is sufficiently fragmented for individual hunting, and the less fragmented the prey school, the more coordination is required. Coordination is also assumed to have diminishing returns so that $y$ always stays between 0 and 1. This is reflected in the first term on the right hand side of Equation (5.2). Parameter $c$ controls the predators’ propensity to coordinate while hunting ($c > 0$).

- It is assumed that the predators are not coordinating when they are actually catching prey. Thus coordination naturally decreases in the absence of other forces. This is reflected in the second term on the right hand side of Equation (5.2). Parameter $d$ controls the predators’ dispersion rate ($d > 0$).

The dynamical system is thus given by

$$\frac{dx}{dt} = ay(1-x) - bx, \quad (5.1)$$

$$\frac{dy}{dt} = c(1-x)(1-y) - dy, \quad (5.2)$$

and its domain of definition is $\mathcal{D} = [0, 1] \times [0, 1]$. In the rest of this chapter, we will use the dot notation for time derivatives. Let $\dot{x} = f(x,y)$ and $\dot{y} = g(x,y)$, then the quantity

$$\frac{\partial f}{\partial x} + \frac{\partial g}{\partial y} = -ay - b - c(1-x) - d \quad (5.3)$$

is strictly negative for all $(x, y)$ in the compact domain $\mathcal{D}$, thus Bendixson’s Criterion [87] is satisfied and we can conclude that there are no closed orbits entirely contained in $\mathcal{D}$. In addition, we can easily verify that the flow of system (5.1–5.2) is
directed inward everywhere on the boundary of the domain:

- \( x = 0 \Rightarrow \begin{cases} \dot{x} = ay > 0 & \text{when } y > 0, \\ \dot{x} = 0 \text{ and } \dot{y} = c > 0 & \text{when } y = 0, \end{cases} \)

- \( x = 1 \Rightarrow \dot{x} = -b < 0, \)

- \( y = 0 \Rightarrow \begin{cases} \dot{y} = c(1-x) > 0 & \text{when } x < 1, \\ \dot{y} = 0 \text{ and } \dot{x} = -b < 0 & \text{when } x = 1, \text{ and} \end{cases} \)

- \( y = 1 \Rightarrow \dot{y} = -d < 0. \)

Thus \( D \) is an \( \omega \) limit set \([87]\) and since it does not contain closed orbits, it must contain at least one asymptotically stable fixed point.

We find the fixed points of (5.1–5.2) by simultaneously solving for \( x \) and \( y \) the following equations corresponding to \( \dot{x} = \dot{y} = 0. \)

\[
\begin{align*}
ay(1-x) &= bx, \quad (5.4) \\
c(1-x)(1-y) &= dy. \quad (5.5)
\end{align*}
\]

Since all four parameters are strictly positive, there are two fixed points in \( \mathbb{R}^2 \) which can be expressed as

\[
\begin{align*}
x_1 &= \frac{2ac + b(c + d) - \sqrt{b(4acd + b(c + d)^2)}}{2c(a + b)}, \quad (5.6) \\
y_1 &= \frac{-b(c + d) + \sqrt{b(4acd + b(c + d)^2)}}{2ad}. \quad (5.7)
\end{align*}
\]

and

\[
\begin{align*}
x_2 &= \frac{2ac + b(c + d) + \sqrt{b(4acd + b(c + d)^2)}}{2c(a + b)}, \quad (5.8) \\
y_2 &= \frac{-b(c + d) - \sqrt{b(4acd + b(c + d)^2)}}{2ad}. \quad (5.9)
\end{align*}
\]
Clearly, $y_2$ is strictly negative thus $(x_2, y_2) \not\in \mathcal{D}$. Therefore, $(x_1, y_1)$ is the one and only fixed point in $\mathcal{D}$ and since $\mathcal{D}$ is an $\omega$ limit set, $(x_1, y_1)$ is asymptotically stable. Figure 5.8 illustrates the flow of the system converging towards the fixed point for a given set of parameters.

For any choice of parameters, the system starting from any initial state $(x_0, y_0) \in \mathcal{D}$ will eventually end up at the equilibrium. In other words, in a given environment, rational predators and prey will always maintain the degree of coordination and fragmentation corresponding to this environment’s equilibrium. It is important to note that the parameters $a$, $b$, $c$ and $d$ are not individual but collective parameters. If a cheater decided to behave differently, then it would affect some of these parameters for the whole population, because they represent averages for the population.

Figure 5.8: Flow of system (5.1–5.2) over domain $\mathcal{D}$ for parameters $a = b = c = d = 1$. The red dot represents the one and only equilibrium in $\mathcal{D}$. The flow is directed inward everywhere on the boundary of the domain and there are no closed orbits so the equilibrium is asymptotically stable in $\mathcal{D}$.

It is easy to see from Equation (5.7) that $y_1$ is always strictly positive, which proves that under the assumptions given above, some degree of coordination is always
required. Now to answer the question if a mixed strategy between coordinated and solitary hunting can ever have a chance to evolve, we have to define what the benefits for predators look like. As stated above, the predators can only catch and eat prey when they are not taking part in coordinated hunting, and their success depends on the fragmentation of the prey school. Therefore, in this model, their net benefits can be considered to be proportional to \( \varphi = x_1(1 - y_1) \). Note that \( \varphi \) depends only on the four parameters \( a, b, c \) and \( d \).

\( \varphi \) does not have a global maximum over the full parameter space. However, it is reasonable to assume that \( a \) and \( b \) are fixed since predators have no influence on them. When \( a \) and \( b \) are fixed, there is a global maximum of \( \varphi \) obtained for \( c = d \), corresponding to a stable strategy for the predators to adopt in order to maximize their benefits. When \( c = d \), equations (5.6–5.7) simplify to

\[
\begin{align*}
x_1 &= 1 - \frac{b}{\sqrt{b(a + b)}}, \\
y_1 &= \frac{\sqrt{b(a + b)} - b}{a},
\end{align*}
\] (5.10)

which do not depend on \( c \) (or \( d \)), and

\[
\varphi = \frac{a + b - \sqrt{b(a + b)}}{a}.
\] (5.12)

Thus predators have no incentive to coordinate, but no restrictions either.

The question is now whether environments in which predators get large benefits while having a high degree of coordination exist. To answer this question, a numerical optimization procedure (gradient descent with box constraints, using Julia’s Optim.jl package version v0.6.1) is used on the full parameter space \( (a, b, c, d) \in [0, +\infty)^4 \) to find sets of parameters which locally maximize the objective function \( \min(\varphi, y_1) \). As can be seen in Table 5.1, examples of environmental conditions in which, at the equilibrium,
predators get large benefits despite a relatively high degree of coordination are not hard to find and they represent a wide range of scenarios.

Table 5.1: Sets of parameters corresponding to local maxima of the objective function $\min(\varphi, y_1)$ (non-exhaustive list). The corresponding environments are remarkable because at the equilibrium, predators have a relatively large degree of coordination and get relatively large benefits.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Equilibrium</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a$</td>
<td>$b$</td>
</tr>
<tr>
<td>1.47</td>
<td>0.17</td>
</tr>
<tr>
<td>10.04</td>
<td>0.64</td>
</tr>
<tr>
<td>59.41</td>
<td>4.11</td>
</tr>
<tr>
<td>0.59</td>
<td>0.00</td>
</tr>
<tr>
<td>152.78</td>
<td>8.18</td>
</tr>
<tr>
<td>10.55</td>
<td>1.85</td>
</tr>
<tr>
<td>5.04</td>
<td>0.86</td>
</tr>
</tbody>
</table>

5.4 Discussion

Using a high-resolution imaging sonar [35], we were able to overcome the difficult problem of measuring predator-prey interactions in the field despite the high turbidity of the environment and without disrupting the fish. The data showed that collective information transfer among prey was impaired and per capita risk increased when prey groups are sufficiently fragmented, and that predators frequently coordinated their attacks in groups of up to five individuals in a line formation. Based on these observations, we hypothesized that coordinated hunting groups may facilitate fragmentation to disrupt the ability of prey to communicate and subsequently increase capture rates.

But coordinated hunting incurs a cost and delays (but hopefully increases) rewards for predators. For it to have a chance to evolve, it must provide better net benefits than alternative strategies. Using a simple dynamical model of the interaction between
predator coordination and prey fragmentation, we found that mixed strategies involving some degree of coordination between predators can maximize their net collective benefits. Furthermore, depending on the environmental parameters, such strategies can require relatively high degrees of coordination. However, more investigation is needed to determine whether or not such mixed strategies are evolutionary stable.

The dynamical model presented here might also apply to other public goods problems. McLeod and Wild [88] devised a dynamical model of population dynamics very similar to ours to provide theoretical support for the ecological constraint hypothesis that strives to explain the emergence of cooperative breeding. The ecological constraint hypothesis states that ecological conditions can deter individuals from breeding independently leading them to breed cooperatively to make the best of a bad situation. It is well supported empirically but the model in [88] proves that ecological constraints can influence the evolution of cooperation even without direct fitness benefits to the helpers.

The present study did not attempt to evaluate the model for realistic values of the model’s parameters. It would be interesting to try to fit these parameters based on field measurements of predator-prey interactions. In particular, field data could be obtained for different species exhibiting similar predator-prey dynamics, or the same species but in different environmental conditions, as a mean of evaluating the predictive power of the model in terms of predator coordination and prey groups fragmentation. These questions might be relevant for studying the effect of fisheries because fishing nets might affect both fragmentation of prey schools and predator coordination through any or all of the parameters of the model. Once in possession of numerical value for the parameters of the model, either obtained from statistical data or derived from first principles, an extended Kalman filter can be used to dynamically estimate prey schools’ fragmentation and predator coordination for real datasets.
Chapter 6

Conclusion

In this thesis, I explored various aspects of collective information processing using empirical data, both experimental and from the field, as well as mathematical and computational models inspired by these empirical systems.

As a preliminary to the subsequent chapters, in chapter 2 I developed a computational method for reconstructing the visual fields of elliptical individuals in the plane and dealing appropriately with the complex patterns of occlusion that inevitably occur. I validated this method by reproducing published results obtained using reconstructed visual fields of schooling fish (golden shiners).

The design of this model was inspired by and calibrated for the schools of golden shiners that I had the chance to observe for hours, both directly or through recorded videos, throughout my PhD. I made every effort both in designing and in describing the model to make it as general as possible, and there are many potential directions for extending it. Although I did not include this in my thesis, I did experiments with implementations of classical schooling models where interactions are based purely on visual inputs. The main problem with this is that you cannot really approach creating such a model from a computer simulation perspective like I tried to do because there is an infinite number of ways that rules of interactions can be defined and the parameter
space is too vast to explore. Instead you need to start with observations and data to make sure that the model you create in grounded in the biology. I still believe there is great potential for this kind of visual based model as they use the same kind of inputs but are much more scrutable than models based on machine learning which are getting extremely popular. I also experimented with the effect of turbidity by combining classical schooling models with a light attenuation model and requiring that the contrast between a distant individual and the background, or even between two distant individuals, be sufficient to be distinguishable. One final obvious extension that I did not need to consider since I used data from a species that lives in shallow water in a virtually two-dimensional environment is a three-dimensional version of the model which might be more appropriate for other species. This could also bring up very interesting complications if one wanted to take into account the properties of light underwater at different depths depending on the angle at which light rays reach the observer.

In chapter 3, I studied how direct visual information enters a fish school, and showed that it is not as straightforward as it might seem since both the global state of the school as well as the individuals’ detection capabilities (like having a blind angle) can greatly influence the number of early detectors of a potential threat. I also studied the structure of the visually mediated interaction network and showed that again, the global state of the school was important but that nevertheless, information was able to spread at all times and from all directions.

With the rise of giant online social networks like Facebook, Twitter, and others, the analysis of social networks’ properties is booming. I believe that although the interaction networks of fish schools and other similar aggregations of animals have many things in common with these social networks, they also provide something additional: not only have they been under selection pressure but they are also much more dynamic. When a predator blazes through a fish schools, the interaction network
of the prey can change dramatically and very quickly in the vicinity of the attack. These rapid changes and their effects on the group as a whole, as well as the more casual reconfigurations that happen all the time within fish schools are in my opinion a great future direction of research in this area.

In chapter 4, I studied how changes in behavior at the group level, namely the increased collective vigilance of the group when risk is perceived in the environment, can result from very simple changes in the behavior of the individuals and found that the best way of facilitating the propagation of alarms was for individual to simultaneously increase their sensitivity to social cues and adjust their rules of motion to form tighter schools.

There are many factors influencing the behavior of schooling fish, and it is sometimes necessary to analyze multiple behaviors simultaneously. A more comprehensive approach gives a fuller picture and can reveal some unexpected interactions between different behaviors. Here I looked at two simple behaviors and found that the effect of the combination is greater than the sum of the effect of each isolated behavior. That’s a fairly common property of complex systems and goes to show that taking into account other parameters and behaviors can yield even more interesting results. In the Couzin Lab, Matt Grobis is expanding on the preliminary experiments we did together and will soon be able to advance the state of the art in the study of fish behavior in risky environments in his own PhD thesis.

In chapter 5, I departed slightly from the collective information flow theme to explore one case of collective information usage. In [35], we recorded and analyzed tracks of predatory fish and their schooling prey during very dynamic hunting events. The analysis revealed that the fragmentation of the prey schools increases the per capita risk of the members of these schools and that predators form coordinated hunting groups, and we hypothesized that coordinated hunting groups may facilitate fragmentation to disrupt the ability of prey to communicate and facilitate their capture.
I then developed a simple dynamical model of the coarse grain interaction between a group of prey and a group of predators to show that mixed strategies, where predators spend a non-negligible proportion of their time coordinating their attacks despite being unrelated to each other and incurring a cost, allowed them to increase their net benefits compared to solitary hunting, and maximize them relative to other similar mixed strategies.

The data collected in [35] has a very high spatial and temporal resolution but the acoustic images are still too noisy to be able to track individual prey (predators were fortunately large enough that they could be accurately tracked). However sonar technology is improving and so are automated tracking tools and it is fair to assume that it will soon be possible to track entire schools with great precision which should open new avenues for the analysis of field data. The model I proposed in this chapter is intentionally very simple which means that it can be improved and built upon in numerous ways. While it is a simple model with fairly strong assumptions, these kinds of models have sometimes proved to be quite good fits to real complex systems and I would love for someone to try and fit this model to a real system to measure its predictive power. And it remains to be proved that the mixed strategies involving coordination among predators are evolutionary stable.

Throughout these chapters, I strived to attack the problems from different levels, the individual versus a small number of neighbors versus the whole group, since one of the most fascinating aspect of collective behaviors is how pervasive they are at all levels of biological organization. The issue of “crossing scales” and in particular developing the mathematical tools to do so has been a great motivation during my PhD and I hope that this thesis contributes, if only a little, to this endeavor.
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