Emergent Schooling Behavior in Fish

by
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Abstract:

Emergence is seen in the schooling behavior of many fish populations. The simple rules that govern individual fish behavior lead to collective motion and complex patterns within larger fish populations. This paper looks at the experimental observations of both individual fish behavior and the schooling behavior that arises within larger populations. The broad features of theoretical models which try to simulate schooling in fish are discussed. The current state of both simulation and observation are assessed, and future research goals are suggested.

1 Introduction

Schooling in fish is an emergent state of fish behavior in which a group of fish move together in a coordinated fashion and form patterns. The patterns formed range from simple ellipsoids to complicated vortex arrangements depending on the fish species and circumstances. Fish in schools often have a regular spacing and move very uniformly in the same direction. Schooling is observed across a wide variety of fish species and is believed to function primarily as an anti-predation mechanism. Schools are fairly long term structures and can maintain a pattern even though individual fish are always coming and going[6]. Schooling is distinct from other types of fish grouping in that it is not driven by external factors. That is to say, schooling fish move together, but are not simply all headed for the same goal (i.e. towards a food source). Rather they are attracted to each other by an internal force and stay in a group at times when they do not necessarily have a common goal.

Schooling behavior is an emergent property. Fish are not intelligent enough to create these regular patterns by choice. Further, the high density of many schools prevents them from even seeing most of the other fish in the school, so they lack the information to know their place in the larger structure. The fish are driven simply to be near each other. It is simple behavioral rules which guide each fish and these result in such fascinating and complex emergent structures.

1.1 Emergence

While governed by only a few simple rules (attraction to their own species, collision avoidance, predator avoidance, desire for food, etc.), fish form complicated long term formations. This is the essence of an emergent state. Emergence in physics involves inanimate systems taking on complex patterns that are not expected from the simple forces driving them. Almost the same is true of fish. The main difference is in the nature of the forces involved. In physics it is fundamental forces like gravitation (which form galaxies) and magnetism (responsible for emergent properties in magnetic materials). In fish the cause of the attraction is internal; however, it also results in the formation of complex structures strikingly similar to those seen in physics. The structure of one type of schooling is similar to a crystal lattice with preferred orientation and spacing[7]. Another is clearly reminiscent a swirling galaxy (see fig. 1). The fact that the forces governing fish behavior are internal to the fish make the problem of emergent fish schooling, in some respects, a much more difficult problem than emergence in physics. The complication arises because the rules governing fish behavior are much less well understood and are potentially much more complex than the simple forces that lead to emergence in physics.

1.2 Why Study Fish Behavior?

Aside from trying to understand how these complex patterns arise, schooling is an interesting topic because of the need to understand the fish populations that we rely on heavily for food. Since it is so tied up in fish behavior, understanding schooling will hopefully yield insight into the health of fish populations in the wild as well as within man made fisheries. Understanding fish schooling is a necessary part of understanding fish biology as a whole and will likely be a key in understanding the ecosystems of the ocean.

The study of schooling in fish and other aggregations in nature is also very interesting for the possibilities of creating such aggregations artificially. Models that can accurately predict fish behavior could be useful for solving many problems. We could solve the traffic and networking problems of the future with similar theories, and could construct robotic or nano-machine swarms obeying simple principles individually but able to complete complicated tasks as a whole[1].

1.3 Work So Far

To date work in this field has been focused in two areas: observations and simulations. Observations conducted in the lab and in the wild attempt to pin down the nature of the individual behaviors that lead to collective patterns. Simulations model the fish and plot their movement based on simple rules. Due to the complexity of both of these tasks, there has been a rather large disconnect between the observations and the simulations. Unfortunately, neither is really developed far enough for meaningful comparison. Recent advances in computational ability, however, have facilitated advances in both observation and simulation. More powerful computers allow for greater tracking ability in observations, and allow simulation of a larger numbers of fish. Advances have also allowed simulations to operate in three dimensions rather than two which had limited earlier efforts. Despite these advances it is still clear that there is a long way to go before these models can be meaningfully compared with observation in anything more than a qualitative sense.

2 Observation/Experiment

There are two main goals to the experiments into fish schooling. The first is simply to observe in the wild or in a laboratory the various features of the fish schools themselves. That is, to observe and measure the size of the school, its density, or the orientation of the fish within the school. The second is to investigate the behavior and sensory faculty of individual fish. By observing how one fish responds to its environment or how a few fish respond to each other it is hoped that some general rules will become apparent for fish-

fish interactions. Understanding these fish-fish interactions is crucial to the efforts to simulate fish schools.

2.1 General Features of Fish Schooling

Schooling occurs in over 50% of species of fish at some point in their lifespan [7]. Because of this there is a huge variety in the types of schooling behavior that are observed. It ranges from simple groups of fish traveling together to complicated swirling arrangements. The simple arrangements are the most commonly studied. In this case the fish form an ellipsoid and are characterized by an approximately constant density and a high degree of polarity[6]. Other configurations of fish schooling include the vortex and milling structures. In these arrangements fish swirl around in tornado or hurricane-like structures. These structures generally occur in fish that are not moving over large distances and have settled in one area to feed or mate. The sheer variety in fish and types of schooling is a major problem in trying to understand how fish school. Observations made about one type of fish may be completely at odds with those of a different type.

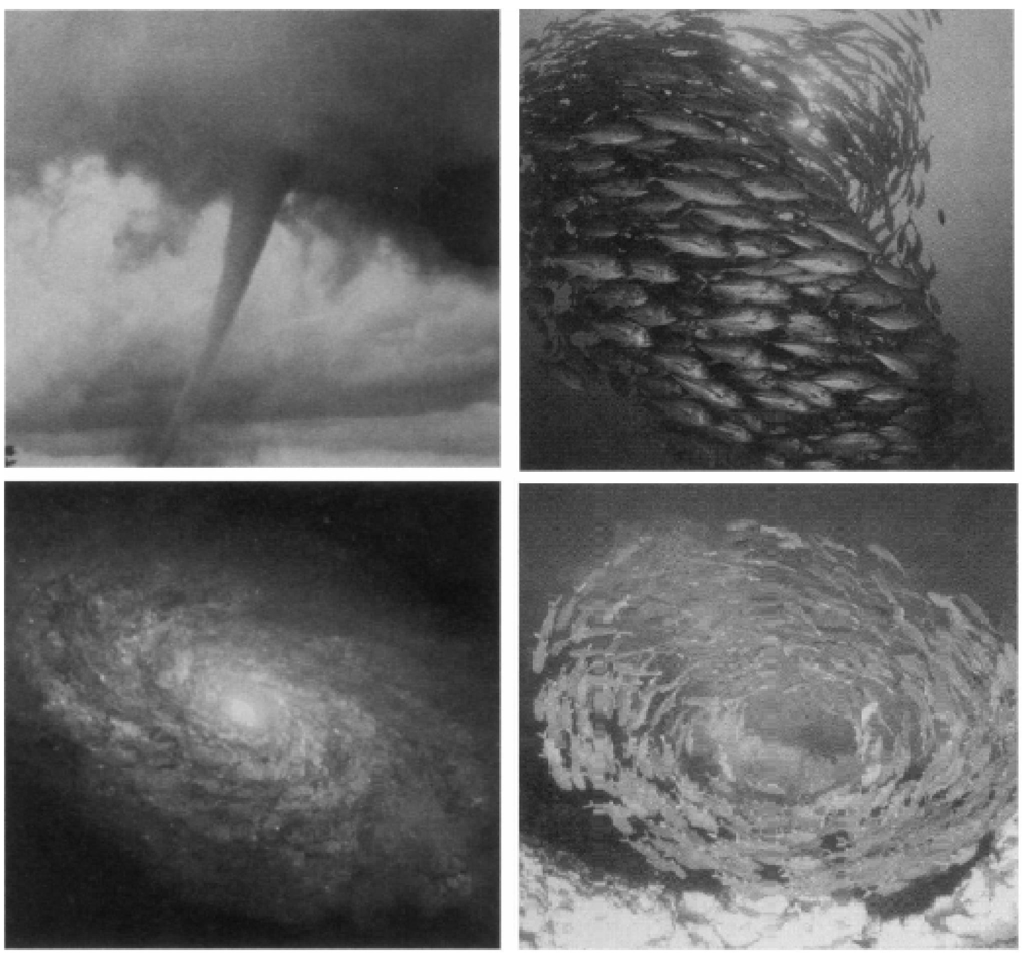

Figure 1: Notice the striking similarities between emergent structures in inanimate systems and those seen in fish schooling. Left: tornado and galaxy, Right: fish in vortex and milling structures configurations (Adapted from [7]).

Further, observed behavior of single fish or even small schools is not necessarily a good indicator of how large schools will behave. Looking for the underlying behavioral responses which lead to schooling is thus a very complicated endeavor.

2.2 Advantages of Schooling

Observations of fish schools in the wild make it clear that schooling does confer a great deal of advantage to those fish that join it. The main advantage is in predator detection and avoidance[3]. While an individual fish has limited vision, the school as a whole has a greater field of view and will often be able to detect predators more easily. Upon detection the fish can signal to each other through behavioral changes and the group as a whole can attempt to escape. The escapes are sometimes seen as "flash expansions" where the group suddenly disbands and all members shoot off in random directions. Other responses include "fountain" formations in which the school separates, only to reform behind the predator[3]. Another benefit the school has is that when a predator makes an attack it will often become confused by the large number of fish in the school and end up unable to focus on one target. Beyond the anti-predator mechanism schools provides are increased foraging ability (again due to the greater number of fish looking for food) and greater proximity for mating[4].

While schooling provides many advantages, there are also disadvantages. Some predators, marine mammals especially, specifically target the large groups and are able to take advantage of their high density. Humans too take advantage of schooling as the schools are easy to locate on sonar and it is easy to net a large population with relatively little effort[5, 7]. Large schools also run the risk of depleting local resources and endangering their survival. Ultimately the variety in species of fish that school and the variety in types of schooling speak both to the evolutionary advantage of schooling, and the fact that there are not very strict requirements for complex behavior to emerge out of simple tendencies.

2.3 Observations of Schooling Fish

Attempts have been made to quantify the formations in fish schools in several different ways. A typical experiment conducted in the laboratory is to set up a tank of moving water with a small school of fish in it. The fish are then photographed or videotaped as they swim. The photographs are analyzed typically for several parameters, notably the nearest-neighbor-distance, and the angle of orientation between nearby fish[4]. These give fairly good measures of the density of the fish school and the degree of relative polarization. A typical experiment of this type can be found in [4]. These measurements have improved drastically with improved computer tracking software but are still fairly limited due to the difficulty in obtaining three dimensional trajectories over a long time scale[7]. The measurements are generally only possible with small species of fish where a significant number will fit in a tank and tracking can only be done consistently over short periods of time. While these types of measurements provide some useful information they often take place in rather limited, artificial circumstances.

Observations in the wild have generally been limited to only the most general characteristics of the schools. Qualitatively much can be said about their shape and behavior, but little conclusive quantitative information is available making it difficult to compare features of laboratory and simulated schools to those in the wild. However, more recently technological advances have lead to promising results for the future of these measurements. Sonar technology has developed to the point where three dimensional density maps can be made of fish in the wild[5]. While this area of research is fairly nascent, it is clear that, in the future, quantitative data will be able to be obtained of fish in the wild, outside of the artificial laboratory circumstances.

2.4 Observations of Individual Fish

Observations of individual fish or small groups have also been made in an attempt to isolate those behaviors which lead to schooling. There have been a multitude of studies which try to track the so called optokinetic response in fish. This is the mechanism by which the fish see and react to other fish in the school and change their position or orientation to stay in the school[4]. Studies to measure this response include placing a fish in a tank with a mirror and measuring its response to its reflection (i.e. whether it attempts to swim near the reflection or away from it) as well as its response to a moving background image. A typical experiment of this type can be found in [4]. The understanding of the optokinetic response may be key in understanding how fish school. However, it must be noted that this system will differ drastically from species to species.

Observations have shown that some of the expected properties necessary for schooling are seen in smaller groups of fish, unfortunately the behavior of a few fish is often rather different from the behavior of fish within a larger school. While they still tend to come together and move together, the shapes they travel in are significantly different from the shapes of larger schools and thus it is difficult to generalize to larger schools.

2.5 The Current State of Fish School Observation

The current state of experimental/observational efforts to understand fish schools is still rather limited. While advances are being made in measurements in the wild and improved tracking of fish in the laboratory, many difficulties remain. It is still a major difficulty to accurately track fish position for a large number of fish over a large amount of time. Detailed tracking of the velocities of individuals within large dense schools is still impossible. Observations in the wild, though progressing, are still very limited.

3 Simulations

The theoretical aspect of fish schooling has been approached primarily with simulations. In general these simulations attempt to account for schooling formations by modeling each fish as governed by certain simple rules. Most involve some differential equations which are then integrated numerically to get a time dependant velocity for each fish. The exact differential equations and rules by which the fish interact vary across the many efforts, but many different forms are able to achieve some aspect of schooling behavior. I will focus on one type of model which is particularly illustrative of the main features of these simulations.

3.1 Common Features of Most Models

In the model used by D'Orsogna et.al. the fish are set to obey a rather simple equation[1]:

$$m\frac{\partial \vec{v}_i}{\partial t} = (\alpha - \beta |\vec{v}_i|^2)\vec{v}_i - \vec{\nabla}_i U(\vec{x}_i)$$

Here each fish is treated as an object subject to certain forces. It has its own motive force (the α term) which, combined with a velocity dependant drag force (the β term), tends to bring the fish to a constant speed. There is also a force due to some potential which is used to model the attraction/repulsion of each fish to each other fish in the school, this is the so-called social force[5]. The potential that generates the social force is the main difference between the models and it is essentially a completely unknown quantity experimentally. Proposed potentials vary significantly and encompass both very simple and rather complex functions.

Some of the simplest (and in many senses the most illustrative) just assume a form with a exponential attractive potential effective generally at large distances to model the general trend of fish to congregate with others of their kind, and a separate repulsive exponential potential to model the necessity for collision avoidance at a much shorter range. This is the simple potential of D'Orsagna et.al.[1]:

$$U(\vec{x}_i) = \sum_{j \neq i} [C_r e^{\frac{-|\vec{x}_i - \vec{x}_j|}{l_r}} - C_a e^{\frac{-|\vec{x}_i - \vec{x}_j|}{l_a}}]$$

The constants l_r and l_a are used to set the length scale of the repulsive and attractive forces respectively. The constants C_r and C_a set the relative amplitudes of these forces.

More complicated potentials are generally based on some assumption of how the fish actually interact with each other. Some of these start to take into account the nearest neighbors nature of the forces. That is, since the fish are only able to see those few other fish near them they will respond only to those few they can see. In other studies attempts are made to include random noise in some fashion in order to simulate differences in fish perceptions, size or ability. More complicated potentials are often based on some assumptions about how fish will respond to each other, though they are often given without much experimental evidence and amount to little more than educated guesses. Many of these guesses give reasonable results, but not categorically more accurate than the simpler models. In general even when some potential is assumed it will have several parameters, and in most models some values for these parameters will yield some aspect of schooling behavior. Unfortunately many papers do not fully explore the phase space of these parameters which makes it difficult to understand how the model results in schooling[7].

3.2 Principle Results

The main features that most models predict are related to a few different types of schooling. The first is the simple case where fish move in a common direction with a near-uniform spacing with an elliptical shape. Efforts have been made to calculate the density, the polarity, and shape of this pattern. This is useful especially in comparison to laboratory experiments where measurements are primarily made of the orientation and nearest neighbor distance which can be fairly directly compared to the polarity and density. Since the fish in this formation have a relatively uniform velocity and are spaced at fairly regular intervals, some models proceed in analogy to emergent states in magnetic materials[8]. The other, perhaps more exciting, form of schooling which some models deal with is that of the vortex or mill. In these cases simulated fish form fascinating circular patterns which mimic those observed in some species of fish. Unfortunately there is much less experimental data regarding these types of schooling, so it is difficult to say whether these models get anything more than the qualitative shape of the vortex correct.

In a recent paper by Hemelrijk et.al. a model was used to predict the simple ellipsoidal schooling shape[2]. The model in this paper used up to two thousand simulated fish and simulated them in three dimensions. They also take into account the density dependence of visibility in deciding which nearest neighbors their fish should respond to. This effort also utilized a rather complicated potential function. Interesting predictions are made in regard to the shape of the front of the school, the relative polarization of the fish and the density variation within the school. The model confirms the ellipsoidal shape seen in many schools. The most interesting feature is the prediction of an area of high density towards the front of the school (see fig. 2). Their model confirms several qualitative aspects of observed fish behavior. Of note are that larger population schools tend to be denser, and that slower groups become more polarized. Since this model predicts certain interesting features, especially regarding the density distribution it will be interesting to see if observations can confirm or refute this.

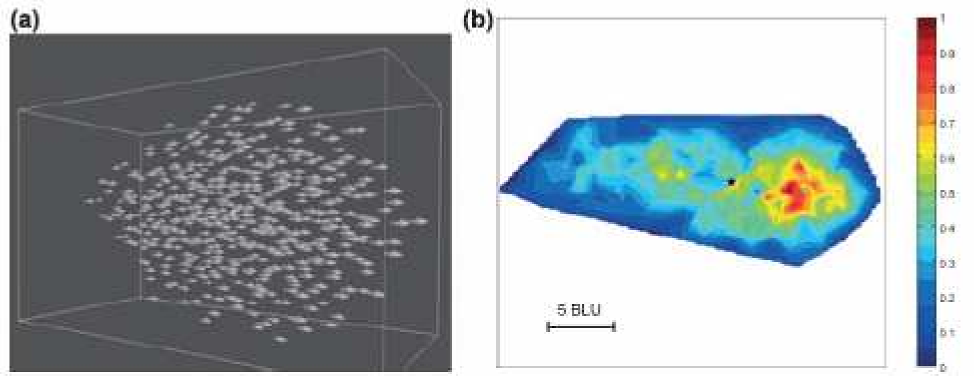

Figure 2: a) Shape and b) density distribution predicted by the model in [2]. Note the three dimensional ellipsoidal pattern the school assumes and the high density at the front of the school (picture taken from [2]).

In a paper by D'Orsagna et.al. a simple model was used to try to map the phase diagram for animal aggregations that following simple exponential attraction and repulsion[1]. These results are interesting partly in that they do not assume very much about the animals in the model, and since there is relatively little information about how the fish actually respond to one another it is useful to see exactly how little is necessary to mimic the behavior seen in the wild. The most interesting part of this work is that it predicts the more complicated forms of schooling behavior: the vortex and milling states. The phase diagram produced is also highly interesting in that it predicts how various parameters in the model can be changed to move from one type of schooling to another. Since the model is rather general it seems very promising that several types of schooling are predicted. It makes sense, then, that different types of schooling are seen in different fish since they will obviously have somewhat different responses to one another. While this model is simple, it has several parameters that the authors have adjusted across the whole phase space. The result is a comprehensive picture of what properties of fish schools can be achieved with such a simple model. This is a necessary starting point before further, more complicated models can be completely understood. If a behavior can be achieved with a simple rule, it is not necessary to complicate the model with guesses regarding the complicated ways in which real fish interact.

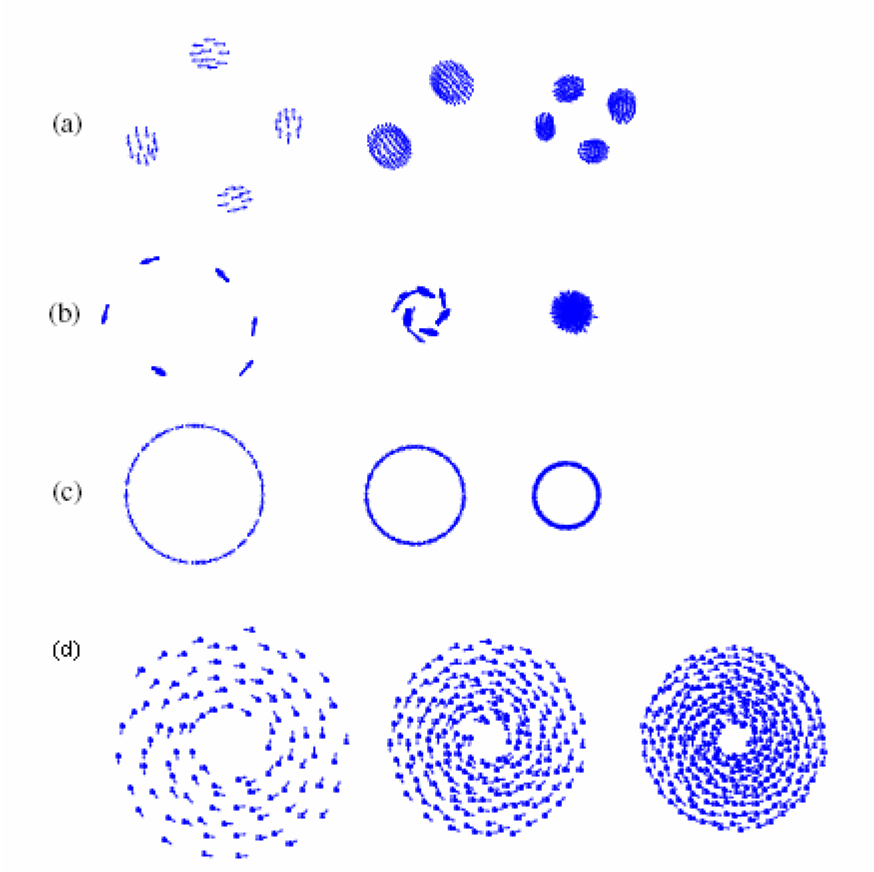

Figure 3: Simulation results from several regions of the phase diagram produced in [1], left to right is increasing the number of fish being simulated. Most interesting are a) and d) which bear striking resemblance to the ellipsoidal and milling structures seen in fish schools (Adapted from[1]).

3.3 Problems Apparent in Some Modeling Schemes

Many efforts seem to assume too much about the fish in order to model them. There are many models which try to explain the schooling behavior by having the simulated fish try to match their velocity to that of neighboring fish. Other models make fish try to orient themselves in the direction of their neighbors, and others still give the fish a preferred distance to other fish. In these cases it is interesting to note that certain features that are believed to be emergent phenomenon in fish are essentially forced into the models[7]. By making fish preferentially line up with each other and match velocities, one should not be surprised to find that the simulated fish travel in the same direction at the same speed. However, this elucidates an important point; there is no reason to assume that this is not, in fact, the type of behavioral rules that real fish are following. It is entirely possible that they are following a set of rules which more deterministically yields what seem to be emergent phenomenon. This illustrates a key area where experiments, and observations should be made; models would be very much more consistent if the actual manner in which fish react to each other was better understood. However, even if real fish obey such velocity/orientation matching rules there are still several interesting emergent phenomenon to be explained including patterns such as the vortex or mill which would still be considered emergent phenomenon.

3.4 Current State of Fish School Simulation

For some time simulations were limited to very few fish (about a hundred or fewer) and to only one or two dimensions[7]. The conclusions drawn from such simulations are hard to extrapolate to the huge schools of often millions of fish that are observed in the ocean. Only recently have computers become powerful enough to handle larger fish populations (in the thousands) and handle three dimensions. The jump to three dimensions is likely to change a lot in how the models perform. It will be very interesting to see how future models behave in three dimensions and with larger fish populations.

4 Discussion

The work done so far in studying schooling behavior in fish is very interesting. Observation and laboratory experiments have shown the tendency of individual fish to congregate and that the nature of this behavior leads to cohesive and stable long-term structures. Further, simulations show that even very simple rules can give rise to very complicated patterns which are strikingly similar to those observed in the wild. While both observation and simulation have made great progress in recent years, there are still hurdles to overcome.

4.1 Main Problems in Fish Schooling Research

The main problem that is evident in this work is that the simulations are so disconnected from experiments. While the simulations predict qualitative features, little is done in a quantitative sense to connect these to experiments. On the other hand the experiments aimed at determining individual fish behavior seem too primitive to really get at what the simulations need. That is, they often focus on features of the schools (density polarity etc.), or individual fish behavior, but not their behavior within the schools. An understanding of fish behavior in the schools will be needed to get an accurate social force for the simulations.

Up till now researchers constructing the models seem to have to guess at what a reasonable potential might look like and see if schooling behavior results. The fact that even the simplest potentials lead to schooling illustrates a problem here: if any random guess yields schooling behavior, simply guessing a function and checking will not be sufficient. The simulations may be best served by analyzing simpler potentials more completely as in [1] and waiting until sufficient evidence is available to construct accurate models. Another difficulty in studying fish schooling is the massive number of fish species that school. Observations and predictions that are valid for one species will not, necessarily hold for other species.

4.2 Potential Solutions

The obvious solution is to have greater collaboration between experiment and simulation. However, it is clear that neither the simulations nor the experiments are at the point where they can handle schooling quite as it occurs in the wild. Simulations remain limited in the number of fish they can simulate and only recently have they moved to three dimensions. Observations in the wild are difficult and it could be some time before large scale velocity tracking is possible. Even in the laboratory systems to track the velocities of fish over a large time frame are just becoming possible. It seems that the clear missing link is observations of individual fish within the school. To accurately model the fish behavior, it must be known how the fish react not to one or two other fish, but to the group as a whole. It is unlikely that a fish in a very large school will account for each of the fish near it individually; rather, it will react to the group as a whole. This type of information cannot be achieved by simply measuring the spacing between fish in the school, or their relative orientation. It can only be acquired by tracking the velocity (in three dimensions) of several fish within the school to see how they react to each other over a long period of time.

4.3 Conclusions

Because the simple models can account for many of the features of fish schooling behavior does not mean that the fish, in fact, follow such simple rules[6]. However, the simple schemes can be the most illustrative of what is actually leading to the schooling behavior. The exact dynamics of how the fish are attracted/repelled may be hideously complicated in real life, but it seems that the simple models can account for the broad features fairly well. As experiments come to better understand how fish interact, the models will not need to guess at what potential to use for fish-fish interactions, those things will be known. What the models have to contribute, then, is not in guessing at these potentials, but rather in understanding what features of these potentials lead to schooling. This can best be achieved by studying the simpler models.

Ultimately the understanding of fish schooling is set to grow by leaps and bounds as new technologies are put to use in both experimental and computational efforts. It will be fascinating to see how these new developments confirm or overturn current theories. It can only be hoped that, going forward, experimental and computational scientists will work more closely than they have in the past to develop a more cohesive understanding of this very interesting and important topic.

5 References

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