

EVOLUTION OF FISH SCHOOLS:

A THEORETICAL STUDY BY AGENT-BASED SIMULATION
AND GAME-THEORETIC ANALYSIS

Wen-Chi Yang

A thesis submitted to
The University of Birmingham
for the degree of
DOCTOR OF PHILOSOPHY

School of Computer Science
College of Engineering and
Physical Sciences
The University of Birmingham
1st Submission: April 2016
2nd Submission: January 2017

UNIVERSITY OF
BIRMINGHAM

University of Birmingham Research Archive

e-theses repository

This unpublished thesis/dissertation is copyright of the author and/or third parties. The intellectual property rights of the author or third parties in respect of this work are as defined by The Copyright Designs and Patents Act 1988 or as modified by any successor legislation.

Any use made of information contained in this thesis/dissertation must be in accordance with that legislation and must be properly acknowledged. Further distribution or reproduction in any format is prohibited without the permission of the copyright holder.

ABSTRACT

The research work reported in this thesis aimed to identify the underlying mechanism which drives fish to evolve into schooling behaviour. Although the adaptive dynamic to cause this collective movement has been widely studied from various aspects, the previous perspectives still contain different blind spots, and the causation of this adaptation is still far from discovered.

Based on agent-based simulations and game-theoretic analyses, this thesis investigated the proposed issue through the following three main research questions. First, can a model be built with less bias from the preconceived knowledge? Secondly, can the evolution of prey's schooling behaviour be simulated under individual selection? Thirdly, can the schooling behaviour be evolutionarily stable given predators are also adaptive? By addressing these three research questions, a more comprehensive answer to this topic gradually emerged. Finally, it is inferred by the simulation and derivation that the schooling pattern in nature can be an evolutionarily stable state, in which the prey adopt the collective departure strategy and the predators can develop various hunting tactics.

To reduce the bias of preconceived knowledge, two attempts were made when building a spatial-explicit agent-based model. First, the limited range of candidate strategies for prey agents to develop has been addressed by introducing the algorithm NeuroEvolution of Augmenting Topologies (Stanley & Miikkulainen, 2002) into the model. This algorithm generates a fish agent's behavioural strategy automatically in an open-ended search space. Hence, designing potential strategies in advance is unnecessary. Moreover, beneficial strategies can be developed even if they are unreported. Secondly, to validate whether the model designs which involved ecological knowledge may lead to considerable bias, the authenticity and credibility of the model were studied according to popular suggestions in the ecological domain. The validation of authenticity was to verify whether its settings accord with the empirical data of fish. The validation of credibility was to analyse the sensitivity of parameters and improve the

robustness of the model against noises. These efforts maintain that the findings and extensions from this model will be persuasive.

The simulation outputs of this relatively unbiased model displayed an unreported adaptive dynamic, that is, the collective departure scenario. It was demonstrated that when the fish agents evolve under individual selection, they tend to move into the safe centre of their groups as predicted by the selfish herd scenario (Hamilton, 1971). This tendency finally causes compact groups, where marginal prey cannot move into the centre for their safety. In this situation, prey agents develop the collective departure strategy, by which the marginal agents leave the border of their groups together to expose the inner neighbours. Hence, the moving schools emerge since no agent prefers to stay on the margin of a stationary herd. This is the first scenario to explain the evolution of schooling by evolutionary selfishness, and the second research question is addressed.

Based on the findings of the collective departure strategy, a coevolution system of predators' and prey's behavioural adaptations was constructed. It was demonstrated and analysed that there are evolutionarily stable states in this coevolution system. In these stable states, prey always adopt the collective departure strategy and cause the emergence of the schooling pattern. In contrast, depending on the strength of predators, as the level of the extra energy cost to chase a moving school, the adaptive strategies can be various. For example, if predators are strong, they should evolve to attack the central position of prey aggregates. Otherwise, they should evolve to attack the marginal prey, known as the marginal predation (Parrish, 1991). These derived adaptations are consistent with the appearance of predator-prey interactions in open waters. Hence, the third research question has been addressed.

This research is the first work to demonstrate and derive that the schooling behaviour of group-living fish can be evolutionarily stable in the predator-prey coevolution system. The agent-based simulation provides the evidence of the assumptions made in the game-theoretic analyses, and the game-theoretic studies validate that the simulation outputs are reasonable and accurate. The findings have made a breakthrough in the understanding of natural evolution in the marine world. It is hoped that this thesis can make a significant contribution to the debate on this topic.

I would like to dedicate this thesis to my parents.

ACKNOWLEDGEMENTS

First, I would like to express my deepest gratitude to my parents. Without their support and enduring encouragement, this thesis would not have been possible. They trust me heartily no matter how many frustrations and challenges I have met. This thesis is dedicated to them.

Secondly, I am sincerely most grateful to my wife, Mrs. Hsin-Ru Chen. Her unending support helped me to keep my belief and passion when the path was not smooth. I have kept in mind that she gave up her career to be with me for the duration of my research.

During the past four years, I have received lots of help and guidance from my supervisor, Dr Shan He. He was always happy to discuss with me and share his knowledge with me so that the interesting research works in this thesis can be done. I would like to sincerely thank him for leading me into the beautiful academic world.

My appreciation is also due to many academic staff at the University of Birmingham, such as Prof Jon Rowe, Prof Xin Yao, Prof Peter Tino, Dr David Parker and Dr Rami Bahsoon, for their patient guidance of my research. I also wish to thank my dear teachers in Taiwan: Prof Yung Shi Lin, Prof Cheng-Yuan Liou and Prof Jeng Chyan Chen. They have never hesitated whenever I asked for their help.

Lastly, I want to especially thank Prof J. Eric Wilkinson, Emeritus Professor of Education, University of Glasgow, UK and Professor, University of Taipei, Taiwan. This thesis cannot be done without his valuable comments and suggestions.

CONTENTS

Chapter I	Introduction.....	1
Chapter II	Literature Review.....	8
2.1	Terminology.....	10
2.2	Ecological Observation.....	12
2.2.1	Defensive Tactics of Prey Fish.....	13
2.2.2	Hunting Tactics of Predators.....	14
2.3	Mechanism and Reasons.....	16
2.3.1	Swarm Behaviour and Self-organisation.....	16
2.3.2	Survival Benefit of Schooling Fish.....	17
2.3.3	Competition within a Group.....	19
2.4	Computational Simulation.....	21
2.4.1	Self-organising Models.....	22
2.4.2	Evolutionary Models.....	24
2.5	Validation in Ecological Modelling.....	28
2.5.1	Authentic Model.....	29
2.5.2	Robust Simulation.....	32
2.5.3	Evolutionary Stability.....	34
Chapter III	Modelling the Behavioural Evolution of Prey Fish.....	42
3.1	Background.....	43
3.2	Model.....	47
3.2.1	Two Perceptions of Local Surroundings.....	49
3.2.2	Reaction by Two Elementary Behaviours.....	52
3.2.3	Evolutionary Procedure.....	54
3.2.4	Implementation of NEAT Algorithm.....	55

3.2.5	Originality of Model Design.....	59
3.3	Quantification.....	61
3.4	Validation of Authenticity.....	64
3.4.1	The Sensory Perceptions.....	65
3.4.2	The Elementary Behaviours.....	65
3.4.3	The Predation Risk.....	67
3.4.4	Other Issues.....	68
3.5	Validation of Credibility.....	70
3.5.1	Alternative Selection Scheme.....	70
3.5.2	Other Parameter Scans.....	75
3.6	Discussion.....	77
Chapter IV	Evolving the Adaptive Strategy of Schooling Fish.....	79
4.1	Background.....	80
4.2	Method.....	83
4.3	Result.....	85
4.3.1	Emergence of the Schooling Pattern.....	85
4.3.2	Transition of Adaptive Strategies.....	88
4.4	Analysis.....	96
4.4.1	Collective Departure Scenario.....	96
4.4.2	Exceptions of Collective Departure Scenario.....	102
4.5	Discussion.....	104
Chapter V	Coevolution between Prey Fish and Predators.....	106
5.1	Background.....	107
5.2	Model.....	110
5.2.1	Model Framework.....	110
5.2.2	Selection and Adaptation at the Both Sides.....	112
5.2.3	Self-organising Mechanism of Prey.....	117

5.3	Result.....	125
5.3.1	Adaptation of Prey.....	125
5.3.2	The Emergent Patterns.....	128
5.3.3	Adaptation of Predators.....	131
5.4	Analysis.....	135
5.4.1	Deriving ESSs at the Prey Side.....	136
5.4.2	Deriving ESSs at the Predator Side.....	138
5.5	Discussion.....	140
Chapter VI	Conclusion.....	143
6.1	Summation of Research Works.....	144
6.2	Contribution.....	147
6.2.1	The Proposed Collective Departure Strategy.....	147
6.2.2	The ESS in Predator-Prey Coevolution.....	149
6.2.3	The Adjustments to Reduce Modelling Biases.....	151
6.3	Limitations and Further Works.....	153
6.3.1	Influence of Other Factors to the Simulation.....	153
6.3.2	Evidence of Collective Departure Scenario in Fish.....	154
6.3.3	Analogy of Collective Departure Scenario to Other Animals...155	
	References.....	157

LIST OF FIGURES

2.1	The Rock-paper-scissors Game.....	39
3.1	Sensory Range and Two Perceptions.....	50
3.2	Decision Making by Repulsion and Attraction.....	52
3.3	Categorisation of Positions	62
3.4	RPFC Metric vs. Group-level Index.....	63
3.5	Minimal Turning Radius.....	69
3.6	Performance of Selection Schemes.....	73
3.7	Performance of Replacement Rates.....	74
3.8	Risk Distribution by Arena Length.....	75
4.1	Positional Frequencies at the Final Stage.....	86
4.2	Emergent Patterns in Evolution.....	87
4.3	Positional Frequencies at the Individual Level.....	89
4.4	Adaptive Strategies in Evolution.....	90
4.5	Frequency-dependent Risk Distribution	92
4.6	Probabilities of Positional Changes.....	93
4.7	Density and Frequency of Swarm Centre.....	94
4.8	CDS's Adaptation to Different Positions.....	95
4.9	An Idealised Circular 2D Swarm.....	99
4.10	Adaptive Dynamic of CDS.....	100

5.1	Diagram of the Self-organising Mechanism.....	119
5.2	Prey's Adaptation under $X = (X^P, 0.9X^P, X^M, 0)$	126
5.3	Prey's Adaptation given a Dangerous Centre.....	127
5.4	Full-range Map of Emergent Patterns.....	129
5.5	Two Specific Risk Distributions.....	130
5.6	Adaptive Dynamic of Predators.....	133
5.7	Evolutionarily Stable States.....	134
5.8	ESSs versus Optimal States.....	135
5.9	ESSs at the Prey Side.....	137
5.10	ESSs at the Predator Side.....	139

LIST OF TABLES

2.1	Terms about Collective Behaviour.....	11
3.1	Parameters of Interaction.....	49
3.2	Parameters of NEAT.....	58
4.1	The Four Evolutionary Stages.....	88

Unexpectedly, when somewhere sheds a faint light, full of uncertainty, awe-inspiring, should one leave the route, and tread a footpath toward to it? In Robert L. Stevenson's story *Eldorado* (1878), those Spanish kept chasing that dim figure, had never stepped back, even if overwhelmed by the shadow of fear. "A strange picture we make on our way to our chimaeras, ceaselessly marching, grudging ourselves the time for rest; indefatigable, adventurous pioneers."

CHAPTER I

INTRODUCTION

This thesis is concerned with the computational simulation and game-theoretic analysis of the behavioural evolution of fish in open waters. In open waters, most species of group-living fish flock into a densely packed aggregate, head in the same direction and swim with a high degree of coordination when they confront predators (Breder, 1967; Shaw, 1978; Magurran, 1990). This collective behaviour has long been referred to as the ‘schooling’ pattern in related biological studies, like Parr (1927), Atz (1953), Aoki (1982), Handegard et al. (2012) and so on. Due to the polarised property of a schooling pattern, there must be some fish in the front position of their group, which lead other fish to move forward. It has been observed and analysed that fish in this front position (referred to as the ‘pioneer’ position in this thesis) undertake a higher predation risk than their followers (Bumann et al., 1997).

Since fish schools generally consist of unrelated individuals and the effect of inclusive fitness is insignificant (Naish et al., 1993; Hauser et al., 1998; Krause et al., 2000), this

phenomenon leads to a pending question why schooling fish can be pioneers unselfishly (Parrish & Edelstein-Keshet, 1999). The paradox is that: if pioneers in a fish school incur a higher risk than those followers, a selfish fish which always hides in the crowd should gain better survival fitness. Therefore, evolution should not drive fish into the schooling pattern since those fish willing to be pioneers should be replaced by the selfish ones according to the principle 'survival of the fittest'.

However, the schooling pattern has been observed in various species of gregarious fish when they are under a predatory hazard (Shaw, 1978). To discover the reason for these adaptations, explanations from various perspectives have been proposed. For example, some empirical studies have reported that these schooling formations can reduce the average risk on fish individuals, which may result from the confusion effect (Milinski & Heller, 1978), dilution effect (Turner & Pitcher, 1986), information transfer effect (Lima, 1995) and so on (Krause & Ruxton, 2002). These findings imply that the benefit at the group level may relieve the degree of short-term selfishness in evolution.

On the other hand, some studies doubt the influence of group benefit in evolution and emphasise the adaptive dynamic undergone by selfish individuals (Dawkins, 1976; Williams, 1966). For example, Hamilton (1971) demonstrated that the herding phenomenon can be explained by evolutionary selfishness, known as the selfish herd scenario. To further explain the formation of a moving school from the same viewpoint, individual difference and evolutionary trade-offs are the two primary proposed reasons. The first reason is that the different needs or endowments among fish individuals can cause fish of some characters prefer to lead the group (Conradt & Roper, 2009; Eshel et al., 2011). In other words, it is believed that there is a fixed group of pioneers in a school. The second reason is that the higher predation risk of being a pioneer can be

mediated by the foraging benefit (Krause, 1992; Olson et al., 2015). It implies the schooling formation is more likely to happen in a foraging stage. Both reasons lead to some conflicts with the empirical data.

The agent-based simulation has been employed to study the evolution of the collective movement since Reynolds (1993) and Werner & Dyer (1993). It is considered more persuasive to illustrate a natural complex system by this kind of models because they avoid a large degree of abstract simplifications compared to those models built from the view of the whole population (Grimm et al., 2005; Schellinck & White, 2011). Among this kind of models, Wood & Ackland (2007) showed that both a stationary herd and a moving school can be the final emergent patterns in evolution, and all schooling agents have the same probability of being pioneers temporarily. However, different outputs also exist. For example, the simulation in Guttal & Couzin (2010) demonstrated that a subgroup of agents should become permanent leaders to cause the collective motion in evolution, and the simulation in Olson et al. (2013) displayed that schooling is a transitional state toward to stationary herds under individual selection and adaptation.

So far, explanations about the adaptation of schooling behaviour all have their advantages and drawbacks. The viewpoints based on the group benefit can be supported by empirical data, but leave a conflict with the principle of natural selection. The viewpoints based on evolutionary selfishness are theoretically correct, but only the herding behaviour can be explained from this aspect persuasively at present. The computational simulations are possible to disclose implicit causations in the evolutionary trajectory, but their outputs are largely affected by the preconceived knowledge behind the model design. These pros and cons of different viewpoints have

resulted in debates and studies on this topic for decades, which are reviewed in Chapter II.

In this thesis, the question why fish have evolved into the schooling pattern is investigated by computational simulations and game-theoretic analyses. The general aim of the research is to solve this pending question, which can be achieved through addressing the three main research questions of this thesis sequentially. First, can a computational model be constructed with less preconceived bias in its design? Secondly, can this relatively unbiased model simulate the evolution of fish schools under individual selection? Thirdly, when the adaptation at the predator side is considered, can fish agents evolve into a schooling pattern?

The first research question considers that since the simulation outputs largely depend on the model design, methods to reduce the potential bias of the involved knowledge then become fundamental. To address this question, related concerns about the authority and credibility of an ecological model are highlighted. In addition, the bias from an arbitrarily designed set of potential strategies in previous works has also been reduced. The works about the construction of an evolutionary model with an open-ended solution space, as well as its validation, are put in Chapter III. The second research question considers whether evolutionary selfishness under individual selection is sufficient to drive fish agents into the schooling pattern by the model. If it is possible, the viewpoints based on individual selection are supported, and the reason of this adaptation can be inferred from the simulation. On the other hand, if the model demonstrates that individual selection cannot drive fish agents into the schooling pattern, the viewpoints based on the group benefit are supported, and the selective forces at the higher level should be studied. These experiments and analyses are displayed in Chapter IV. The last

research question further considers the coevolution between prey fish and their predators. If it is demonstrated that the schooling pattern can evolve when predators are also adaptive, the answer to the pending question can be more complete. This attempt is described in Chapter V.

In Chapter III, the issue about model construction and validation is studied. To simulate fish behaviour and the emergent patterns, a spatial-explicit agent-based model is built, in which the fish agents interact with one another in a virtual arena as the appearance of real fish. To simulate the evolutionary dynamic of prey fish, the NEAT algorithm (Stanley & Miikkulainen, 2002) is employed, which evolves neural networks through a genetic algorithm and the complexity of networks, as the numbers of links and nodes in a neural network, increases with generations automatically without an upper bound (Stanley & Miikkulainen, 2002). Therefore, by letting each NEAT network represent a behavioural strategy of a fish agent, that is, the operation of elementary responses based on local information, the behavioural evolution of fish can be simulated without an artificially predetermined set of potential strategies. To heed previous criticisms on the related simulation works (Grimm et al., 2005; Schellinck & White, 2011), the authenticity and credibility of this model are emphasised and validated. First, whether the settings and parameters of the proposed model are consistent with the empirical data is analysed thoroughly. Secondly, the robustness of this evolutionary model, which indicates the ability to reproduce consistent and reliable outputs given a noisy environment, and the sensitivity of model parameters are experimented and reported.

Based on the proposed model, the research question about whether schooling can be the simulation output is addressed in Chapter IV. It is demonstrated that the schooling pattern can evolve through the mechanism of individual selection. In the model, this

adaptation usually increases the predation risk of the whole population, which implies that the group benefit can be irrelevant to the adaptation of schooling in nature. Through a theoretical analysis, the collective departure scenario is proposed. It indicates that under individual selection, the tendency of herding, as the selfish herd scenario (Hamilton, 1971), will finally result in a tightly packed and relatively stationary swarm where no peripheral fish can enter the central position of the crowded flock. In this situation, leaving the swarm with few companions can be more adaptive than staying on the periphery, so the stationary swarm will be replaced by moving groups, or to say, schooling patterns, in evolution. The excess fitness of this strategy is earned from exposing central fish of a swarm after the collective departure, which exposed fish have to share the predation risk during a predatory hunt.

In Chapter V, the adaptation of predators' hunting strategies is considered. That is to say, if predators' feeding preferences are adaptive, can fish evolve into the schooling pattern? It is demonstrated that the behavioural coevolution of predators and prey can reach certain evolutionarily stable states. Depending on the energy difference between chasing a moving school and hunting a stationary herd, the adaptive strategies at the predator side can be various. If this difference is greater than a threshold, predators should evolve into the 'marginal predation' (Parrish, 1991), that is, attacking the border of a prey group. This adaptation can be observed in most predatory fish and dolphins (Parrish, 1991; Vaughn-Hirshorn et al., 2013). If this energy difference is small, the predators should evolve to hunt the centre of a prey group. This tactic can be observed in killer whales and humpback whales (Simila & Ugarte, 1993; Wiley et al., 2011). In contrast, prey aggregation forms the schooling pattern by the collective departure strategy in any evolutionarily stable states.

The research studies in this thesis illustrate a complete picture of the behavioural evolution of gregarious fish as well as their predators in open waters. It is inferred that natural selection at the individual level can drive prey fish and their predators into an evolutionarily stable state, where the prey fish exhibit the schooling pattern and the predators usually display a preference of marginal predation. This schooling pattern can be a self-organising phenomenon from the adaptive strategy of collective departure, by which peripheral fish leave the border of a group together. These findings are consistent with fieldworks and empirical studies to a significant extent and have broadened the understanding of the evolution of fish schools in nature.

CHAPTER II

LITERATURE REVIEW

The research of animals' social behaviour has been a significant field in Ecology (Krause & Ruxton, 2002; Couzin & Krause, 2003). One popular subject is the collective behaviour of fish, especially when under predatory threats (Krause & Ruxton, 2002). In this situation, fish immediately flock into a compact aggregate and move in coordination (Magurran, 1990).

Two questions behind this phenomenon have been proposed for half a century (Sumpter, 2006): viz., by what mechanism can those relatively simple fish perform such sophisticated behaviours? Why have these behaviours developed in evolution? At present, the first question in general seems to be solved, that is, fish can simply interact with other nearby fish, and the local interaction among individuals can result in a certain collective behaviour, known as the self-organising phenomenon (Couzin & Krause, 2003). However, detailed interpretations of the local interaction are still diverse (Schellinck & White, 2011).

The answer to the 'why' question has not reached a consensus. The most popular viewpoint is that survival pressure is the primary evolutionary force (Krause & Ruxton,

2002). Relevant explanations are the information transfer effect (Lima, 1995), the confusion effect (Milinski & Heller, 1978) and the dilution effect (Turner & Pitcher, 1986), which indicate that the collective behaviour of a fish aggregate brings the survival benefit to its members. On the contrary, the benefit of a group has long been considered doubtful to drive the evolution of fish individuals by other academic schools (Hamilton, 1971; Dawkins, 1976; Williams, 1966), despite that a more convincing explanation has not been proposed.

Computational models have been introduced to inspect viewpoints about the ‘how’ question for decades, for its capability to simulate the self-organising mechanism of social agents (Grimm et al., 2005; DeAngelis & Grimm, 2013). In fact, current understanding of fish’s self-organising phenomenon has largely relied on the spatial-explicit agent-based models (Schellinck & White, 2011). In these models, fish agents are put into a virtual place to interact with one another under a set of rules.

In recent years, the attempts to employ computational models to gain insight into the ‘why’ question have begun (Wood & Ackland, 2007; Olson et al., 2013; Olson et al., 2016b). These few works simulated the evolutionary trajectory of prey population by spatial-explicit agent-based models, and used their outputs to support certain viewpoints and propose causal inferences. The outputs of these evolutionary simulations, however, can even conflict with one another due to different preconceived knowledge behind their model settings.

In the following sections, after clarifying the definition of certain ambiguous terms, the above summation is reviewed in detail, from Chapter 2.2 to Chapter 2.4 sequentially. In Chapter 2.5, the validity of an evolutionary model in Ecology is discussed from the

three aspects: the authenticity of a model, the robustness of a simulation and the convergence of an evolutionary process.

2.1 Terminology

First, the terms used to describe collective behaviours and patterns of fish individuals are clarified. Following the conformity of related studies, for example, Parr (1927), Atz (1953), Aoki (1982), Couzin et al. (2002) and Handegard et al. (2012), the term ‘schooling’ is introduced to indicate the coordinated and cohesive movement of a fish aggregate, and a schooling aggregate is referred to as a ‘school’. To describe other two collective patterns highlighted by related works, following the usage in Parrish & Edelstein-Keshet (1999), Couzin et al. (2002), Deutsch et al. (2012), Tunstrom et al. (2013) and so on, the term ‘swarm’, or ‘swarming pattern’, is adopted to mention a relatively stationary group where individuals move with a low coordination; the term ‘milling pattern’, or ‘milling group’, is adopted to mention a stationary aggregate which individuals circle about the centre of the group in coordination.

The terms ‘herd’ and ‘flock’ are used based on their usual definitions, as to mention a cohesive aggregate, no matter it is a school, a swarm or a milling group. Similarly, their verbs are used to mention the behaviour to form cohesive aggregates. As a complement, the term ‘shoal’, which is usually adopted to mention a fish aggregate without the emphasis of the collective pattern, was sometimes used to refer ‘schooling’ or ‘swarming’ in different contexts (Delcourt & Poncin, 2012). This term is avoided in the thesis to reduce possible ambiguity.

Table 2.1: Terms about Collective Behaviour

Term	Definition	References
‘schooling’	The behaviour to move in coordination with nearby individuals so that a moving aggregate emerge.	Parr (1927), Atz (1953), Aoki (1982), Couzin et al. (2002), Handegard et al. (2012), etc.
‘school’	A moving aggregate where individuals move in coordination and head in the same direction.	
‘swarming’	The behaviour to move towards nearby individuals in low coordination so that a relatively stationary aggregate emerges.	Parrish & Edelstein-Keshet (1999), Couzin et al. (2002), Deutsch et al. (2012), Tunstrom et al. (2013), etc.
‘swarm’	A relatively stationary aggregate where individuals move in low coordination.	
‘milling group’	A relatively stationary aggregate where individuals cycle around the centre in coordination.	
‘herd’ / ‘flock’ / ‘group’	An aggregate (which can be a school, a swarm, a milling group or others), or the formation of an aggregate.	Hamilton (1971), Aoki (1982), Couzin et al. (2002), Deutsch et al. (2012), etc.

Secondly, the usage of the two terms in this thesis, ‘evolution’ and ‘coevolution’, are clarified. In Ecology and Biology, the term ‘coevolution’ is a specific concern of ‘evolution’, which focuses on the interactive influence of different species or objects in evolution, like the ‘coevolution’ of predators and prey, or the ‘coevolution’ of heterogeneous proteins (Thompson, 1989).

However, in Computer Science, particularly in the subdomain Evolutionary Computation, an evolutionary system is labelled ‘coevolutionary’ if the performance (usually referred to as the fitness value) of a solution (which can represent a strategy, an individual, a set of parameters and so on) is influenced by other solutions in the population (Paredis, 1995; Watson & Pollack, 2001). For example, the multi-player prisoner’s dilemma game is a ‘coevolutionary’ system since the utility of a strategy depends on other players’ strategies (Miller, 1996). In contrast, the term ‘evolution’ is used when a solution’s performance can be evaluated without the consideration of other solutions in the population, for example, the successful times of a solution in a typical

pole balancing task (Wieland, 1991). According to this definition, evolution of a prey population should be a ‘coevolutionary’ system if each prey’s survival fitness depends on not only its behavioural strategy but also other prey’s strategies.

To make the statement in this thesis consistent with the proposed ecological topic, the definition and usage of ‘evolution’ and ‘coevolution’ are kept with the ecological domain, for example, ‘evolution of prey’ and ‘coevolution between predators and prey’. However, it should be noted that all the mentioned evolutionary models in this thesis, from previous works to the proposed models, are ‘coevolutionary’ systems given the definition in Evolutionary Computation.

Thirdly, the term ‘fitness’ usually mentions the evaluated value of a solution’s performance in Evolutionary Computation (Haupt & Haupt, 2004). It is not exactly the same as a solution’s reproduction probability, although they are positively correlated. In contrast, ‘fitness’ usually equals the reproduction probability, or the reproduction rate, in Evolution Theory and Evolutionary Game Theory (Hammerstein & Selten, 1994). In this thesis, the usage of this term conforms to the definition in Evolutionary Computation.

2.2 Ecological Observation

The interaction between prey fish and their predators in open waters is a splendid natural sight. At the prey side, an aggregate of fish individuals responds to the predatory attacks as a coordinated unit, and exhibits dramatic evasive tactics like moving, morphing, splitting and merging (Magurran, 1990). At the predator side, predatory fish and cetaceans have developed sophisticated hunting strategies against the prey

aggregation (Domenici, 2001). In the sequent content, this real-world phenomenon is depicted as background for further discussion.

2.2.1 Defensive Tactics of Prey Fish

Aquatic vertebrates exhibit different evasive strategies when facing the predation hazard. One common and efficient defence is hiding into reefs or rifts (Krivan, 1998). Unfortunately, this method is not an option for fish with their habitat in open waters, like in the pelagic zone of the ocean, where finding a refuge to reduce the predation risk is denied.

For these fish, collective motion has been developed under predatory threats (Shaw, 1978). A dramatic example is when the pelagic forage fish, like herrings (*Clupea harengus*) and sardines (*Sardinops sagax*), encounter their predators (Clua & Grosvalet, 2001; O'Donoghue et al., 2010). In this situation, countless prey fish flock tightly and move in high coordination with one another in front of those predatory fish and cetaceans. This unique response of vigilant prey fish is known as 'schooling' (Breder, 1967), also referred to as 'polarisation' (Partridge, 1982) and 'compact' (Magurran & Pitcher, 1987). More examples of the schooling behaviour are in dwarf herrings (*Jenkinsia lamprotaenia*), polllocks (*Pollachius pollachius*) (Partridge, 1982), minnows (*Phoxinus phoxinus*) (Magurran & Pitcher, 1987), and so on (Seghers, 1974; Hoare et al., 2004; Tien et al., 2004).

The biological mechanisms to establish this schooling pattern have been well investigated since Parr (1927). Empirical studies showed that the degree of coordination of schooling fish is decreased considerably when their eyes are covered (Parr, 1927; Atz, 1953; Partridge, 1982). Therefore, vision has been suggested as the fundamental

function for fish to maintain a schooling pattern. In addition, the influence of the lateral lines, a biological system to detect the surrounding water flow, has also been reported (Partridge, 1982; Faucher et al., 2010). When fish's lateral lines are temporarily damaged, the frequencies of body collisions and isolated fish both increase (Faucher et al., 2010).

2.2.2 Hunting Tactics of Predators

Different from the identical adaptation of prey fish in open waters, the adaptations of predatory fish and cetaceans vary largely among species. Nevertheless, their hunting tactics can be organised in general by dividing predators into the following three types (Domenici, 2001): relatively small predators (around ten times larger than their prey fish), relatively large predators (around 100 times larger than their prey fish) and extremely large predators (around 1000 times larger than their prey fish).

For those relatively small predators, the 'marginal predation' is a significant feeding preference (Parrish, 1991). That means the predator prefers to eat those prey at the boundary of a group, rather than those in the centre. Examples are bass (*Micropterus salmoides*), goldfish (*Carassius auratus*) (Romey et al., 2008), and bullgill (*Lepomis macrochirus*) (Ioannou et al., 2012). This preference has been well depicted in Romey et al. (2008). The experiment showed that, given a prey group on the water surface, a predatory fish directly below this group still attacks the marginal prey, even if they are more distant to the predator than the central ones.

Those relatively large predators are the primary predators in the pelagic zone of the ocean, and have developed multifarious hunting strategies (Parrish, 1991; Domenici, 2001). For example, when a swordfish (*Xiphias gladius*) or a sailfish (*Istiophorus*

albicans) feeds on schooling prey, it uses its long bill to ‘slash’ at the prey group and then catches those attacked and injured fish (Domenici et al., 2014). The thresher shark (*Alopias pelagicus*) ‘whips’ the prey group by its tail to receive a similar result (Oliver et al., 2013). These predators have evolved their weapons to hunt prey aggregation solitarily.

Moreover, some species of relatively large predators have developed coordinative group hunting strategies. For example, when dolphins, such as spinner dolphins (*Stenella longirostris*) and dusky dolphins (*Lagenorhynchus obscurus*), feed on schooling fish, they ‘herd’ these prey into a milling aggregate (Benoit-Bird & Au, 2009; Vaughn-Hirshorn et al., 2013). The participant dolphins can vary from 3 to 300, depending on the breed (Vaughn-Hirshorn et al., 2013). A typical process of this hunting tactic is each dolphin first swims through the side or bottom of the fish school without direct feeding attempts, known as the ‘herding pass’ (Benoit-Bird & Au, 2009). After several times of herding passes, prey fish are centralised into a huge milling aggregate. Dolphins then begin to consume fish at the side of the milling ball, that is, exhibiting the marginal predation (Vaughn-Hirshorn et al., 2013).

To those extremely large predators, that is, large sharks and whales, a school of prey fish can be treated as a food unit (Parrish, 1991). For example, when a humpback whale (*Megaptera novaeangliae*) attacks schooling fish, it first expels air bubbles below the prey school to drive stunned fish into a dense aggregate. Then it consumes the whole aggregation from the bottom to the water surface through a bite (Wiley et al., 2011). Killer whales (*Clupea harengus*) can also exhibit a group hunting behaviour similar to dolphins, without the appearance of marginal predation (Simila & Ugarte, 1993).

2.3 Mechanism and Reasons

Focusing on the schooling pattern of gregarious fish when they confront predators, the following two questions have been studied for decades (Sumpter, 2006): how do fish exhibit this schooling pattern? Why have they developed this behaviour? The former question is about the mechanism to form the collective behaviour and the latter question concerns the mechanism of its adaptation in evolution. Nowadays, the gap between these two topics is inconspicuous (Sumpter, 2006).

In the following section, the swarm behaviour and self-organising phenomenon is introduced to address the ‘how’ question. Subsequently, current understanding and debates of the ‘why’ question are reviewed thoroughly.

2.3.1 Swarm Behaviour and Self-organisation

Two essential characters of a fish school are as follows. First, fish are homogeneous without collaboration or social roles (Partridge, 1980; Ward et al., 2001; Grégoire et al., 2003). That is to say, this collective motion does not consist of certain leaders. Secondly, consensus making is local and limited (Olst & Hunter, 1970; Huth & Wissel, 1994; Hoare et al., 2004). That is to say, fish can only interact with their neighbours and cannot form the schooling pattern on purpose. This collective behaviour, caused by homogeneous and simple individuals, is known as swarm behaviour (Bonabeau et al., 1999; Bouffanais, 2016). Swarm behaviour has been observed among several gregarious organisms, like the murmuration of starlings, the vortex swimming of daphnia, the milling formation of ants, as well as the schooling pattern of fish (Couzin & Krause, 2003; Conradt & Roper, 2005).

Although swarm behaviour can display a sophisticated appearance at the group level, it is usually caused by relatively simple behaviours at the individual level (Bonabeau et al., 1999; Bouffanais, 2016). For example, it has been demonstrated that the collective evasion of schooling fish can be simulated through four simple individual behaviours as below (Inada & Kawachi, 2002). One is moving away from the extremely close neighbours, another is moving towards the relatively distant neighbours, the third one is keeping the distances to the other neighbours, and the last one is escaping from a predator. When these simple reactions are adopted by a population of homogeneous prey agents, the evasive tactics of natural schooling fish during a close attack, like the morphing and merging of an aggregate, can be observed. The phenomenon that simple individuals can result in unexpected group behaviours is referred to as self-organisation (Couzin & Krause, 2003). This mechanism implies that the collective pattern is an ‘emergent’ phenomenon from local interactions.

Since the first self-organising model of fish’s schooling pattern (Aoki, 1982), the studies on the self-organising mechanism in animals have been fruitful (Couzin & Krause, 2003; DeAngelis & Grimm, 2013). One of the most popular tools is the spatial-explicit agent-based model. This kind of model simulates the complex mechanism of self-organisation through the spatiotemporal interactions among a population of simple agents (Schellinck & White, 2011). These simulations are reviewed in Chapter 2.4.1.

2.3.2 Survival Benefit of Schooling Fish

As to the question why fish have evolved into the schooling pattern under predation risk, a prevalent belief is that this formation provides survival benefit to the individuals (Krause & Ruxton, 2002). The three most popular explanations are the information

transfer effect (Powell, 1974; Lima, 1995), the confusion effect (Milinski & Heller, 1978; Hall et al., 1986), and the dilution effect (Foster & Treherne, 1981; Turner & Pitcher, 1986). The first two explanations advocate that schooling brings a functional advantage to fish individuals, which advantages require further mechanisms be involved. The third explanation stresses the survival benefit of living in groups compared with living in isolation, or in smaller groups. This advantage needs no additional mechanism within a group.

The information transfer effect, also termed the 'many-eyes effect' (Powell, 1974) or the 'wisdom of the crowd effect' (Conradt, 2011), predicts that group vigilance can cause a better opportunity for individuals to escape from predators. It is because the detection range of a group is much wider than that of a single individual, and the spreading of danger signals within a group can be quick (Lima, 1995). However, the phenomenon that an individual is less vigilant in a large group may reduce the effect of this collective detection (Roberts, 1996). Recent empirical studies have reported that this information transfer effect occurs in fish schools (Handegard et al., 2012), and the spreading of information becomes quicker as the group size increases (Ward et al., 2008). The mechanism by which group-living animals can improve their decision making in a large group was also modelled theoretically (King & Cowlshaw, 2007).

The confusion effect indicates that the similar characters of prey individuals can reduce the accuracy of a predatory attack (Milinski & Heller, 1978). That is to say, a predator is likely to change its target many times when facing an aggregate of identical prey, which potentially decreases the successful rate of the attacks (Hall et al., 1986). This hypothesis is favoured in invertebrate animals (Smith & Warburton, 1992). On the schooling fish and their predators, supportive evidence had been considered scant

(Morgan & Godin, 1985; Krause et al., 1998). However, some of recent empirical studies inferred the existence of this effect from predatory fish's preference of marginal predation (Romey et al., 2008; Ioannou et al., 2012).

The dilution effect describes that an individual's probability of being targeted by a predator becomes smaller as the size of its group increases (Foster & Treherne, 1981). The precondition of this explanation is that the predator feeds only one prey, or few prey, when it encounters a prey group. Hence, a prey in a large group is less likely to be the unlucky one compared with a prey in isolation or in a smaller group. This viewpoint attracts less criticism since the likelihood of facing predators could be similar between a prey aggregate and a lone prey in the marine world (Turner & Pitcher, 1986). Fieldworks and Empirical studies have supported that fish in smaller groups are more in danger (Morgan & Godin, 1985; Handegard et al., 2012; Domenici et al., 2014).

2.3.3 Competition within a Group

The perspectives in the previous section highlight the survival benefit in a fish school. However, it remains uncertain whether the group benefit can cause the evolution of a schooling pattern, considering that the selective force in nature should fall on individuals rather than groups (Hamilton, 1971; Parrish & Edelstein-Keshet, 1999). This debate has lasted for a half century without a strong solution (Williams, 1966).

Hamilton (1971) underlined the effect of natural selection through a conceptual model. This work demonstrated that evolution can be irrelevant to the group benefit when individual fitness is taken into account. The scenario, known as the selfish herd hypothesis, is that frogs tend to flock into compact herds because every frog prevents itself from staying at the dangerous boundary. This famous work refutes the intuitive

opinion that evolution of a collective pattern must bring some advantage to the population. Following from the argument in Hamilton (1971), it has been pointed out that explaining fish's schooling behaviour by the group benefit could be theoretically incomplete (Parrish & Edelstein-Keshet, 1999; Sumpter, 2009).

However, a conundrum is that fish at the front edge of a school bear a higher risk than the others (Bumann et al., 1997). Moreover, the increase of the school size can aggravate the predation risk of the leading fish (Krause et al., 1998). This biased risk results in an inconsistency that if the individual selection is considered, the evolutionary stability of a schooling pattern should not hold because selfish individuals can gain excess fitness by shirking from staying in the front position (Parrish & Edelstein-Keshet, 1999). In other words, assuming the eaten ones are usually those fish ahead of the others, a mutant fish which always follows some leading neighbours, instead of staying at the front edge occasionally, should be selected in evolution. Consequentially, undergoing natural selection and adaptation, fish's schooling pattern should collapse due to the lack of leading individuals.

To avoid the invalid conclusion that the evolution of fish schools is an exception of natural selection, viewpoints based on the evolutionary trade-offs have been proposed (Krause, 1992; Parrish & Edelstein-Keshet, 1999; Conradt et al., 2009). This kind of perspective considers that although those fish at the front edge of a school undertake higher risk than the others, there is a foraging benefit for them to balance their pros and cons. As supportive evidence, empirical studies have documented that the leading fish can intake more food than their followers (Krause, 1993; DeBlois & Rose, 1996). Also, starving fish are more likely to be in the front position than well-fed fish (Krause et al., 1992). However, this trade-off explanation is not favoured by the fact that fish exhibit

their schooling behaviour especially when in danger of predation (Seghers, 1974; Magurran & Pitcher, 1987; Tien et al., 2004), instead of when in the foraging situation (Hoare et al., 2004).

Recently, individual difference has been emphasised as an influential factor of fish's collective movement. For example, fish with a larger body size are usually observed at the front edge of a school (Krause et al., 2000). The different extent of hunger, as described above, and the biased foraging information (Couzin et al., 2011) can also lead to temporary differences among a fish group. These differences then cause a certain sub-group being in the front position consistently, and hence, cause the collective motion. This kind of explanation implies that there is 'leadership' within a fish group (Krause et al., 2000). A few models have demonstrated how individual difference can drive a population into a moving group with 'leaders' (Couzin et al., 2005; Conradt et al., 2009; Couzin et al., 2011), as well as some evolutionary models have been proposed (Conradt & Roper, 2009; Guttal & Couzin, 2010; Eshel et al., 2011).

However, this kind of collective motion, consisted of constant leaders, is reported mainly when fish are in the foraging situation (Krause et al., 1992; Couzin et al., 2011). When fish perform the schooling pattern in front of predators, the existence of 'leaders' is considered negligible by earlier documents (Partridge, 1980). Unfortunately, no recent investigation considers whether fish schools have 'leaders' under predatory threats.

2.4 Computational Simulation

The ecological experiments have given fruitful speculations to the behavioural mechanism and evolutionary dynamic of fish's schooling pattern. In recent decades,

computational simulation has been employed as a concrete way to test these viewpoints (DeAngelis & Grimm, 2013). One reason is that it provides a greater scope of experiments than empirical works (Grimm et al., 2005). Another reason is that it models the natural complex system better than theoretical derivations (Schellinck & White, 2011). Through computational simulations, a viewpoint or an assumption can be demonstrated and analysed, which is considered more persuasive than purely by the induction and inference from relatively limited ecological findings (Grimm et al., 2005; Sumpter, 2006). In the following sections, the self-organising models are introduced first, which demonstrate how collective patterns can emerge by local behaviours. Subsequently, previous evolutionary models of prey fish, or generally speaking, of prey aggregation, are reviewed.

2.4.1 Self-organising Models

Self-organising models of fish's collective pattern are mainly spatial-explicit agent-based models, which simulate the collective patterns based on spatiotemporal interactions among fish-like agents (DeAngelis & Grimm, 2013). Typically, in this kind of model, agents are homogeneous and their behavioural rules are designed according to certain preconceived knowledge (Schellinck & White, 2011). By simulating these agents' interactions on a computer, the self-organised pattern of the virtual population can support particular perspectives or lead to original inferences (Grimm et al., 2005).

The first significant self-organising model of gregarious fish, and of group-living animals, was contained in Aoki (1982). This model assigned each fish agent a fixed moving speed, a limited sensory range and a blind zone at the rear. The reaction of an agent to its neighbours was designed through a set of simple rules: viz., approaching the

referenced neighbour if it is distant, avoiding the referenced neighbour if it is close, and aligning with the referenced neighbour if the distance is intermediate between the above two. The choice of a referenced neighbour, at each step, is along a probabilistic distribution, by which neighbours ahead of the focal fish are more likely to be chosen, known as the 'front priority'. This work demonstrated that the interaction of these fish-like agents can lead to collective schooling behaviour.

Following the model in Aoki (1982), a novel modification was made in Huth & Wissel (1994). This work underlined the mixed influence of multiple neighbours and designed an agent's movement decision based on up to four referenced neighbours in its sensory range. The simulation demonstrated that the degree of coordination is increased significantly when multiple neighbours are involved in an agent's movement decision. Hence, it implied that the natural schooling fish would make decision based on multiple referenced neighbours. In addition, the influence of the 'front priority' was experimented. The result suggested that without this feature, the emergent collective motion is more similar to the natural fish schools.

Couzin et al. (2002) abandoned the 'front priority' and treated the influence of all neighbours equally important. Additionally, the avoidance behaviour in Aoki's framework (1982) was designed prior to the approaching and paralleling behaviours. This work demonstrated that through expanding the range of parallel orientation, the collective pattern of fish agents transits from a disordered swarm, via a milling group, to a schooling pattern with a high degree of coordination. This work displayed that the transition of fish's collective patterns can be simulated through the adjustment of a single parameter, as the range of parallel orientation. Its simplicity implies the self-

organising mechanism of fish's collective behaviour may be captured to a significant extent.

Although Huth & Wissel (1994) and Couzin et al. (2002) suggested that schooling is better simulated when the influences of neighbours are evenly important, the evidence of this 'front priority' in fish individuals has been reported (Aoki, 1982; Herbert-Read et al, 2011; Katz et al., 2011). In order to mimic the interaction of real fish more realistically, a few works have begun to study the precise positional priority for a fish's decision making (Ballerini et al., 2008; Strombom, 2011; Strandburg-Peshkin et al., 2013).

There have been works to simulate the collective evasion of schooling fish during the close attack of a predator. For example, Inada & Kawachi (2002) have shown that the morphing and merging of a fish school can be simulated. The employed model was similar to the model in Huth & Wissel (1994), with an additional behaviour as escaping from the predator. Based on a similar design, Zheng et al. (2005) compared the fitness of different escaping tactics, and reported that cooperative evasion obtains better fitness than the others. Lee (2006) studied the morphology of fish aggregation given different types of predatory attacks.

2.4.2 Evolutionary Models

Before reviewing the evolutionary models of schooling fish, it should be clarified that although the terms 'predator-prey', 'pursuit-evasion' and 'coevolution' have been widely used in Evolutionary Computation since Benda (1986), their focus is different from the topic here. In Evolutionary Computation, 'predator-prey' models are built to solve complicated tasks or practise artificial intelligence (Hillis, 1990; Ficici & Pollack,

1998; Goh & Tan, 2009). In these cases, a direct fitness function for the aimed goal is difficult to be explicitly defined. By cooperation or competition among agents, optimisation can be reached through a simpler fitness function (Haupt & Haupt, 2004; Bouffanais, 2016). The common focus of these techniques is put on optimisation of solutions rather than on evolutionary dynamics of the natural predator-prey interaction (Nowak & Sigmund, 2004).

With the concern of natural evolution in animal behaviours, some evolutionary simulations had focused on the competition between a predator and a prey. For example, Cliff & Miller (1995) and Nolfi & Floreano (1998) demonstrated how the coevolution between a prey agent's evasive strategy and a predator's chasing strategy leads to a balance of both fitness values. By these simulations, the 'red queen hypothesis' (Van Valen, 1973), which assumed a predator-prey coevolution is an arms race without endpoints, was highlighted and supported. However, the findings from this kind of one-on-one interactions are rarely considered to be an analogy to the evolution of gregarious animals and their collective behaviours because the intraspecies competition in a species, which influences the evolution much more than the interspecies competition (Connell, 1983), was overlooked.

The first evolutionary model focusing on animals' collective behaviour can be traced back twenty years (Reynolds, 1993). However, the link between a computational simulation and the natural evolution of collective motion has only been established in recent years (Wood & Ackland, 2007). These evolutionary models are typically a combination of a self-organising model and a genetic algorithm. The self-organising model is to simulate agents' spatiotemporal interaction as well as the emergent patterns.

The genetic algorithm is employed to simulate the evolutionary mechanism of natural selection and adaptation.

Genetic algorithms are computer programmes that inspired from natural evolution (Holland, 1975). In a genetic algorithm, there is a population of 'chromosomes', each of which represents a strategy, a solution or an agent, depending on the design. A typical evolutionary process is as follows (Haupt & Haupt, 2004). First, each chromosome is assigned a score, referred to as a fitness value, based on its performance in a given task. Then, according to the principle of 'survival of the fittest', a chromosome's reproduction probability and elimination probability are given based on its relative performance in the population. Finally, before entering the next generation, offspring are reproduced by the operation of crossover and mutation on the selected chromosomes. This process is repeated so that the dynamic of natural evolution is mimicked.

Earlier works, like Reynolds (1993) and Werner & Dyer (1993), were more similar to games of artificial agents. That is to say, given rewards and dangers in an arena, agents can evolve to develop an effective movement to gain better fitness. These preliminary works, however, drew a framework to simulate collective behaviour in evolution, that is, a spatial-explicit agent-based model combining with a genetic algorithm. Moreover, agents in these models were designed with sensory perceptions so that decision making can be adaptive to the surroundings.

Ward et al. (2001) simulated the behavioural coevolution of prey fish and their predators. In this model, a fish's eyes and lateral lines were simulated as two sensory perceptions of an agent, and a neural network was employed to connect the movement

decision with local information from these sensors. Although the output may not be as appealing, this is the first work to consider a real fish's perceptions and responses in evolution.

Since Oboshi et al. (2003), Aoki's framework (1982) of the design of a fish agent has been introduced to evolutionary models. Based on the predefined attraction, repulsion and paralleling behaviours in Aoki (1982), the simulation can be more robust and the output can be more similar to the appearance of real fish. In this kind of evolutionary models, the adaptation of a fish individual is simulated by evolving certain parameters of a chosen self-organising model. For example, the agent design in Oboshi et al. (2003) was based on Inada & Kawachi (2002). Through a genetic algorithm, the adaptive weight of escaping behaviour was studied.

Wood & Ackland (2007) designed agents based on the model in Couzin et al. (2002), with an additional escaping behaviour. The evolution of prey agents was simulated by evolving the movement speed and the orientation range, that is, neighbours in which can trigger a prey's paralleling behaviour. This work exhibited that two Nash equilibria (should also be evolutionarily stable states according to its description) of collective patterns can be reached. One is a compact milling group of low-speed agents and the other is a polarised moving school of high-speed agents. This work stated that the milling aggregation is invasion-free although individuals in this pattern incur higher predation risk. Hence, the findings supported the selfish herd hypothesis (Hamilton, 1971). The significance of this work is that it is the first work to introduce game-theoretic concepts to validate the simulation (Sumpter, 2009).

Similar to Wood & Ackland (2007), Ioannou et al. (2012) introduced the agent design in Couzin et al. (2002) and evolved the agents by the orientation range, where the designs different from Wood & Ackland (2007) were the fixed speed and the lack of escaping behaviour. Instead of setting an artificial predator to hunt the prey agents, Ioannou et al. (2012) used a real predatory fish, bluegill sunfish, to hunt the virtual prey agents and drive the evolutionary simulation. It showed that the bluegill sunfish preferred the isolated prey to prey aggregation, preferred the marginal prey to the central prey, and preferred the swarming prey to the schooling prey. It was demonstrated that these feeding preferences always drive the evolution of the virtual prey agents into the schooling pattern.

A series of latest works (Olson et al., 2013; Olson et al., 2016a; Olson et al., 2016b) simulated the evolution of prey aggregation as well as the coevolution between prey and predators with minimal predetermined rules. These works abandoned Aoki's framework (1982) and designed an agent's movement decision at a rather basic level, as turning right or turning left, based on the information from the visual perception. Olson et al. (2013) demonstrated that schooling is a transitional state and can be replaced by disordered swarms and milling groups in evolution. Olson et al. (2016a) experimented whether the cohesive swarming pattern can evolve given different hunting strategies. Olson et al. (2016b) demonstrated that prey's swarming behaviour and the predator's hunting strategy can form an evolutionary cycle in coevolution.

2.5 Validation in Ecological Modelling

Ecological modelling aims to investigate the dynamic in a natural system by the tool of computational models, mainly spatial-explicit agent-based models (DeAngelis &

Grimm, 2013). The targets can be fish in the ocean, trees in a forest, birds in the air, and so on (Grimm et al., 2005). After the review of the related computational models, the validation of an ecological model is discussed here.

Validation in ecological modelling is largely different from normal procedure in Computer Science. Typically, a computational algorithm can be validated through a relatively objective measurement, like the accuracy or the running time. In contrast, evaluating the significance of an ecological model is fairly descriptive, and has been one of the important pending questions in Ecology itself (Sutherland et al., 2013). The most popular concern is the authenticity of a model, that is, whether a model can represent the targeted system in nature (Rohani et al., 1997; Grimm et al., 2005; Schellinck & White, 2011). Focusing on evolutionary simulations, the robustness of a model and the game-theoretic analysis of the outputs have also been highlighted (Grimm et al., 2005; Sumpter, 2009). These three perspectives of a model's validity are discussed in this subchapter.

2.5.1 Authentic Model

Computational simulations have revealed many underlying mechanisms of ecological systems qualitatively (Grimm et al., 2005). For example, from the emerged collective patterns demonstrated in Couzin et al. (2002), one can infer how gregarious animals, like fish, birds, ants and insects, can form a milling torus or a moving group (Couzin & Krause, 2003). However, similar patterns among different systems are possible to be driven by different mechanisms (Breckling et al. 2006; Giardina, 2008). To better understand whether the findings of a model is suitable to predict a certain targeted system, or which design among various models (with qualitatively similar outputs) can

better illustrate a particular system, the quantitative analysis of a model has recently been highly emphasised in the ecological domain (Parrish et al., 2002; Couzin & Krause, 2003; Breckling, et al. 2006; Giardina, 2008). By this analysis, the authenticity, or ‘realism’ in Grimm et al. (2005), of a model’s parameter setting, agent design and simulation outputs is concerned based on empirical data (Couzin & Krause, 2003; Grimm et al., 2005). Nevertheless, it is not a debate between qualitative models and quantitative models; instead, the quantitative analysis has improved the understanding of the qualitative features in an ecological system (Wiegand et al., 2003; Breckling et al. 2006).

To validate an ecological model by its authenticity, two general principles have been widely agreed (Parrish et al., 2002; Grimm et al., 2005; Schellinck & White, 2011). One is that the complexity of a model should be in a reasonable range. The other is that the analogy between a model and the reality should be strong.

Focusing on the first principle, a successful model should illustrate a complex system to a considerable extent, at the same time with as simple and clear settings as possible (Grimm et al., 2005). There is a trade-off between simplification and meticulousity. Obviously, if a model is too simple, the output then becomes uninformative (Parrish et al., 2002). On the contrary, if a model is too complicated with numerous parameters, the essence of the targeted system is not revealed (Parrish & Edelstein-Keshet, 1999). It remains a tough task for model designers to decide which elements of the real system should be included. Some systematic approaches have been suggested in Grimm & Railsback (2012).

Certain computational models of gregarious fish have attracted criticisms from this aspect. For example, models based on mathematical tools have been criticised as too abstract to the direct ecological interest (Schellinck & White, 2011). On the other hand, simulating fish schools based on Aoki's framework (1982) has been criticised as predictable at the beginning due to the simplified setting of parallel orientation (Parrish & Edelstein-Keshet, 1999). Sumpter (2006) suggested that a simplification should be with reasons because no individual really follows simple rules.

Focusing on the second principle, an ecological model is meaningful only if its settings and outputs both resemble the natural system (Rohani et al., 1997; Grimm et al., 2005). About the model setting, the parameters and the design of a model should be consistent with the empirical data to a considerable extent (Parrish et al., 2002; Schellinck & White, 2011). Many criticisms on previous models are from this aspect. For example, even though averaging the influences of all neighbours for decision making can mimic the natural schooling pattern well (Huth & Wissel, 1994; Couzin et al., 2002; Wood & Ackland, 2007), criticisms on this design have been made due to its inconsistency with the empirical data (Parrish & Edelstein-Keshet, 1999; Ballerini et al., 2008).

About the authenticity of model outputs, an analogical mapping from the simulation outputs to the targeted system should be obvious (Grimm & Railsback, 2012). Unfortunately, comparison between a simulation output and a natural complex system can still be arbitrary. A popular way is through a visualisation, which can be found in Aoki (1982), Couzin et al. (2002), Wood & Ackland (2007) and all the reviewed models. Furthermore, most of these works provided specific quantifications to add credit to the statement, despite that the quantified values can still be inconsistent to the empirical data (Parrish et al., 2002).

2.5.2 Robust Simulation

An agent-based model's credibility is increased if the emerged pattern can be reproduced consistently against noises (Rohani et al., 1997) and be insensitive to parameters to an extent (Grimm et al., 2005). In other words, a simulation is more significant if it is robust to a noisy environment and parameter adjustments in a wider range. Since simulating the evolution of a prey population is typically based on a 'coevolutionary' system of genetic algorithms, that is, a solution's payoff relies on the frequency of different solutions in the population (Angeline & Pollack, 1993; Watson & Pollack, 2001), studies from Evolutionary Computation are informative to enhance the consistency and reliability of simulation outputs in a noisy simulation environment. However, the different focuses between Evolutionary Computation and ecological modelling should be highlighted.

In Evolutionary Computation, a genetic algorithm is employed typically to solve optimisation problems, by which an acceptable solution to the given objective function can be retrieved from a vast searching space effectively and efficiently (Beasley et al., 1993). For this purpose, dwelling on a local maximum, or even an intermediate state, is considered an evolutionary failure (Beasley et al., 1993; Watson & Pollack, 2001). To avoid this situation, techniques to improve the searching scheme have been widely studied, like annealing (Ingber & Rosen, 1992), niching (Horn et al., 1994) and so on (Haupt & Haupt, 2004). In contrast, the 'coevolution' systems in nature, like the evolution of a fish population undergoing individual selection, are usually without an explicit objective function to evaluate the simulation effectiveness (Watson & Pollack, 2001). In these cases, 'evolutionary stability' in Game Theory is more suitable to verify whether a simulation has reached its convergence (Nowak & Sigmund, 2004), the

concept of which is introduced in the next section. In this part, computational designs to avoid simulation failure in ecological modelling are reviewed.

The reproduction probability of an individual should be positively correlated to its fitness value, as the score of its performance, to guarantee a more adapted population in the next generation (Holland, 1975). The original version of this mapping defined an individual's reproduction probability by the ratio of its fitness value to the overall fitness values in the population (Holland, 1975), known as the 'roulette wheel selection' (Goldberg, 1989). However, the reproduction probability may not be commensurate with the fitness value assigned by a given evaluation function (Baker, 1987; Whitley, 1989). In this situation, a more effective and robust way is to evaluate this probability based on the ranking sequence (Whitley, 1989; Jadaan et al., 2005; Noraini & Geraghty, 2011). This type of selection schemes are known as the 'rank selection' (Baker, 1987), by which an adjusted fitness value, as the rank of an individual's performance score in the population, is assigned to calculate the reproduction probability. A popular scheme is the 'tournament selection', which practises the rank selection by a competition among randomly chosen individuals (Goldberg & Deb, 1991). Additionally, present works in Evolutionary Computation usually adjust this mapping to cause the effect of speciation, by which the group selection is simulated (Haupt & Haupt, 2004). Focusing on the evolutionary models of fish, Wood & Ackland (2007) adopted the roulette wheel selection. Other works did not provide clear descriptions of their selection schemes.

To simulate the replacement of individuals in a population, the reproduction and elimination of a population can occur between every two generations (Holland, 1975), known as the 'generational reproduction'. An alternative is that individuals reproduce offspring and die out continuously without a significant gap, as the 'steady-state

reproduction' (Syswerda, 1991). Related studies have shown that the steady-state reproduction performs better than the generational reproduction in many environments (Syswerda, 1991; Davis, 1991; Vavak & Fogarty, 1996). However, it was reported that the effectiveness of a steady-state reproduction can reduce in a noisy 'coevolution' system (Paredis, 1995), which can be improved by a dynamic reevaluation of the fitness values (Paredis, 1995; Vavak & Fogarty, 1996). The replacement method in most of the evolutionary models in Ecology, like Wood & Ackland (2007) and Olson et al. (2013), is the steady-state reproduction, by which few offspring are generated to replace few worst-performed agents between every two generations.

The evaluation function to assign fitness values to individuals can be subject to constraints. It has been considered an inefficient method to eliminate or repair infeasible solutions through additional mechanisms (Michalewicz, 1995). A more practical technique is to apply a penalty to those infeasible solutions through an adjusted evaluation function (Richardson et al., 1989; Carlson, 1995). This technique defines a new evaluation function by combining the original function with its constraints through a penalty multiplier or similar skills (Joines et al., 1994; Michalewicz & Attia, 1994). Hence, the same system can be operated as without constraints by this new evaluation function. Another technique to avoid infeasible solutions is to modify the genetic operator, so that the offspring individuals are guaranteed to be feasible (Michalewicz, 1995).

2.5.3 Evolutionary Stability

Evolutionary stability is one of the most persuasive concepts on natural evolution (Hammerstein & Selten, 1994; Nowak & Sigmund, 2004). This concept considers that a

state can be an endpoint of the evolution only if it cannot be perturbed by few mutants in a given set of alternative strategies (Smith, 1982). Not only used to describe a state of a population (which can represent human beings, animals, etc.), evolutionary stability is also used to describe a strategy (which can represent genetic traits, behavioural phenotypes, etc.) when all individuals in a population exhibiting this strategy leads to an evolutionarily stable state (Smith, 1982). For example, a population of ‘defect’ players in a one-shot (no repeated interactions) prisoner dilemma game is an evolutionarily stable state, and the ‘defect’ strategy is an evolutionarily stable strategy (Hammerstein & Selten, 1994).

Before a brief review of the special cases and limitations of evolutionary stability, the original definition of evolutionary stability in Smith (1982) is displayed as follows. It should be noted that in principle, evolutionary game theories only consider 'symmetric' games, where the payoff of a strategy is independent from the individual who adopt it, or to say, the utility/payoff/fitness function is unique (Hammerstein & Selten, 1994). Given a set of potential strategies, X , and an infinite population exhibiting the strategy $p \in X$, this state is defined evolutionarily stable if and only if any small proportion, $\epsilon < \epsilon^*$, of a different strategy $q \in S$, is less adaptive in this population than the resident strategy p . Mathematically to say, $\forall q \in X, q \neq p$,

$$\exists \epsilon^* > 0, \forall \epsilon < \epsilon^* \quad u_p = u(p|(1 - \epsilon)p + \epsilon q) > u_q = u(q|(1 - \epsilon)p + \epsilon q) \quad (2.1)$$

where $u(x|d)$ denotes the utility of strategy x in state d , and $(1 - \epsilon)p + \epsilon q$ is the perturbed state after strategy q 's invasion, where the proportions of strategy p and strategy q are $1 - \epsilon$ and ϵ , respectively. This inequality guarantees strategy q will be eliminated and replaced by strategy p in evolution. As all alternative strategies are

considered ($\forall q \in X$), strategy p is defined as an evolutionarily stable strategy and the state that all individuals adopt strategy p is an evolutionarily stable state. In most traditional games, the interactions among individuals are randomly paired (or to say, individuals are completely mixed), and hence the probability for an individual to encounter a certain strategy is equal to the frequency of this strategy in the population (Hammerstein & Selten, 1994). In this situation, the utility of adopting a strategy in a state can be rewritten as

$$u(x|ad_1 + bd_2) = au(x|d_1) + bu(x|d_2). \quad (2.2)$$

Hence, the inequality to reach evolutionary stability can be rewritten as, $\forall q \in X, q \neq p, \exists \epsilon^* > 0, \forall \epsilon < \epsilon^*$,

$$u_p = (1 - \epsilon)u(p|p) + \epsilon u(p|q) > u_q = (1 - \epsilon)u(q|p) + \epsilon u(q|q). \quad (2.3)$$

If $u(p|p) > u(q|p)$, there must be a sufficiently small ϵ^* to satisfy the inequality. If $u(p|p) < u(q|p)$, the inequality cannot hold given a nearly zero ϵ . In the last condition, as $u(p|p) = u(q|p)$, this inequality is equivalent to $u(p|q) > u(q|q)$. Therefore, the common form of evolutionary stability is derived, as the following two conditions (Smith, 1982):

$$u(p|p) > u(q|p) \text{ or } u(p|p) = u(q|p) \& u(p|q) > u(q|q). \quad (2.4)$$

An evolutionarily stable strategy needs not to be a pure strategy. It can be a mixed strategy like $x = (tx_1, (1 - t)x_2)$, where x_1, x_2 denote pure strategies and $t, 1 - t$ are the probabilities of adopting the associated pure strategies (Hammerstein & Selten, 1994). Most traditional games are based on the precondition that individuals are randomly paired and mixed strategies are flexible. This precondition leads to the property of

symmetry in an evolutionary game: an evolutionarily stable state in a symmetric game must be a symmetric equilibrium, where all individuals adopt the same strategy (Smith, 1982; Hammerstein & Selten, 1994). That is to say, an evolutionarily stable state must contain a single evolutionarily stable strategy. As a complement, Bishop & Canning (1978) derived that given individuals are randomly paired, if the mixed strategy x is evolutionarily stable, then $u(x_1|x) = u(x_2|x) = u(x|x)$, and any pure strategies, as x_1 or x_2 , are not evolutionarily stable. This theorem is not contradictory to the property of symmetry in an evolutionary game.

Only when a mixed strategy is inflexible, an evolutionarily stable state can be a ‘polymorphic’ state where the population exhibits a fixed distribution of various pure strategies (Smith, 1982). For example, the gender distribution among human beings forms a polymorphic stable state, where 50% individuals are male and the other 50% are female, but no individual can adopt a mixed strategy to be sometimes male and sometimes female.

The relation between an evolutionarily stable state and a Nash equilibrium is as follows (Hammerstein & Selten, 1994). A Nash equilibrium is a state where no single individual can earn excess profit from changing its strategy (Osborne & Rubinstein, 1994). That is to say, taking the above game for example, given all individuals adopting strategy p is a Nash equilibrium, then $\forall q \in X, q \neq p$,

$$u(p|p) \geq u(q|p), \tag{2.5}$$

where $u(x|d)$ denotes the utility of strategy x in state d , and X is the set of potential strategies.

Comparing this form with the common form of evolutionary stability, it can be observed that the concept of evolutionary stability is a refined subset of Nash equilibrium (Osborne & Rubinstein, 1994; Smith, 1982). Traditional game theories assumed individuals are completely rational and hence, a Nash equilibrium is an endpoint of a game since no single individual can receive better payoff by alternative strategies (Osborne & Rubinstein, 1994). Comparatively, evolutionary stability additionally considers the ‘irrational’ mutants, which happens in natural evolution. When a small proportion of ‘irrational’ mutants has already perturbed a state, evolutionarily stable states are those Nash equilibria which have the tendency to recover and keep being endpoints in a game (Smith, 1982).

Evolutionary stability does not always exist in a game (Hammerstein & Selten, 1994). For example, although the rock-paper-scissors game has a unique Nash equilibrium as $(\frac{1}{3} \text{ rock}, \frac{1}{3} \text{ paper}, \frac{1}{3} \text{ scissors})$ (Figure 2.1A), where no other strategy can earn excess benefit from this state (all strategies’ expected payoffs are 0), it is not evolutionarily stable. As a brief proof, given a population of individuals which all adopt $(\frac{1}{3} \text{ rock}, \frac{1}{3} \text{ paper}, \frac{1}{3} \text{ scissors})$ and forms a Nash equilibrium $(\frac{1}{3} \text{ rock}, \frac{1}{3} \text{ paper}, \frac{1}{3} \text{ scissors})$, when the state is invaded by a small proportion of individuals adopting pure ‘rock’, the perturbed state then becomes $(\frac{1}{3}+ \text{ rock}, \frac{1}{3}- \text{ paper}, \frac{1}{3}- \text{ scissors})$, where $\frac{1}{3}+$ means greater than $\frac{1}{3}$ and vice versa. In this perturbed state, the utility of the resident strategy, $(\frac{1}{3} \text{ rock}, \frac{1}{3} \text{ paper}, \frac{1}{3} \text{ scissors})$, is 0, and the utility of the invasive strategy, pure ‘rock’, is also 0 (Figure 2.1B). Hence, the invasive strategy has no tendency to die out and the original state is changed.

A
POPULATION
p q $1-p-q$
rock paper scissors
INDIVIDUAL
rock
paper
scissors

0	-1	1
1	0	-1
-1	1	0

B
POPULATION
$\frac{1}{3} + \epsilon$ $\frac{1}{3} - \frac{\epsilon}{2}$ $\frac{1}{3} - \frac{\epsilon}{2}$
rock paper scissors
INDIVIDUAL
rock
paper
scissors

0	-1	1
1	0	-1
-1	1	0

Figure 2.1: The Rock-paper-scissors Game

Panel A shows the payoff matrix of the rock-paper-scissors game, by which the utility of adopting ‘rock’, for example, can be calculated as $1 - p - 2q$. When individuals in the population all adopt (1/3 rock, 1/3 paper, 1/3 scissors), that is, $p = q = 1/3$, no other strategy can gain better payoff in this population. Hence, it is a Nash equilibrium. Panel B shows this Nash equilibrium is not evolutionarily stable. For example, given a small proportion of individuals, denoted by ϵ , have changed their strategies into pure ‘rock’, the payoff of (1/3 rock, 1/3 paper, 1/3 scissors) in this perturbed state is not better than that of the invasive strategy, pure ‘rock’, so that the pure ‘rock’ individuals have no tendency to die out in evolution.

Traditional game theories do not focus on the reachability of a Nash equilibrium (Osborne & Rubinstein, 1994). However, in evolutionary game theory, the adaptive dynamic, as the evolutionary trajectory, of an evolutionary game has also been widely studied and modelled (Hammerstein & Selten, 1994). For example, Nowak & Sigmund (2004) has concluded that even if an evolutionarily stable state exists in a game, it can be unreachable through any evolutionary trajectory. The absence of evolutionary stability in a system has been observed in the real world. For example, the adaptation of male body colours in a population of side-blotched lizards (*Uta stansburiana*) displays a periodic cycle and cannot be converged (Sinervo & Lively, 1996).

The preconditions of evolutionary stability do not always hold. For example, game-theoretic studies have demonstrated that the interaction among individuals in a population is not necessarily randomly paired in a spatial game (Nowak & May, 1992). In this kind of games, limited dispersal of individuals can result in a local interaction among specific strategies and violates the common form of evolutionary stability

(Nowak & May, 1992). In addition to this exception, in many ‘coevolutionary’ systems in Evolutionary Computation, the search space is ‘open-ended’ (Ficici & Pollack, 1998), that is, there are always potential solutions able to invade the current one. Since the set of potential strategies is difficult to be defined completely, the analysis of evolutionary stability cannot be applied to these systems. An analogy in nature is the alien species brought by humans. An ecological equilibrium can be no longer stable when the invader does not belong to the original set of animals (Mooney & Cleland, 2001).

Few ecological works have begun to introduce this game-theoretic concept for the validation of their simulation outputs. For example, Wood & Ackland (2007) stated that their simulation outputs are Nash equilibria through the observation “*when simulations are started from one evolved state, then this state is maintained even in conditions where the other state usually evolves. This indicates that two distinct Nash equilibria—states from which no individual boid can benefit from changing its behaviour—exist on the fitness landscape of the model*”. As a complement, since this work allowed irrational mutants during their evolutionary simulation, the two states should also be evolutionarily stable based on the definition. Also, Guttal & Couzin (2010) verified whether a converged state is evolutionarily stable by testing the invasive ability of certain mutants by computational simulation. In detail, after a population of agents evolves into a certain pattern, this work perturbed this state by putting a small proportion of invasive agents into the resident population. Then, it demonstrated that, given various sets of invasive agents, the perturbed pattern can always recover to the original state after a few generations. Although these attempts are not a formal proof of

evolutionarily stability, the significance of analysing the evolutionarily stable states of an evolutionary simulation has been highlighted (Sumpter, 2009).

CHAPTER III

MODELLING THE BEHAVIOURAL EVOLUTION OF PREY FISH

This chapter addresses the first main research question, about how to reduce the bias when building a computational model to simulate fish's behavioural evolution, from the following four specific topics:

- A model to evolve strategies based on an open-ended solution space
- A bottom-up metric to quantify the simulation outputs
- The validation of the model from the aspect of realistic settings
- The validation of the model from the aspect of reliable outputs

In this work, an evolutionary model is proposed to study fish's adaptation under the survival pressure. The employed genetic algorithm of the model is NEAT (Stanley & Miikkulainen, 2002), which evolves neural networks through a genetic algorithm. Different from many of previous evolvable neural networks, which networks' complexity, such as the number of nodes, links and layers, were usually predesignated (Haupt & Haupt, 2004), a neural network in the NEAT algorithm can evolve from a rather basic structure to a complicated composition of nodes and links without a

limitation of its complexity. By adopting NEAT networks to implement the behavioural strategies of fish agents, the evolutionary simulation can be viewed as based on an open-ended solution space, which covers all possible strategies a fish agent can develop to control its elementary behaviours based on the acquired information (Stanley & Miikkulainen, 2002). Hence, the bias of manually designed solution space in previous works can be largely reduced. To quantify the simulation output, a measurement based on the bottom-up categorisation is proposed. Compared with traditional methods, this metric illustrates evolutionary states in a wider range. Finally, according to the validation principle in ecological modelling (described in the following section), authenticity and credibility of this model are both analysed to reduce potential biases from the model setting.

Although the inconsistency between a model and the targeted system always exists, the proposed model in this chapter has reduced many significant biases in previous works from the three aspects. First, the predesignated small range of potential strategies in previous models is replaced by an open-ended solution space. Secondly, some significantly unrealistic settings in different previous works are improved. For example, this model forbids the physical overlaps and allows agents to make decision based on current surroundings. Thirdly, the influence of selection schemes to the robustness of agent-based models is emphasised and analysed.

3.1 Background

With the rapid growth of computational capability, simulation has become a powerful tool to investigate complex systems in animals (DeAngelis & Grimm, 2013). These ecological simulations are typically agent-based and spatial-explicit models, which hold

a population of agents in a virtual arena and mimic the real-world system by spatiotemporal interactions among these agents (Couzin & Krause, 2003; Schellinck & White, 2011). The advantage of this kind of simulation is that the abstract formulations are largely avoided compared with traditional theoretical models (Schellinck & White, 2011; DeAngelis & Gimm, 2013). Therefore, the implicit causality of a natural system is inferred more directly and clearly.

One of the most successful usages of simulation is to reveal the self-organising mechanism of group-living fish's collective movement (Schellinck & White, 2011). For example, Aoki (1982) demonstrated that fish schools can be an emergent pattern by agents of simple behaviours. Huth & Wissel (1994) compared various behavioural settings and found that fish's schooling pattern is better mimicked when decision making relies on multiple neighbours. Couzin et al. (2002) showed that the transition between fish's collective patterns can be displayed by adjusting a certain behavioural preference of agents. These simulations have largely improved the understanding of fish's behavioural mechanism (Couzin & Krause, 2003).

After the success of modelling fish's behaviours by computers, simulation has recently been employed to study the behavioural evolution of fish (Sumpter, 2006). That is to say, why should fish develop these simple behaviours in evolution? However, at present, simulations on this topic are less significant due to the diverse outputs from different designs. For example, Wood & Ackland (2007) demonstrated that the survival pressure can drive fish agents into one of the two states: a milling herd or a moving school. On the contrary, schooling was the only evolutionary result in Oboshi et al. (2003) and Ioannou et al. (2012). On the other hand, Olson et al. (2013) demonstrated

that schooling should be an intermediate phase in evolution and should be replaced by milling herds and stationary swarms.

The inconsistency among the previous evolutionary simulations highlights the issue of preconceived biases in ecological modelling. For example, if the work in Wood & Ackland (2007) is considered more successful due to its ‘reasonable’ output (Sumpter, 2009), the validation then biases to the preconceived knowledge and reserves no significance for the experiments by simulation. Unfortunately, validation in ecological modelling has been highly contested (Rohani et al., 1997; Parrish et al., 2002; Schellinck & White, 2011), and a convincing metric to score ecological simulations still seems impractical. Nevertheless, two fundamental principles have been widely agreed, which are realistic settings and reliable outputs (Grimm et al., 2005; Schellinck & White, 2011).

The most important factor of a valid ecological simulation is that the setting should accord with the empirical data (Parrish et al., 2002; Grimm et al., 2005; Schellinck & White, 2011). Otherwise, the output cannot be an analogy to the targeted natural system. For example, although fish schools can be mimicked vividly by averaging the influences of all neighbours (Huth & Wissel, 1994; Couzin et al., 2002), this setting has become disputed after unfavourable empirical evidence was found (Ballerini et al., 2008; Katz et al., 2011). From this viewpoint, the model in Wood & Ackland (2007) may not be as valid because at least two of its settings violate the empirical data considerably. One is that an agent’s decision making in this model is also evenly influenced by all neighbours. Another is that the paralleling behaviour of its agents is not observed in the real fish (Tien et al., 2004; Katz et al., 2011). Comparatively, Olson et al. (2013) designed the movement of agents without predetermined rules. This design

is more realistic to a certain extent, despite its output, as the crucial part of a model, may be unrealistic.

The credibility of a model is increased if its outputs are less sensitive to potential noises and parameter adjustments (Rohani et al., 1997; Grimm et al., 2005), which property is also referred to as the ‘robustness’ of a demonstration (Grimm et al., 2005). Related techniques to improve an evolutionary model’s ability to reproduce consistent and reliable outputs have been developed for decades in Evolutionary Computation (Haupt & Haupt, 2004). However, rare ecological models have acquired this knowledge. For example, Wood & Ackland (2007) designed an unscaled proportional fitness selection in its genetic algorithm, which scheme has been proven less robust than others (Whitley, 1989; Blicke & Thiele, 1995; Reeves, 2003; Noraini & Geraghty, 2011). Moreover, almost none of the previous works reported quantitative analyses about the robustness of their simulations and the sensitivity of their parameter settings, the neglect of which may cause concern about the reliability of the outputs.

In this chapter, an evolutionary model is built to reduce preconceived biases in previous works and its validation is emphasised. After building the model based on an open-ended solution space in Chapter 3.2, the validity of this model is highlighted from the three aspects. First, for an objective description of the simulation outputs, the quantification is discussed in Chapter 3.3. Secondly, to validate the authenticity of this model, a comprehensive comparison of the model, the empirical data and previous works is reported in Chapter 3.4. Thirdly, in Chapter 3.5, the parameters are scanned to understand their influences to the simulation. These elaborate analyses construct a solid base of the validity of the model outputs and further inferences.

3.2 Model

To investigate the evolution of gregarious fish under the survival pressure, a spatial-explicit agent-based model is built based on a genetic algorithm. The employed algorithm is NeuroEvolution of Augmenting Topologies (NEAT) (Stanley & Miikkulainen, 2002). This algorithm encodes a neural network into a chromosome so that a population of neural networks can evolve through the procedure of selection, crossover and mutation. In the NEAT algorithm, neural networks can be initially given a minimal topology, and complicated structures can be built incrementally along the evolutionary process. Based on this powerful capability, the strategies of agents can be developed from trivial tactics to sophisticated ones automatically, without a predetermined setting of the candidate strategies.

In the proposed model, 100 prey agents are put in a square arena to interact with one another for the survival fitness. To simulate the environment in open waters, the arena is wrapped around, that is, the left boundary connects the right boundary, and the upper limit connects the bottom one. The size is set $500BL \times 500BL$ (body length, as the length unit in the model) to avoid crowding within a feasible computational time. Similar settings are 80 prey agents in a $400BL \times 400BL$ wrapped-around arena (Wood & Ackland, 2007) and 50 prey agents in a $512BL \times 512BL$ wrapped-around arena (Olson et al., 2013).

To simulate predation risk in this virtual arena, the concept, ‘domain of danger’ (Hamilton, 1971), is introduced. It indicates the area where one becomes the nearest prey if a predator is present. As supported by empirical evidence (Mooring & Hart, 1992; Viscido & Wethey, 2002; De Vos & O’Riain, 2010), it is usually assumed that a

prey's predation risk is proportional to its domain of danger (Viscido, et al., 2001; James et al., 2004; Wood & Ackland, 2007). In the proposed model, the calculation of each prey's domain of danger is simplified by randomly putting a rule-based predator in the arena (outside prey's bodies) and letting it chase the nearest prey until a touch. Geometrically, a moving group's domain of danger is different from that of a stationary herd (Bumann et al., 1997). By providing the predator a fixed speed, this skewness in a moving group can be simulated directly.

Each prey has a round body and its diameter is defined $1 BL$ (body length), which is treated as the unit of the length. The overlap between two prey's bodies is considered unrealistic and forbidden in the model (outlined in Chapter 3.2.3). A prey swims in a fix speed and the swimming direction depends on its strategy, subject to a maximal turning angle. The strategy is implemented by a NEAT network, which input is the information from a local sensory range, as the round area of radius R_S with a blind zone at rear (outlined in Chapter 3.2.1), and the output controls a prey's movement decision at each step (outlined in Chapter 3.3.2). In other words, a prey's behavioural strategy is a course of reactions according to local information acquired from its sensors. As different strategies incur different predation risks, the behavioural evolution of the prey agents is then processed undergoing selection, reproduction and elimination (outlined in Chapter 3.2.3 and Chapter 3.2.4).

In the following sections, the agent design and the evolutionary procedure of this model are described and explained, followed by a report about the originality of the proposed model. The general concern of these designs is to accord with the empirical data at the same time avoiding a sharp rise in computational complexity. Comprehensive

validations of this model’s authenticity and credibility are provided in Chapter 3.4 and Chapter 3.5, respectively.

Table 3.1: Parameters for Interaction

Name	Value
Arena Length	500 BL
Prey Speed (SPD)	0.12 BL per step
Predator Speed (PS)	1.125 ~ 5 SPD
Min. Turning Radius (R_T)	0.5 BL
Max. Turning Angle (θ_T)	$\text{asin}(\text{SPD}/2/R_T)$
Sensory Radius (R_S)	15 BL
Angle of Blind Sector	60 degrees
Length of the Attraction Area (ℓ_A)	dynamically decided by each NEAT network at each step (Figure 3.2)
Spreading Angle of the Attraction Area (θ_A)	
Length of the Repulsion Area (ℓ_R)	
Spreading Angle of the Repulsion Area (θ_R)	

3.2.1 Two Perceptions of Local Surroundings

It has been reported that a fish’s movement decision largely relies on the information from its lateral lines and eyes, where the lateral lines sense the moving direction of neighbours (as the vector **dir** in the following content) and the vision distinguishes the distances of nearby fish (as the vector **loc** in the following content) (Olst & Hunter, 1970; Partridge, 1982; Faucher et al., 2010). According to the empirical data, the visual sensor and flow sensor designed in this subchapter are considered to fit the realism of a fish's capability at a reasonable level. A further validation of this design’s authority is put in Chapter 3.4.1.

In the proposed model, each prey agent is assigned a limited sensory range and an agent can only notice those neighbours in this range. It is a circular area of the sensory radius, R_S , except a blind zone, as the behind sector of 60 degrees (Figure 3.1). The perceptions

to retrieve information from the sensory range are implemented as the input of a NEAT network. To simulate the lateral lines, three nodes are used to detect the average direction of nearby prey. To simulate the vision, five nodes are used to depict their average positional distribution. As the predator is designed to distribute the predation risk according to agents' domains of danger, it is unnecessary to let agents identify this predator (Hamilton, 1971). That is to say, the escaping tactics during a close attack is omitted in the present model. With an additional node feeding the constant value one, to provide a computational offset to the neural network, there are nine input nodes in total.

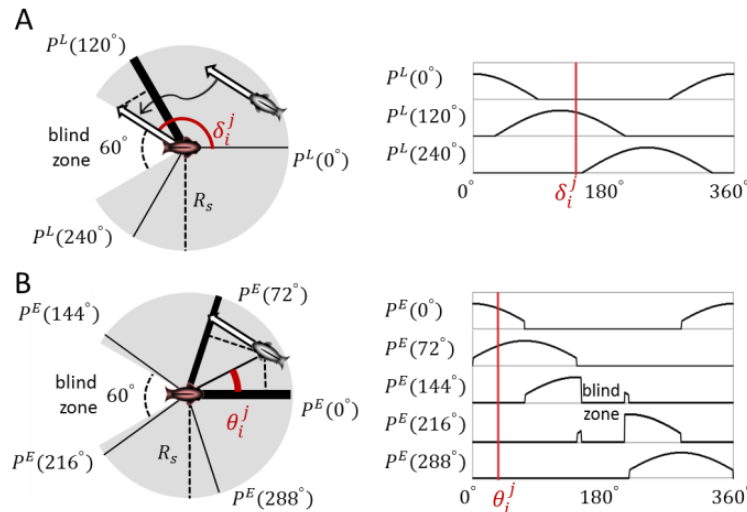


Figure 3.1: Sensory Range and Two Perceptions

A prey agent is given a limited sensory range, drawn as the grey area. The information in this sensory range is acquired by the simulated lateral lines, as in subfigure A, and the simulated eyes, as in subfigure B. The lateral lines report the average direction of prey neighbours, and the eyes report the positional distribution of them. The two plots at the right hand side display the detection range of these sensors. Specifically, it is set 72° towards the both sides in the visual system so that a nearby prey triggers exactly two visual sensors.

Given that the vector loc_i denotes the location of fish i , the unit vector dir_i denotes the moving direction of fish i , δ_i^j is the angle between dir_i and dir_j (Figure 3.1A), and Z_i^S contains the indices of those prey in fish i 's sensory range, here the three input nodes, $P_i^L(0^\circ)$, $P_i^L(120^\circ)$ and $P_i^L(240^\circ)$, of the simulated lateral lines are valued by

$$P_i^L(x) = \sum_{j \in Z_i^S} \frac{\varphi(\cos(\delta_i^j - x), 0)}{\|\mathbf{loc}_j - \mathbf{loc}_i\|^2},$$

$$\text{where } \varphi(y, z) = \begin{cases} y, & \text{if } y > z \\ 0, & \text{otherwise.} \end{cases} \quad (3.1)$$

The cosine value of $(\delta_i^j - x)$ calculates the similarity between \mathbf{dir}_j and the vector which rotates \mathbf{dir}_i by x degrees (Figure 3.1A). The function φ is a threshold in order to accumulate the influences of referenced prey. The denominator portion provides the information of distance, by which a closer prey results in a larger value, as suggested in Viscido et al. (2002). According to the values of these three input nodes, the average direction of nearby prey can be estimated. For example, if $P_i^L(0^\circ)$ is significantly larger than the two others, fish i can recognise that it swims in coordination with its neighbours. Since this design has simplified a fish's lateral system into 3 numeric signals, additional noises are not added into this flow sensor.

Similarly, the visual perception is simulated as a greyscale based on the five input nodes: $P_i^E(0^\circ)$, $P_i^E(72^\circ)$, $P_i^E(144^\circ)$, $P_i^E(216^\circ)$ and $P_i^E(288^\circ)$. Given θ_i^j is the angle between \mathbf{dir}_i and $\mathbf{loc}_j - \mathbf{loc}_i$ (Figure 3.1B), the corresponding values of these nodes are

$$P_i^E(x) = \sum_{j \in Z_i^S} \frac{\varphi(\cos(\theta_i^j - x), \cos(72^\circ))}{\|\mathbf{loc}_j - \mathbf{loc}_i\|^2},$$

$$\text{where } \varphi(y, z) = \begin{cases} y, & \text{if } y > z \\ 0, & \text{otherwise.} \end{cases} \quad (3.2)$$

The nonzero threshold, $\cos(72^\circ)$, is set to ensure agents can identify the presence of leading neighbours. By this setting, $P_i^E(0^\circ) > 0$ if and only if there is at least one neighbour at the front sector between the angles 72° and -72° , or equivalently, in the

range $0^\circ \sim 72^\circ$ or $288^\circ \sim 360^\circ$ (Figure 3.1B). Like the case of designing the flow sensor, additional noises are not considered in this simplified visual sensor.

3.2.2 Reaction by Two Elementary Behaviours

The two elementary behaviours exhibited by real fish are attraction and repulsion, by which fish approach relatively distant neighbours and avoid the extremely close ones (Partridge, 1982; Tien et al., 2004; Katz et al., 2011). When a fish has multiple neighbours, those ahead of this fish are more influential to its decision making (Aoki, 1982; Herbert-Read et al, 2011; Katz et al., 2011). The agents in the proposed model are designed to develop their strategies on the basis of these two elementary behaviours, with a front priority of the referenced neighbours. The validation of this design's authority is put in Chapter 3.4.2.

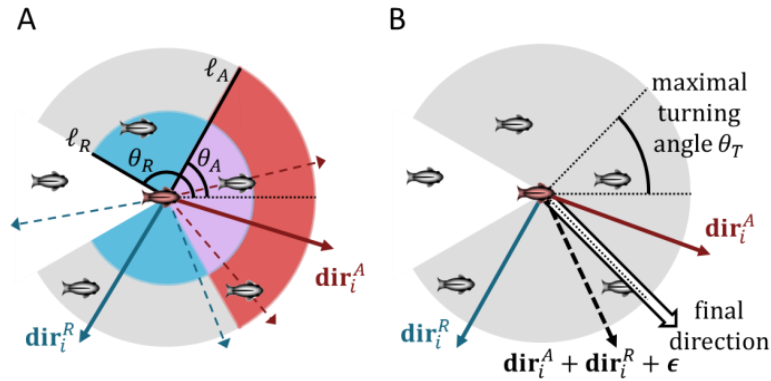


Figure 3.2: Decision Making by Repulsion and Attraction

A movement decision is made through the mediation of attraction and repulsion. As subfigure A illustrates, the attraction-triggered range is defined by the length ℓ_A and the spreading angle θ_A ; the repulsion-triggered range is defined by the length ℓ_R and the spreading angle θ_R . In subfigure A, a fish is in the attraction-triggered range (the red area), a fish is in the repulsion-triggered range (the blue area), and one fish is in both ranges (the purple area). Calculation of the attraction behaviour, or the repulsion behaviour, is to average all the corresponding vectors of the fish in its range. In this example, there are two fish. Subfigure B shows that the final direction is the sum of the attraction vector and the repulsion vector, with a slight noise, subject to a maximal turning angle.

At each step, the nine input nodes provide local information to the NEAT network, and through the nodes and links in the hidden layer, four output nodes are set to define the triggered ranges of attraction (approaching a prey) and repulsion (avoiding a prey), by which the final movement is mediated. To draw the triggered range of attraction, two output nodes are used to determine its length, ℓ_A , and spreading angle, θ_A , by which two parameters, a fan-shaped area is defined to represent this range (Figure 3.2A). Similarly, the length, ℓ_R , and the spreading angle, θ_R , to draw the triggered range of repulsion is controlled by another two output nodes (Figure 3.2A). To accord with the area of the sensory range, the maximal length of both triggered ranges is the sensory radius, R_S , and the maximal spreading angle of both ranges is 150° , considering the blind zone (Figure 3.2A).

A fish's attraction behaviour, \mathbf{dir}_i^A , is defined as a scaled vector of the sum of all the directions from its location toward to those prey in its triggered range (Figure 3.2A). In detail, given Z_i^A contains the indices of those prey in fish i 's attraction-triggered range, \mathbf{dir}_i^A is assigned a zero vector if $Z_i^A = \emptyset$, and when $Z_i^A \neq \emptyset$,

$$\mathbf{dir}_i^A = \frac{\mathbf{dir}_i^{A'}}{\max(\|\mathbf{dir}_i^{A'}\|, 1)}, \quad \text{where } \mathbf{dir}_i^{A'} = \sum_{j \in Z_i^A} \frac{\mathbf{loc}_j - \mathbf{loc}_i}{\|\mathbf{loc}_j - \mathbf{loc}_i\|}. \quad (3.3)$$

This design follows Huth & Wissel (1994), Couzin et al. (2002) and Wood & Ackland (2007), but the normalisation of $\mathbf{dir}_i^{A'}$ is adjusted to happen only when the length of $\mathbf{dir}_i^{A'}$ is greater than one, which adjustment reduces the noise from an unnecessary scaling-up. Similarly, given Z_i^R contains the indices of prey in fish i 's repulsion-triggered range, the repulsion behaviour, denoted as the vector \mathbf{dir}_i^R , is $\mathbf{0}$ if $Z_i^R = \emptyset$, and when $Z_i^R \neq \emptyset$, it is calculated by

$$\mathbf{dir}_i^R = \frac{\mathbf{dir}_i^{R'}}{\max(\|\mathbf{dir}_i^{R'}\|, 1)}, \quad \text{where } \mathbf{dir}_i^{R'} = \sum_{j \in Z_i^R} \frac{\mathbf{loc}_i - \mathbf{loc}_j}{\|\mathbf{loc}_i - \mathbf{loc}_j\|}, \quad (3.4)$$

as summing and scaling all the directions away from those prey in its triggered range (Figure 3.2A).

After the calculation of the two elementary behaviours, a fish's final direction is the unit vector of $\mathbf{dir}_i^A + \mathbf{dir}_i^R + \epsilon$, subject to a maximal turning angle (Figure 3.2B), where the noise ϵ is set as the vector $0.01 \times \mathbf{dir}_i$ rotated by $\epsilon \sim N(0,5)$ degree. Although the influences of all prey in a triggered range are averaged, the priority of leading neighbours (Katz et al., 2011) is preserved by the setting of spreading angles. Through a dynamic change of these triggered ranges, an adaptive degree of the priority can be developed for survival benefit.

3.2.3 Evolutionary Procedure

The performance of a prey, or equivalently, its strategy as well as its NEAT chromosome, is evaluated based on the eaten times (the times that the predator touches it) and the overlapping times (the times that a prey overlaps its body with others). This design is to estimate the survival fitness and prevent the unrealistic interaction at the same time (Carlson, 1995). Specifically, the fitness value of prey i is set as

$$u_i = (1 - T_i^E/T^H) - \lambda T_i^O/T^H, \quad (3.5)$$

where T_i^E and T_i^O denotes fish i 's total eaten times and total overlapping times, respectively, and T^H is the total hunting attempts of the predator. Hence, $1 - T_i^E/T^H$ is the survival probability of fish i in a hunt. The multiplier λ is a penalty to handle the overlap-free constraint $T_i^O/T^H = 0$. In the experiment, T^H is set to 300 for a sufficiently

large sampling size; λ is set to 0.1 to allow few mistakes and reduce the evolutionary difficulty, which can effectively forbid unrealistic overlaps after about ten generations, as 0~2 times per agent per 10000 steps.

The mapping from the fitness value to the reproduction probability in the original NEAT algorithm operates a niching technique to optimise the performance. This usage causes additional assumptions, however, when linked to the evolutionary mechanism in nature. To be more analogous with the natural selection, the exponential rank selection is adopted after the comparative experiments in Chapter 3.5.1. Given $rnk(u_i)$ as the rank of prey i 's fitness value in the population, the associated reproduction probability, r_i , is

$$r_i = \frac{1.16^{-rnk(u_i)}}{\sum_{j=1}^N 1.16^{-rnk(u_j)}} \approx 0.16 \times 0.862^{rnk(u_i)} \text{ (given } N = 100\text{)}. \quad (3.6)$$

Based on the reproduction probabilities, K pairs of prey agents are selected as the parents. Through the operation of crossover and mutation by the NEAT algorithm, K offspring of the selected parents are reproduced to replace the same amount of worst-performed ones. These $100 - K$ better-performed agents and K offspring agents compose the population in the next generation. The replacement rate is set $K = 17$ according to the experiments in Chapter 3.5.1.

3.2.4 Implementation of NEAT Algorithm

The NEAT chromosome of each prey agent, $C_i = \{(l_m^n, w_i^{mn})\}$, is a set of weighted links, where l_m^n is a link from node m to node n , and the weight of this link in C_i is w_i^{mn} . As a distinctive structure of the NEAT algorithm, each link is labelled an unique innovation number, x_m^n , in a global set, $Inno = \{(l_m^n, x_m^n)\}$, which records the time this link first

appears in the population (Stanley & Miikkulainen, 2002). By these innovation numbers, a NEAT network can be represented as a sequence of ordered links, or to say, a chromosome, so that it can be evolved by a genetic algorithm. The maximal innovation number of all links in C_i is denoted as I_i^{MAX} and the maximal innovation number in the population is denoted as I^{MAX} .

Based on the agent design, there are nine input nodes, labelled from 0 to 8, and four output nodes, labelled from 9 to 12. The initialisation of each agent's NEAT chromosome is

$$C_i \xleftarrow{\text{assign}} \{(l_0^9, \epsilon()), (l_0^{10}, \epsilon()), \dots, (l_1^9, \epsilon()), \dots, (l_8^{12}, \epsilon())\}, \quad (3.7)$$

where $\epsilon()$ is a generator of white noises, following the normal distribution $N(0,0.01)$. In other words, the simplest network is built at beginning, by 36 weighted links from each input node to each output node. At the same time, the set of innovation numbers is initialised as

$$Inno \xleftarrow{\text{assign}} \{(l_0^9, 1), (l_0^{10}, 2), \dots, (l_1^9, 5), \dots, (l_8^{12}, 36)\}. \quad (3.8)$$

Hence, $I^{MAX} = 36$, as well as $I_i^{MAX} = 36$, initially.

There are two steps to reproduce an offspring chromosome (Stanley & Miikkulainen, 2002). The first step is to generate a new chromosome by a crossover from the parents' chromosomes, in order to inherit the beneficial network components of parents. The second step is to allow mutation of links and nodes with a small probability, by which operation beneficial innovations are possible to happen in evolution. The probabilities are suggested 0.08 for link mutation and 0.03 for node mutation (Stanley & Miikkulainen, 2002), which parameters are adopted in the model.

To implement the crossover, denoting the offspring as C_o and its parents as C_i and C_j , all links belonged to both C_i and C_j are inherited by C_o . Each of these links in C_o , said l_m^n , receives a weight value as $w_i^{mn} + \epsilon()$ or $w_j^{mn} + \epsilon()$ with even probability. For those links only owned by one parent, assumed C_i , they are inherited by C_o as $(l_m^n, w_i^{mn} + \epsilon())$ with a given probability. This probability is set to 1.0 if this link's innovation number, x_m^n , is greater than I_j^{MAX} ; otherwise, it is set to 0.5. The motivation of this setting is to protect newly invented links for their potentials.

After inheriting the links and weights from the parents, the offspring C_o has a small probability to operate mutation. There are two kinds of mutations: the link mutation and the node mutation. To practise the link mutation, a link, said l_m^n , which is not belonged to C_o but both node m and node n are in C_o , is created in C_o , with the weight $\epsilon()$. If this link appears in the population at the first time, it is given the innovation number $I^{MAX} + 1$ and then added to the global innovation set, *Inno*.

To practise the node mutation, a link belonged to C_o is chosen, said l_m^n , and segmented into two links l_m^t and l_t^n . That is to say, a node, t , and two links, l_m^t and l_t^n , are created in C_o and the original link, l_m^n , is abandoned. If $w_o^{mn} > 0$, the weights of l_m^t and l_t^n , as w_o^{mt} and w_o^{tn} , are both set to the square root of w_o^{mn} . Otherwise, w_o^{mt} is set to the square root of $|w_o^{mn}|$ and then $w_o^{tn} = -w_o^{mt}$. This design guarantees $w_o^{mt} \times w_o^{tn} = w_o^{mn}$, and hence the original function will not be largely affected after adding a node. After assigned the innovation numbers $I^{MAX} + 1$ and $I^{MAX} + 2$, respectively, both of these links are added to the global innovation set, *Inno*.

As the last part of the implementation, the method to construct a neural network from a NEAT chromosome, $C_i = \{(l_m^n, w_i^{mn})\}$, is as follows. At first, the default network is built

by 9 input nodes, labelled from 0 to 8, and 4 output nodes, labelled from 9 to 12. Then, the weighted links in C_i are put into the network sequentially along the ascending order of their innovation numbers (Stanley & Miikkulainen, 2002). If adding a link, said l_m^n , to the network can cause a loop, for example, node m to node n to node t back to node m , l_m^n is treated as a recurrent link with a delay unit Z^{-1} (Stanley & Miikkulainen, 2002). By setting the delay unit, the value of node m toward to node n delays one time step. In other words, the value that node n receives through link l_m^n is actually node m 's value at the previous step. On the one hand, this design is to prevent an infinite loop in the neural network; on the other hand, the capability of a neural network is extended due to the memories brought by these recurrent links. To operate a NEAT network in the proposed model, the values of the eight sensors and the offset node are directly set as the inputs, which values are generally between zero and one. Two output values of the network are multiplied by R_S to represent the values of ℓ_A and ℓ_R . The other two are multiplied by 150 degrees to represent the values of θ_A and θ_R . Since the output values are handled numerically, the activation function of a node is set to only compress excessive values outside the range $[0,1]$ and keep any value in this range unscaled.

Table 3.2: Parameters of NEAT

Name	Value
Input nodes	9
Output nodes	4
Activation function	$\varphi(x) = \begin{cases} 0, & \text{if } x < 0 \\ 1, & \text{if } x > 1 \\ x, & \text{otherwise} \end{cases}$
Recurrent links	YES
Node disability	NO
Pr. of link mutation	0.08
Pr. of node mutation	0.03
Noise	$\epsilon() \sim N(0,0.01)$

3.2.5 Originality of Model Design

The concern of designing the proposed model is to accord with the popular modelling framework in this domain at the same time modifying those settings which have significantly caused biases. Four modifications based on this concern are as follows.

The first one is that physical overlaps are highlighted and strictly forbidden by the penalty of individual fitness (Chapter 3.2.3). Comparatively, almost all previous models in this domain may overlook the influence of physical overlaps, and only smoothly reduced the frequency of overlaps by adding a repulsion force towards those extremely close neighbours (Schellinck & White, 2011). As demonstrated in the next Chapter, the overlap-free setting will reveal some novel evolutionary scenarios which were ignored in overlap-allowed models,

The second modification is providing an open-ended solution space to the evolution of behavioural strategies by the NEAT algorithm. Ward et al. (2001) also evolved fish agents by an evolvable neural network, but only the weights of its neural networks were optimised during the evolutionary simulation. It implies the set of candidate strategies is still restricted although this set is larger and less easily understandable. Comparatively, the NEAT networks can be composed by unlimited links and nodes during the evolutionary simulation, which implies, theoretically, all possible mappings from the local information to the responses are included. Although the present model may be the first work to introduce an open-ended solution space into the evolutionary simulation of animal collective behaviour, it is not novel to evolve intelligent agents by NEAT or other algorithms with open-ended solution space (Ficici & Pollack, 1998; Bouffanais, 2016). For example, Stanley & Miikkulainen (2004) evolves unreported chasing

strategies between two competitive robots by NEAT because of the advantage of its open-ended solution space.

The third modification is that the parallel orientation behaviour, that is, following the neighbours' directions, is abandoned and only the attraction and repulsion behaviours are provided to fish agents. The popular design of fish agents' behaviours is based on the triggered ranges of the three predesignated elementary behaviours: attraction, repulsion and paralleling orientation (Schellinck & White, 2011). However, the setting of paralleling orientation has been disputed since only the attraction and repulsion behaviours can be observed in real fish (Parrish et al., 2002; Tien et al., 2004; Katz et al., 2011). On the other hand, Romanczuk et al. (2009) and Guttal et al. (2012) have demonstrated how locusts exhibit a collective motion only by individual attraction and repulsion. However, the displayed collective behaviours in these models are not reasonably similar to fish schools (Strombom, 2011). Based on the hints from the locus models, the traditional design of fish agents' triggered ranges is modified with an additional spreading angle, so that the unrealistic parallel orientation behaviour can be abandoned.

The fourth modification is the design of local sensors. This consideration can be seen in Werner & Dyer (1993), Ward et al. (2001) and Olson et al. (2013), and hence is not originally proposed in the model. For example, the most similar implementation is in Olson et al. (2013). This work segments a fish agent's sensing range into 100 sectors, each of which is detected by a binary sensing unit: if any fish neighbour is in the sector, the unit returns the value 1; otherwise, the value 0 is returned. The modification from this design is to reduce the sensing units from 100 into 3 (for the flow sensor) or 5 (for the visual sensor) by changing the binary signals into numeric signals. Through this

improvement, the number of a neural network's input nodes is largely reduced so that the complexity to evolve an effective mapping from the input to the output, as an agent's strategy, decreases considerably and the simulation outputs can be more stabilised and repeatable.

3.3 Quantification

To describe the emergent patterns in a spatial-explicit agent-based model, specific quantifications have been developed in many previous works (Parrish et al., 2002). For example, the degree of coordination in a fish aggregate is usually measured based on the addition of all individuals' directions (Huth & Wissal, 1994; Couzin et al., 2002). According to the length of this sum vector, a moving school can be distinguished from a disordered swarm or a milling herd due to the large value. However, these metrics can only measure a single aggregate, and lose their effectiveness when fish flock into multiple groups. A simple instance is when two fish schools moving in opposite directions, in which case, the sum of their directions is mediated to a small vector, as the situation of a swarm.

In the proposed model, fish agents are given the ability to leave their neighbours, as free as to herd together. Therefore, a state of multiple groups is a common situation during an evolutionary process. Instead of clustering these groups from a global view, the bottom-up metric, RPFC, is originally designed by the research work to quantify collective patterns simply and effectively, as drawn in Figure 3.3. The metric takes advantage of each agent's sensory perceptions, by which an agent's positional status, at each time step, can be categorised into one of the following six types: R, P, Fm, Fc, Cm and Cc (Figure 3.3). According to the average frequencies of these six positional types

in a population, three collective patterns can be identified, as the schooling pattern (composed of P, Fm and Fc), the swarming pattern (composed of Cm and Cc) and the dispersal pattern (composed of R).

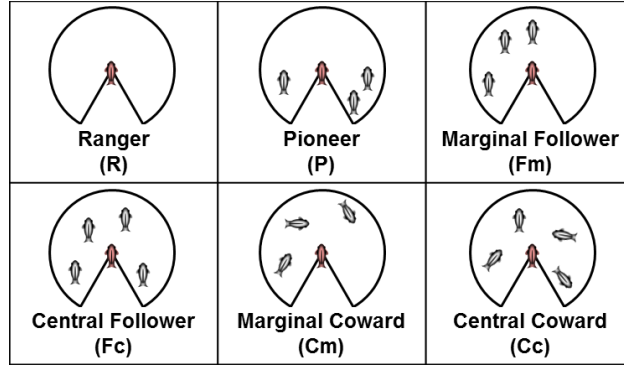


Figure 3.3: Categorisation of Positions

Each fish agent at each step can be categorised into exactly one position: ranger (without neighbours in the sensory range), pioneer (schooling without leading neighbours), marginal follower (schooling with leading neighbours and without neighbours at some other side), central follower (schooling and surrounded by neighbours), marginal coward (not schooling, and not surrounded by neighbours) and central coward (not schooling, and surrounded by neighbours). This categorisation is based on an agent’s sensory perceptions, which ensures that an agent can recognise these positional differences.

The implementation of the RPF metric is as follows. If an agent’s five visual sensors are all zero, which means there is no neighbour in its sensory range, this agent reports its position as ‘ranger (R)’. For those agents with neighbours, an agent is considered ‘schooling’ if

$$P^L(0^\circ) > \omega(P^L(120^\circ) + P^L(240^\circ)), \quad (3.9)$$

where $\omega = 2$ based on the experiment in Figure 3.4. This condition means an agent’s neighbours are on average in a direction similar to that of itself, and if the condition is not satisfied, the agent is considered ‘swarming’ at this step.

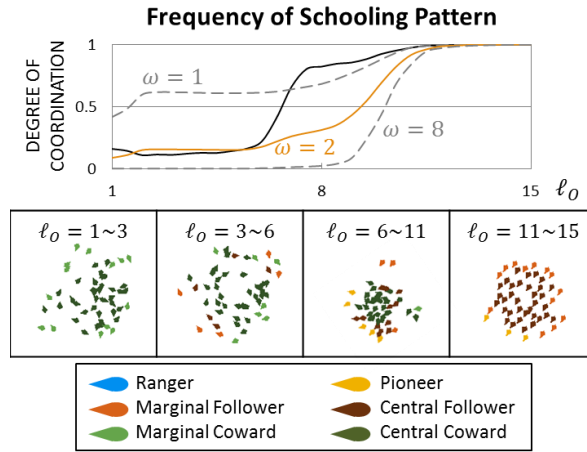


Figure 3.4: RPFC Metric vs. Group-level Index

The model in Couzin et al. (2002) showed that the increase of ℓ_0 , as a parameter of the tendency of parallel orientation, can lead the collective pattern to transit from a disordered swarm, via a milling group and a relatively disordered school, to a highly coordinated school, which outcome is duplicated as the visualisation. To quantify the degree of coordination, the length of the sum vector of all individuals' directions was used in the referenced work, which measurement is duplicated as the black line. As a comparison, the proposed RPFC metric displays that the swarming pattern and the schooling pattern can also be recognised clearly given $\omega \geq 2$. Specifically, a disordered swarm and a milling herd cannot be separated by both of these two metrics, which was measured by another group-level metric in the referenced work. Besides, the relatively disordered school moves through the repulsion behaviours by overlapped agents, which is not a potential state in the proposed overlap-free model.

Subsequently, for further analyses in the latter chapter, a schooling agent is subdivided into one of the three positions according to the information from its visual sensors: viz., 'pioneer (P)', if $P^E(0^\circ) = 0$, which means there is no neighbour in the front sector of 144° ; 'central follower (Fc)', if all of its five visual sensors are greater than zero, which means it is surrounded by neighbours; and 'marginal follower (Fm)' if none of the both. It should be noted that the 'straggler' of a moving school is not separated from followers, in consideration of the existence of a blind zone at the rear. Lastly, a swarming agent is subdivided into one of the two positions: 'central coward (Cc)', if all of its visual sensors are greater than zero, and 'marginal coward (Cm)', otherwise. The term 'coward' is chosen to describe swarming individuals according to the appearance that these agents prefer to hide in the crowd rather than being 'pioneers' or 'rangers'.

Since the proposed categorisation is based on an agent's two perceptions, it is guaranteed that these positional differences can be recognised by the fish agents.

Although an agent often changes its position with time, the distribution of these positions in the population is highly stable, except when the population size is too small. Specific exceptions are when a ranger is followed by other agents in its blind zone, a follower is actually in a huge milling aggregate, and two parallel pioneers are not followed by other agents. These errors, however, are insignificant to the measured results in the model. Hence, more complicated categorisations are prevented.

Apart from the proposed RPF metric, the nearest neighbour's distance (NND), as the distance between one and its nearest neighbour, is introduced to quantify the flocking degree of agents and the level of crowd density in a group. This metric has been widely used as a measurement of the crowding degree in animals (Parrish et al., 2002). There are k -NND metrics (Ballerini, 2008), as the k th nearest neighbour's distance, to reduce the influence of exceptional situations, like pairs. Since there is no survival benefit to pairwise couples in the model, NND is adopted for its simplicity.

3.4 Validation of Authenticity

An ecological model can be significant only if it does not directly contradict the targeted natural system. This is reflected mainly from whether the settings in a model are supported by the empirical data (Parrish et al., 2002; Grimm et al., 2005; Schellinck & White, 2011). Here the authenticity of the proposed model is investigated with a comparison of the previous works.

3.4.1 The Sensory Perceptions

As mentioned in Chapter 3.2.1, a fish's eyes and lateral lines have been proven fundamental to its decision making (Partridge, 1982; Faucher et al., 2010), and the acquisition of information is local and limited (Olst & Hunter, 1970; Hoare et al., 2004). Previous evolutionary models of social agents, like Werner & Dyer (1993), Ward et al. (2001) and Olson et al. (2013), also designed a visual perception for their agents to make dynamic decisions based on local information, among which the agents in Ward et al. (2001) were even given a flow sensor, offering the function of lateral lines. According to the empirical data and the popular settings, the design of these perceptions in the proposed model should be valid and necessary.

In contrast, the agents in Oboshi et al. (2003), Wood & Ackland (2007) and Ioannou et al. (2012) were designed to make static decisions without the reference to current surroundings. That is to say, an agent's behavioural strategy has been decided once the agent is created, and cannot exhibit different responses under different surroundings, for example, being on the periphery or in the centre. This unrealistic limitation of decision making seems disputed when simulating the evolution of fish.

3.4.2 The Elementary Behaviours

Empirical studies have shown that attraction and repulsion are the two elementary behaviours when fish interact with one another (Partridge, 1982; Katz et al., 2011). The front priority, as the larger influence of those neighbours ahead, has also been observed from fish (Aoki, 1982; Katz et al., 2011). Many previous self-organising models have simulated these features effectively (Aoki, 1982; Huth & Wissel, 1994; Inada & Kawachi, 2002), where an additional behaviour, parallel orientation, was set in order to

simplify the interplay of the two elementary behaviours. However, this simplification has become disputed after more empirical studies were made (Parrish et al., 2002; Tien et al., 2004; Katz et al., 2011).

The evolutionary models in Oboshi et al. (2003), Wood & Ackland (2007) and Ioannou et al. (2012) adopted the framework in Aoki (1982) and evolved certain parameters to simulate fish's behavioural adaptation. Both of these works remained the disputed setting of individual paralleling. Other works, such as Ward et al. (2001) and Olson et al. (2013), evolved agents' behaviour from a rather basic level, that is, deciding the moving direction based on the local information. The latter modelling style treats all the behavioural features of real fish as a consequence of adaptation and hence contains much fewer preconceived assumptions. However, possibly subject to the heavy complexity to develop sophisticated movements from such basic level, both of these works (as well as the earlier models in the present study based on this setting) cannot simulate the evolution of fish's schooling behaviour.

In consideration of the computational complexity and the empirical evidence, this model simulates a fish's movement based on the predesignated attraction and repulsion behaviours, with a front priority of the referenced neighbours. Fish's escaping behaviour during a close attack, which was designed in Inada & Kawachi (2002), Zheng et al. (2005) and Lee (2006) to investigate the morphology of fish schools, is discarded in the model. It is because the predator is set to draw a risk distribution proportional to an individual's 'domain of danger' (Hamilton, 1971), and the predator-prey interaction during a physical attack is irrelevant to this concept. The issue is further explained in the next section.

3.4.3 The Predation Risk

Hamilton (1971) proposed the concept, ‘domain of danger’, to estimate the predation risk on prey individuals. It is the area where a prey becomes the nearest one if a predator appears. Therefore, a prey with a large domain of danger implies it may incur higher predation risk. The positive correlation between the domain of danger and the predation risk has been supported by ecological evidence (Mooring & Hart, 1992; Viscido & Wethey, 2002; De Vos & O’Riain, 2010). However, there are also exceptions caused by specific predators.

These exceptions have been mentioned even in Hamilton’s original paper, since the precondition of this concept is that the predator should hunt the nearest prey and only hunt one prey. This assumption does not hold if the predatory fish, for example, prefers to attack those prey in the central position. In this situation, the correlation between the domain of danger and the predation risk is reversed (Hamilton, 1971; Parrish, 1991). This kind of feeding preference has been observed in the pelagic ocean, as in sailfish (Domenici et al., 2014), thresher shark (Oliver et al., 2013) and killer whales (Simila & Ugarte, 1993).

Considering the generality of this concept, most models about prey’s behavioural evolution still adopted the ‘domain of danger’ to simulate predation risk (Viscido, et al., 2001; James et al., 2004; Wood & Ackland, 2007). On the other hand, there have been some works to simulate the evolution of prey under different hunting strategies (Hirsch & Morrell, 2011; Olson et al., 2016a). However, the outputs seem relatively less

informative at present, due to the lack of a strong connection with the natural adaptations in animals.

To outline the general situation of gregarious fish's behavioural evolution, the risk distribution in the present model still follows the concept of 'domain of danger'. However, the limitation of this setting has been noticed in the above paragraphs. A comprehensive model of the coevolution between predators' feeding strategies and prey's collective patterns will be built in Chapter V.

3.4.4 Other Issues

The minimal turning radius of fish has been studied decades ago (Webb, 1976; Domenici & Blake, 1997). This radius, termed R_T , draws the smallest circular path for a fish to turn around (Figure 3.5A), and is measured around $0.2 BL$ in many species of prey fish, as well as predatory fish and cetaceans (Domenici, 2001). Geometrically, as shown in Figure 3.5B, this value is relevant to the maximal turning angle, θ_T , and the moving speed, SPD, as

$$R_T = SPD/2/\sin(\theta_T) \quad (3.10)$$

or

$$\theta_T = \text{asin}(SPD/2/R_T). \quad (3.11)$$

Unfortunately, almost all simulations of fish neglected this metric and only set the maximal turning angle and the moving speed intuitively. Hence, unrealistic values of an agent's minimal turning radius are usually observed in the previous model. For example, in Couzin et al. (2002), the minimal turning radius of an agent is $2.88 BL$

according to the settings that $\theta_T = 10$ degrees and $SPD = 1 BL$. In Olson et al. (2013), Olson et al. (2016a) and Olson et al. (2016b), this radius is 3.59 through $\theta_T = 8$ degrees and $SPD = 1 BL$. In Wood & Ackland (2007), the incorrect relation, $\theta_T SPD^2 = 12.5$ was used, where $R_T = 2.31 \sim 286 BL$ in its experimental range $SPD \in [1, 5]$. These unrealistically large radii directly affect the authenticity of the simulations. In the proposed model, the minimal turning radius is set $0.5 BL$, the speed is set $0.12 BL$ per step, and hence the maximal turning angle per step is derived as 7 degrees.

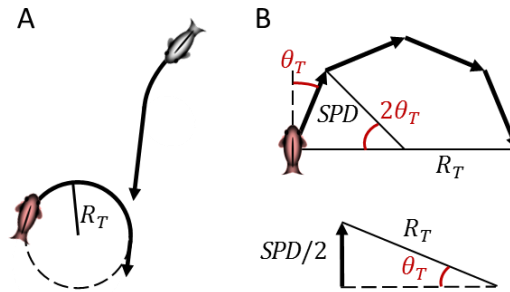


Figure 3.5: Minimal Turning Radius

The minimal turning radius, R_T , draws the minimal circle for a fish to turn around, as in subfigure A. The relation between R_T , the speed (SPD), and the maximal turning angle per step (θ_T) is displayed in subfigure B.

The small amount of prey agents has been mentioned as unrealistic compared to the real fish school of countless individuals (Rohani et al., 1997; Parrish et al., 2002). Subject to the computational time, however, it is impractical to simulate thousands of agents. In this thesis, this criticism is addressed by the associated game-theoretic analyses of the simulation outputs. The derived results from these analyses are insensitive to the population size, which can be from 100 to infinite. Hence, these analyses support that in the proposed model, 100 agents are sufficient to represent the adaptation of countless individuals in a fish population.

Almost all of the related works designed their fish agents with a fixed moving speed (Schellinck & White, 2011), which is obviously unrealistic since a real fish can speed up and slow down. The only agent-based model which allowed its agents to adjust the speed is in Wood & Ackland (2007). It demonstrated that given a fixed predator speed, the adaptation of prey's speed is influential to the evolutionary results. The setting of adaptive speeds is abandoned in the proposed model due to the computational difficulty. However, the influence of speed is included in the extensive model in Chapter V.

3.5 Validation of Credibility

To maintain reliable outputs in a noisy environment, relevant adjustments and parameter scans are made in this subchapter, including the choices of the selection scheme, the selection intensity and the replacement rate in the coming section, and the influences of other parameters.

3.5.1 Alternative Selection Scheme

In a genetic algorithm, crossover, mutation and selection are the three backbones of the computational performance (Haupt & Haupt, 2004). These components of the employed algorithm, NEAT, have been well analysed and validated by the original work (Stanley & Miikkulainen, 2002). However, the selection scheme in NEAT involves niching and speciation, which causes an inconsistency, or to say, additional assumptions, when natural selection and evolutionary selfishness are simulated. The proposed model abandons this selection scheme and chooses an alternative among three popular schemes which conform to the mechanism of individual selection.

The first candidate is the proportional fitness selection, which was the selection scheme of the original genetic algorithm in Holland (1975). This scheme is defined as

$$r_i = \frac{\max(u_i, 0)^{I_{PF}}}{\sum_{j=1}^N \max(u_j, 0)^{I_{PF}}}, \quad (3.12)$$

where the maximum function is to discard negative values; u_i and r_i are the fitness value and the reproduction probability of agent i , respectively. I_{PF} is an index of the selection intensity, also termed the selection pressure, of this scheme (Blickle & Thiele, 1995). When I_{PF} increases, the selection biases to the best few agents and reduces the diversity of a population.

The second candidate is the exponential rank selection, which puts an exponential weight on the better-performed agents based on their ranks (Blickle & Thiele, 1995). Given I_{ER} is the index of this scheme's selection intensity, and $rnk(u_i)$ is agent i 's rank in the population by its fitness value, this scheme defines the reproduction probability as

$$r_i = \frac{I_{ER}^{-rnk(u_i)}}{\sum_{j=1}^N I_{ER}^{-rnk(u_j)}}. \quad (3.13)$$

The last candidate is the tournament selection (Goldberg & Deb, 1991), in which scenario the best agent among randomly selected I_{TR} agents is chosen. As the selection pressure increases with the size of the base group, the integer I_{TR} is also the index of this scheme's selection intensity (Blickle & Thiele, 1995). Mathematically, the reproduction probability by this scheme is

$$r_i = \frac{I_{TR}}{N} \prod_{j=0}^{I_{TR}-2} \frac{N - rnk(u_i) - j}{N - 1 - j}. \quad (3.14)$$

It should be noted that, when the selection intensity is sufficiently high, the exponential rank selection and the tournament selection can draw extremely similar distributions over the reproduction rates in a population (Blickle & Thiele, 1995). However, these selection schemes are significantly different given low selection intensity. For example, when $I_{TR} = 2$, the tournament selection is reduced to the linear rank selection (Goldberg & Deb, 1991; Blickle & Thiele, 1995; Reeves, 2003), as

$$r_i = \frac{2}{N} \times \frac{N - \text{rnk}(u_i)}{N - 1} = \frac{2}{N(N - 1)} [N - \text{rnk}(u_i)]. \quad (3.15)$$

This distribution cannot be considerably fitted by the exponential rank selection with any selection intensity. Hence, these two selection schemes are both kept as candidates.

To experiment the robustness of these candidates in the proposed model, the average NND of the population in the 200th generation is chosen to be the index. The reason is as follows. As overlaps are forbidden by a hard punishment on the fitness value, agents quickly adapt to isolation and this tendency results in a large NND. However, flocking without overlaps, which implies a small NND, is more adaptive than being isolated because of the smaller domain of danger (Hamilton, 1971). From the computational aspect, it is a difficulty to develop a flocking behaviour and avoid overlaps at the same time. Hence, the performance of a selection scheme can be measured by the average NND of a population in an early generation. The 200th generation is chosen since it is long enough for agents to develop the tactic to flock without overlaps at the same time spending short computational time. However, other reasonable choices of the representative generation are insensitive to the findings.

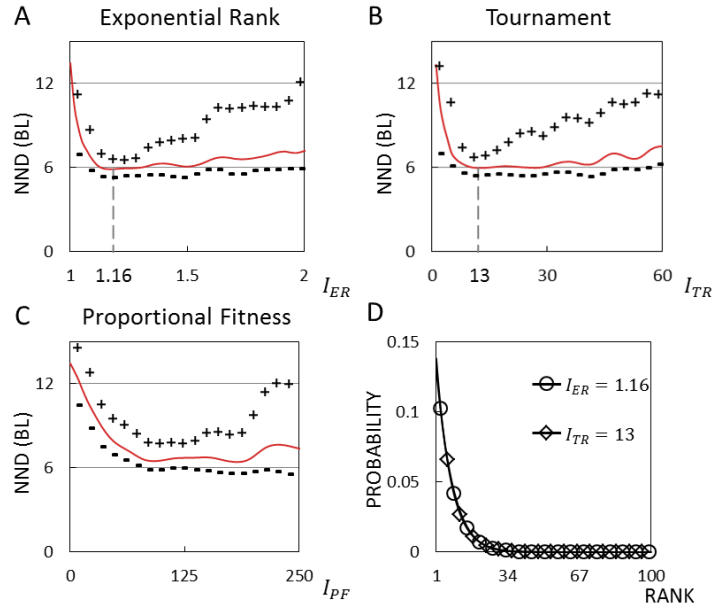


Figure 3.6: Performance of Selection Schemes

As flocking without overlaps is an adaptive strategy with a computational difficulty, the average NND of the population in the 200th generation is used as the performance index (the lower the better). Given a selection scheme with certain selection intensity, 100 simulations were run and hence 100 performance indices were collected. Under this selection intensity, the associated point in the red solid line plots the median of these 100 simulations' performance indices, and the plus and minus symbols are the first quartile and the third quartile, respectively. The test of the three selection schemes, as subfigures A to C, suggests that the exponential rank selection with the selection intensity 1.16 and the tournament selection with the selection intensity 13 are both the best. Since the selection intensity of both values are sufficiently high, it can be observed that their distributions are in fact almost the same, as plotted in subfigure D.

Given a selection scheme and its selection intensity, 100 simulations are made to collect their NND values in the 200th generation. The efficiency and robustness of the scheme and its given intensity are reflected by the distribution of these NND values. That is to say, if these simulations result in similar values, the robustness is excellent, and if most of them output a small NND, the efficiency is high. The experiment shows that when the selection intensity is set too small, the efficiency is affected, but when the selection intensity is considerably large, the consistency of simulation outputs is extremely low (Figure 3.6). Specifically, the NND value is much higher by the proportional fitness selection scheme (Figure 3.6 C), which means the preference of this scheme is the worst in the proposed model. The two best choices are the exponential rank selection with

$I_{ER} = 1.16$ and the tournament selection with $I_{TR} = 13$, both of which provides high robustness and efficiency (Figure 3.6A & Figure 3.6B). By plotting the reproduction probabilities of these two settings (Figure 3.6D), it is observed that they draw almost the same distribution, where only the first one-third agents have a considerable chance to reproduce their offspring. In the proposed model, the exponential rank selection with $I_{ER} = 1.16$ is used to replace the original niching selection scheme in NEAT.

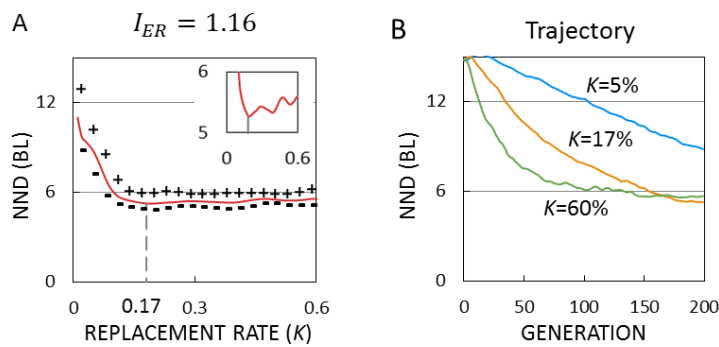


Figure 3.7: Performance of Replacement Rates

Subfigure A shows that the outputs are highly consistent regardless the replacement rate. The only affected factor is the efficiency. However, from the close inspection, as the small plot, the performance of $K=17\%$ is slightly better than the other ones, especially compared to the extremely large values, as shown in subfigure B.

The replacement rate, K , as the proportion of eliminated agents per generation, may influence the performance of a genetic algorithm (Syswerda, 1991; Vavak & Fogarty, 1996). The test based on the exponential rank selection with $I_{ER} = 1.16$ shows that, in the proposed model, the efficiency is enhanced with the increase of K , and the robustness keeps well in all the experimental range (Figure 3.7A). When the replacement rate is extremely large, however, the average NND increases slightly, which may result from the premature situation (Figure 3.7B). According to this test, the replacement rate in the proposed model is set 17%. One reason is that this value performs slightly better than the extremely large values and is more efficient than the

smaller ones. The other reason is that the evolutionary trajectory is a main concern of the research and this value preserves the transitions better than the larger values.

3.5.2 Other Parameter Scans

The arena length is fixed to 500 BL in the present model. However, it does influence the risk distribution in the environment. A smaller arena aggravates the risk on the school margin (P and Fp), and a larger arena endangers the peripheral agents of a swarm (Cm). From the view of the risk distribution, a larger arena is similar to a slower predator, and vice versa (Figure 3.8). Since the analogy from the arena length to the natural environment is less obvious than the predator speed, this parameter is fixed in the proposed model.

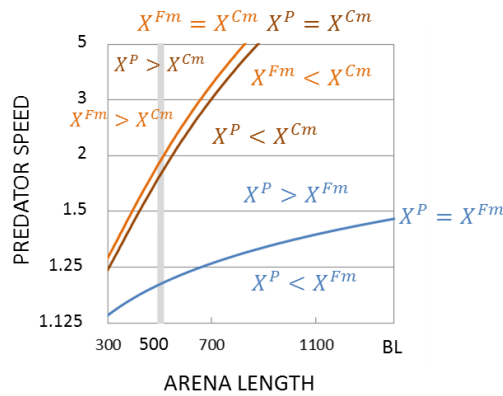


Figure 3.8: Risk Distribution by Arena Length

The influence of the arena length to the predation risk is displayed by a comparison with the predator speed. Since the risk of rangers is always high and the risk of central positions is nearly zero, only the relations between the risks of pioneers (X^P), marginal followers (X^{Fm}) and marginal cowards (X^{Cm}) are shown: the blue curve shows the condition $X^P = X^{Fm}$, the light orange curve is $X^{Fm} = X^{Cm}$ and the dark brown curve is $X^P = X^{Cm}$. When the arena length increases, the risk distribution is influenced as the predator speed becomes slower. For example, the risk distribution of 500 BL arena length and 1.8 SPD predator speed is similar to that of 800 BL arena length and 5 SPD predator speed. In all other experiments in this thesis, the arena length is fixed at 500 BL so that only the influence of different predator speeds is experimented. This experimental range is shown by the grey vertical line.

The influences of the prey speed (SPD) and the minimal turning radius (R_T), as well as the maximal turning angle calculated by $asin(SP/2/R_T)$, are insensitive given a

reasonable range of their values. Specifically, a larger speed and a smaller minimal turning radius, both of which enlarge the maximal turning angle, may cause an evolutionary failure due to the difficulty of making precise movement decisions. On the other hand, a small moving speed aggravates the computational time; a large minimal turning radius affects the flexibility of agents and violates the empirical data (Domenici, 2001). The insensitive ranges of these parameters are $0.06\sim 0.15 BL$ per step for SPD and $0.05\sim 2.00 BL$ for R_T .

The influence of the sensory range is as follows. The area of a blind zone does not obviously affect the simulation in the wide range $0^\circ\sim 90^\circ$, where the number of subgroups increases gradually given a larger blind zone. Although the simulation outputs are insensitive to this setting, it is kept in order to accord with the previous works and empirical data (Schellinck & White, 2011). About the sensory radius, this parameter is generally uninfluential to the result in the range $9BL < R_S < 21BL$. However, a large R_S imposes a heavy load on the computational time due to the increase of neighbours in the sensory range. On the other hand, a small R_S enhances the number of subgroups. It should be noted that since the influence of a neighbour is designed inversely proportional to the square of its distance, a larger R_S is not equal to receiving the information from a wider area.

Lastly, about the role of the white noise, ϵ , although a few models have emphasised its importance (Schellinck & White, 2011), this parameter is dispensable in the model. It is because the difference between each agent's NEAT chromosome has caused a similar effect. If this additional noise is added, agents need more space to avoid overlaps so that the number of subgroups increases. In the present model, the noise is set small, which propose is only to simulate random walks of isolated agents.

3.6 Discussion

Simulation of fish's behavioural evolution has been a rising topic in Ecology. However, the design of a model usually relies on certain ecological knowledge, and hence different predetermined settings have led to different, or even contradictory, simulation outputs. In this Chapter, efforts to construct an evolutionary model with fewer preconceived biases are from the two aspects: the open-ended solution space to evolve strategies and the validation of model settings based on the related concerns.

In the present model, the behavioural strategy of a prey agent is a course of reactions to the local surroundings. In other words, it is a mapping from local information to the elementary behaviours. In previous works, only a small range of potential strategies were chosen to simulate the behavioural evolution of fish, which directly caused a bias as the influence of other strategies outside this range were neglected. This work introduces the NEAT algorithm to reduce the bias of a predesignated strategy set. Because this algorithm evolves its neural networks in an open-ended search space without the limitation of complexity, a prey agent is theoretically possible to adopt any strategy, as the mapping from the acquired local information to the given behaviours, for its fitness. This contribution further provides the present model a capability to evolve beneficial strategies which have not been reported.

For the rest of model settings, according to the ecological concern, the authenticity and credibility of the proposed model is analysed carefully. About its authenticity, most settings of the model are highly consistent to the empirical data, and its unrealistic simplifications are also reported. About its credibility, the insensitive range of each parameter is reported, and the robustness of this model against noises is experimented

and optimised. Specifically, this work emphasises the influence of selection schemes in ecological modelling, which issue was neglected in almost all evolutionary simulations in this field. These experiments may highlight the importance of these techniques in ecological modelling.

It is a fact that every model is a simplification of its targeted system and there must be unrealistic settings in a model. For example, the constant speed and round body shape of every prey agent in the proposed model are different from the real fish, the arena in this model is a 2-dimensional plane rather than a 3-dimensional space, and the sensors designed for the agents are also simplified. Although these simplifications have been widely adopted in the related works (Schellinck & White, 2011), they may still cause a qualitative deviation from the real system to the simulation output. The aim of this work is to propose a model which has avoided some considerable biases in previous models, so that it can simulate the underlying mechanism of fish's behavioural evolution more convincingly. In future works, whether any of the adopted simplifications in the present model is qualitatively influential in evolution will be studied (discussed in Chapter 6.3.1).

CHAPTER IV

EVOLVING THE ADAPTIVE STRATEGY OF PREY FISH

This chapter addresses the second main research question, about whether the evolution of prey fish's schooling pattern can be demonstrated and explained under individual selection, by investigating the four specific research questions:

- Can schooling evolve under a selective force on individuals?
- What is the adaptive strategy which causes the schooling pattern?
- What is the profit earned from this strategy?
- In what environment can this strategy be evolutionarily stable?

Based on the spatial-explicit agent-based model outlined in Chapter III, the simulation demonstrates that, given selection at the individual level, the selfish herd scenario (Hamilton, 1971) is a fundamental mechanism in evolution. That is to say, prey agents always prefer to be at the protected centre rather than the dangerous boundary. This preference then leads the population into disordered swarms, that is, relatively stationary aggregates in which agents exhibit a low degree of coordination. Interestingly, as the selective force keeps falling on the agents, these swarms will finally

become too crowded for marginal agents to occupy the safe centre. In this situation, schooling consistently emerges due to an unreported adaptive strategy, named ‘collective departure’: leaving the risky boundary with few companions to expose interior agents. Through the game-theoretic analysis, one can interpret how ‘collective departure’ brings survival fitness to a prey individual by sharing the predation risk with others. Moreover, a prediction is also proposed on the evolution of gregarious prey under various conditions.

This chapter reveals some novel viewpoints on the evolution of fish's collective motion. First, fish schools can evolve by the force of individual selection, regardless of the group benefit. Secondly, schooling can be a self-organising phenomenon by the adaptive strategy for local interaction: ‘collective departure’. Thirdly, the biased risks among positions within a group can be the essential factor for fish to evolve into a schooling pattern.

4.1 Background

Schooling is a coordinated movement of gregarious fish that can be commonly observed in open waters (Breder, 1967; Shaw, 1978). Formation of this collective motion has been known as a self-organising phenomenon. In other words, fish only interact with their nearby neighbours, and these local interactions indirectly lead to the emergence of a schooling pattern (Couzin & Krause, 2003; Sumpter, 2006). Various self-organising models have demonstrated how simple behaviours to interact with adjacent individuals can result in this coordinated movement. This may be due to a fish aligning itself with its neighbours (Aoki, 1982; Couzin et al., 2002) or a fish chasing its leading neighbours (Huth & Wissel, 1994; Strombom, 2011).

Previous experiments have shown that the degree of coordination is enhanced when fish individuals are in danger of predation (Seghers, 1974; Magurran & Pitcher, 1987; Tien et al., 2004). Hence, survival pressure is considered the primary force for fish to adapt to this collective motion (Krause & Ruxton, 2002). To explain further why schooling has evolved under survival pressure, traditional focuses are mainly put on benefits to schooling groups. For example, the dilution effect, confusion effect, and information transfer effect are all on the basis that schooling can mitigate predatory attacks towards individuals in an aggregate (Krause & Ruxton, 2002).

However, the benefit of a whole group cannot be regarded as the direct evolutionary reason for a schooling pattern, since the force of natural selection is on individuals rather than groups (Hamilton, 1971; Parrish & Edelstein-Keshet, 1999; Sumpter, 2009). Those explanations underlining the group benefit may neglect that competition does not only appear as fish in a school versus fish not belonging to it, but also presents among fish in the same school. Specifically, in a moving aggregate, those fish at the front edge bear higher predation risk than their followers (Bumann et al., 1997; Krause et al., 1998). Besides, marginal fish are usually in more danger than central ones (Hamilton, 1971; Parrish, 1991). These biased positional risks may allow selfish individuals to profit from occupying secure positions within a group (Hamilton, 1971; Parrish & Edelstein-Keshet, 1999). This possibility implies that, given the selective force at the individual level, a pattern with higher group benefit can be replaced by a worse one (Smith, 1982).

To understand how schooling can evolve through individual selection, self-organising models combined with a genetic algorithm have relatively recently begun to simulate the adaptation of schooling behaviour, like Ward et al. (2001), Oboshi et al.

(2003), Wood & Ackland (2007) and Ioannou et al. (2012). So far, previous models have not taken the ‘internal competition’ into account, as the ability of an agent to recognise its position is limited or lacking in these models. This limitation omits the competition among individuals in the same group, and, as explained in the preceding paragraph, can mislead the evolutionary force away from the individual level.

Recent studies have begun to explain the adaptation of collective motion by individual difference and leadership. Since fish in a group can have different needs, information or endowments (Krause et al, 1998; Krause et al, 2000; Couzin et al., 2011), it is inferred that these differences can cause a certain sub-group of ‘leaders’ to lead the group (Couzin et al., 2005; Conradt et al., 2009; Couzin et al., 2011). Some evolutionary models based on, or close to, this perspective have also been proposed (Conradt & Roper, 2009; Guttal & Couzin, 2010; Eshel et al., 2011). These viewpoints assumed that there are social roles and leadership in a fish school. However, there is scant evidence to support that fish’s schooling pattern under predation risk relies on the role of leaders (Partridge, 1980; Hoare et al., 2004).

By connecting a self-organising model with the NEAT algorithm (Stanley & Miikkulainen, 2002), an evolutionary model was built in Chapter III. To address the research questions in this chapter by the model, its three essential features are emphasised as follows. First, decision making of agents is dynamically based on the local surroundings. Secondly, potentially profitable strategies can be developed automatically without a predesignated strategy set. Thirdly, overlaps between two agents' bodies are strictly forbidden, rather than a smooth control by a repulsive force as in most of the previous models (Schellinck & White, 2011).

4.2 Method

In the simulation, a fixed number of prey agents (100 agents) are put into a 2D wrapped-around arena to interact with one another. Each agent adopts a strategy, implemented by the NEAT neural network (Stanley & Miikkulainen, 2002), to make movement decision based on its local surroundings. The movement decision can be attraction (approaching the neighbours), repulsion (avoiding the neighbours), or the interplay between these two. The endowment of each prey agent is identical, for example, same body length (1BL), same moving speed (1SPD), and so on. The predation risk of these agents is distributed by a rule-based ‘unbeatable’ predator. This predator always chases the nearest prey during a predatory hunt until touching one. Then it is reallocated randomly to start another hunt. The predator’s speed (PS) is an experimental parameter from 1.125 times to 5 times faster than the prey speed. This setting implies that the predation risk of a prey agent is positively correlated to its domain of danger, that is, the area where one becomes the nearest prey to the predator (Hamilton, 1971).

Survival fitness of each prey agent is defined as the survival probability per hunt, subject to the overlap-free constraint, that is, $u_i = (1 - T_i^E/T^H) - \lambda T_i^O/T^H$ (as formula 3.5), where T_i^E and T_i^O are the eaten times and overlapping times of an agent, respectively. T^H represents the predator’s hunting times. The multiplier λ is a penalty to take the constraint $T_i^O/T^H = 0$ into account. After ranking by each agent’s fitness value, the worst 17 agents are eliminated, and substituted by 17 offspring of well-performed agents. Then, the process is repeated 1500 times, or to say, 1500 generations. (Details are provided in Chapter III)

To quantify the output of the simulation, the proposed RPFC metric in Chapter III is adopted to categorise an agent's position, at each step, into the following six types: 'ranger' (R), as an agent with no neighbour, 'pioneer' (P), as an agent at the front edge of a school, 'marginal follower' (Fm), as an agent at the other edge of a school, 'central follower' (Fc), as an agent in the centre of a school, 'marginal coward' (Cm), as an agent on the boundary of a disordered swarm, and 'central coward' (Cc). (Details are provided in Chapter III)

Based on this categorisation, four properties of the collective behaviour exhibited by a prey population are measured as follows. The first property is the positional frequency, which is defined as the ratio of the appearance times of a certain position to the appearance times of all the six positions. For example, given the following observation: at step 0, 10 prey agents are 'rangers', 20 prey agents are 'pioneers', and 70 prey agents are at other positions; at step 1, 20 agents are 'rangers', 30 agents are 'pioneers', and 50 agents are at other positions, then the frequency of the 'ranger' position is $(10 + 20)/200 = 15\%$, the frequency of the 'pioneer' position is $(20 + 30)/200 = 25\%$ and the other four positional frequencies are $(70 + 50)/200 = 60\%$ in total. In the simulation, the positional frequencies are measured based on 30000~50000 steps, so the expected frequencies can well represented.

The second property is the frequency of an emergent pattern, that is, the dispersal, schooling or swarming pattern. It is the summation of the associated positional frequencies: the dispersal pattern's frequency is equal to the frequency of the 'ranger' position, the schooling pattern's frequency is the sum of the frequencies of the 'pioneer', 'peripheral follower' and 'central follower' positions, and the swarming

pattern's frequency is the sum of the frequencies of the 'peripheral coward' and 'central coward' positions.

The third property is the positional risk, which means the probability of being eaten at a certain position per step (Bumann et al., 1997; Krause et al., 1998). It is not directly related to the survival probability, which is measured by $1 - T_i^E/T^H$ in the proposed fitness function, where T_i^E/T^H estimates the probability that prey i will be eaten during a predatory hunt, regardless of time steps. The risk of a certain position is measured as the ratio of the times the predator catches prey at this position to the appearance times of the position. The six positional risks are denoted by $X^R, X^P, X^{Fp}, X^{Fc}, X^{Cp}, X^{Cc}$, respectively.

The fourth property is the probabilities of positional changes. In the simulation, this probability is measured at the individual level. Taking the probability of changing from the 'marginal coward' position to the 'pioneer' position, that is, $pr(Cm \rightarrow P)$, for example, a certain prey's $pr(Cm \rightarrow P)$ is measured by the times it changes from the 'marginal coward' position to the 'pioneer' position over the times it is at the 'marginal coward' position.

4.3 Result

4.3.1 Emergence of the Schooling Pattern

In the experimental range of the predator speed, 578 simulations out of the total 600 simulations demonstrate that the frequency of the schooling pattern is in the majority (exceeding 50%) in the final generation, and is usually significantly higher than the swarming pattern and the dispersal pattern (Figure 4.1A). Thus, the first question of this chapter is answered here. At this stage, prey agents form elongated moving groups, in

which the central positions are scant. In other words, agents are all on the margin of their schools, either being pioneers or marginal followers (Figure 4.1B). Specifically, when the predator speed is greater than 1.8 (organised as fast-predator situations), the faster the predator, the higher the frequency of the swarming pattern emerges (Figure 4.1C). However, the majority is still the schooling pattern.

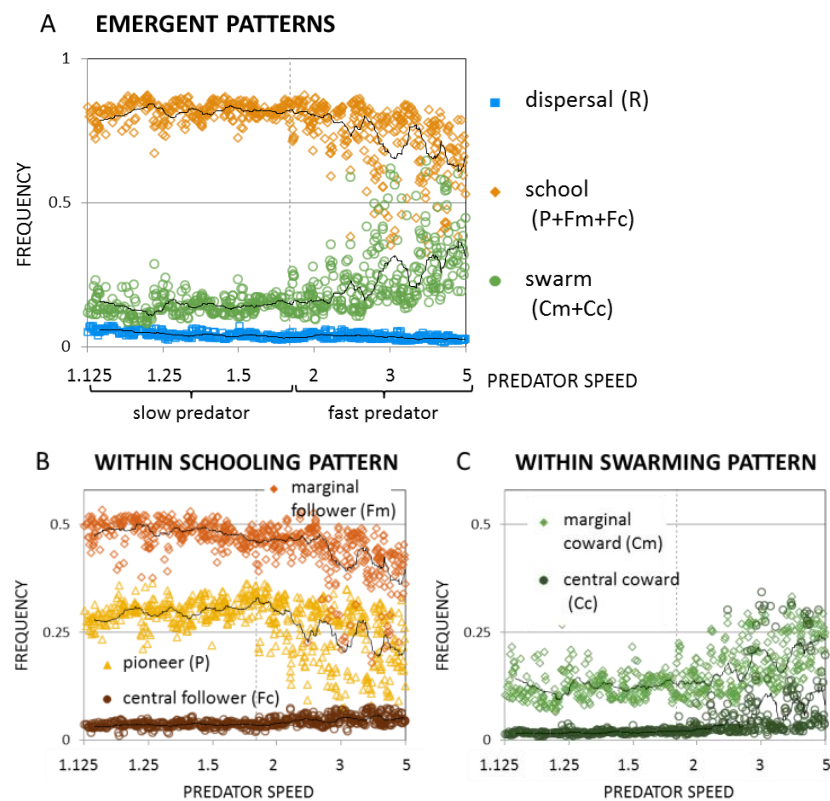


Figure 4.1: Positional Frequencies at the Final Stage

Subfigure A shows the majority of the apparent patterns in the final generation is schooling, regardless of the predator speed. Subfigure B and C show the detailed positional frequencies in the schooling pattern and swarming pattern, respectively. The vertical dotted line at 1.8 divides the results into slow-predator and fast-predator situations. These panels are plotted by 600 simulations in the range $1.125 \leq PS \leq 5$.

As shown in Figure 4.2, a typical evolutionary trajectory (75% of the simulations) is from isolated agents (stage I, named the ‘dispersal stage’ as the isolated agents do not form cohesive groups), via moving flocks (stage II, named the ‘grouping stage’ as small

cohesive herds have been observed) and few huge swarms where prey agents try to enter the central position with a low degree of coordination (stage III, named the ‘swarm stage’ due to the high frequency of the swarming pattern), to a few schooling groups where prey agents move in coordination and lead to a collective motion (stage IV, named the ‘stable school stage’ due to the extremely high frequency of the schooling pattern). These four stages are organised in Table 4.1. The transition from the ‘swarm stage’ to the ‘stable school stage’ can last longer than 500 generations in fast-predator situations ($PS > 1.8$), but the ‘stable school stage’ can be reached consistently before the 1000th generation.

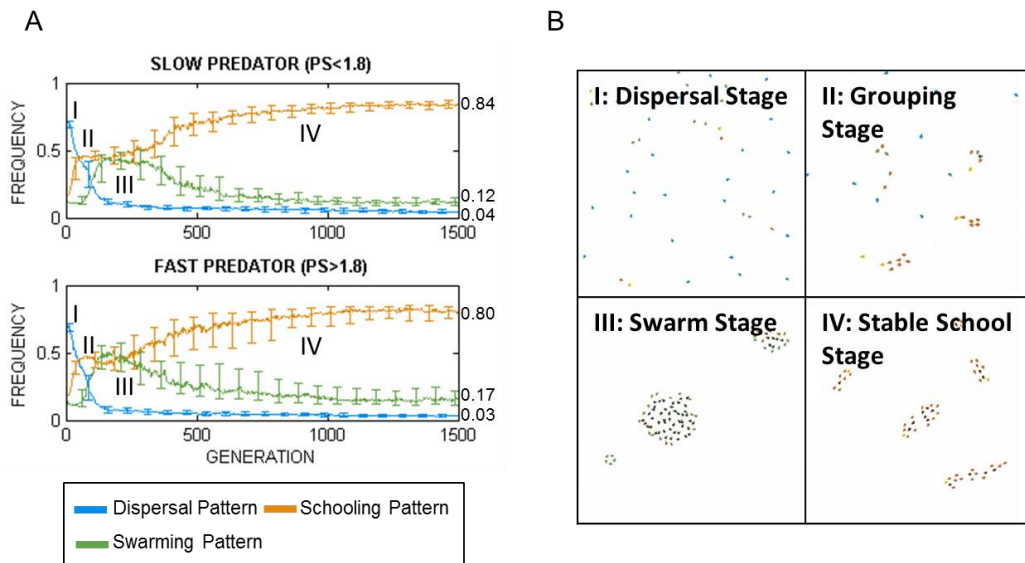


Figure 4.2: Emergent Patterns in Evolution

The curves in subfigure A plot the medians of the associated frequencies among the simulation instances, where the bars show the interquartile ranges. It displays that the emergent patterns in an evolutionary trajectory consistently form four stages sequentially: dispersal stage (I), grouping stage (II), swarm stage (III), and stable school stage (IV), irrespective of a slow predator ($PS < 1.8$) or a fast predator ($PS > 1.8$). Subfigure B provides a visualisation of these four stages.

Table 4.1: The Four Evolutionary Stages

Sequence	Name	Major Collective Pattern
Stage I	Dispersal Stage	The Dispersal Pattern
Stage II	Grouping Stage	The Schooling Pattern
Stage III	Swarm Stage	The Swarming Pattern
Stage IV	Stable School Stage	The Schooling Pattern

4.3.2 Transition of Adaptive Strategies

Evolution at the individual level is a gradient process of selection and adaptation among slightly variant strategies, that is, NEAT neural networks, so that the prey population in each generation is relatively homogeneous and the positional distributions among individuals are similar (Figure 4.3A). In other words, there is no considerable subgroup, such as permanent leaders of a school, observed in the simulations. During an evolutionary trajectory, the adaptive strategies in a prey population are developed and replaced sequentially, which lead to the emergence of the four stages at the population level (Figure 4.3B). The development and transitions of these strategies are discussed as follows.

Within the first ten generations, since hard punishment is applied to the overlapping behaviour, those agents prefer to overlap their bodies with neighbours, by the attraction behaviour, are eliminated quickly. Hence, it is observed that an offspring will carry on the preference of repulsion (Figure 4.4A), which causes the early stage to be full of lone rangers (R) (Figure 4.3A). This ‘avoidance strategy’ (Figure 4.4A) is an adaptation to the overlap-free constraint. From now on, the overlapping times are measured less than 2 times per agent per 10000 steps ($T_i^O/T^H < 2 \times 10^{-4}$), and hence prey agents will develop their strategies only based on the survival fitness, as their eaten times.

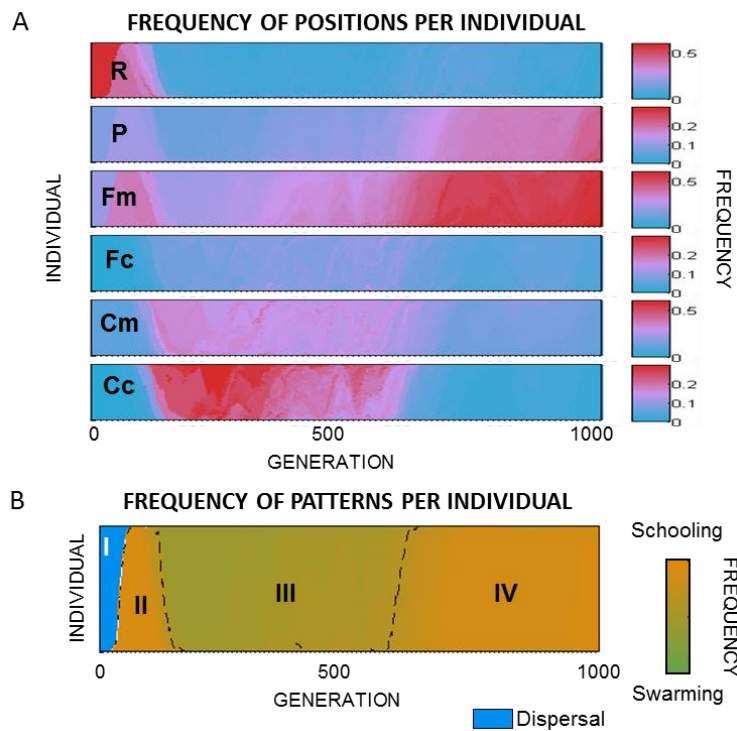


Figure 4.3: Positional Frequencies at the Individual Level

Subfigure A shows the evolution of the six positional frequencies at the individual level. In each heat map, there are 100 rows, each of which represents one prey's positional frequency. It can be observed that the prey population in every generation is generally homogeneous without considerable evolutionary branches. Subfigure B shows the frequency of patterns per prey agent by combining the corresponding positional frequencies, where the blue colour is used if the frequency of 'ranger' is greater than 50%. This panel can be connected to the four stages observed at the population level. Moreover, it shows each of these stages is composed of relatively homogeneous prey agents. These panels are plotted based on a representative simulation given $PS=1.8$. The qualitative results given other predator speeds are the same.

The first transition observed in the present simulations is that aggregated prey will invade isolated ones (Figure 4.2 and Figure 4.3, from I to II). In the dispersal stage, it is measured that being a pioneer of a school (P) has the lowest positional risk, as well as those followers (Fm) also incur lower risk than lone rangers (R) (Figure 4.5A). As analysed by Turner & Pitcher (1986), when the risk of being in groups is less than that of being in isolation, evolution will favour prey which live in groups. The simulations demonstrated that prey evolve to facilitate group formation by pursuing the neighbours ahead of it (being a follower) and being repelled by the rearward neighbours (being a

pioneer) (Figure 4.3A and Figure 4.4B). This ‘pursuit-escape strategy’, similar to what observed in locust aggregation (Romanczuk et al., 2009), then leads to a higher frequency of the schooling pattern and a lower frequency of the dispersal pattern at the population level, and converts the dispersal stage into the grouping stage (Figure 4.2A and Figure 4.3B, from I to II). The transition from isolated prey to gregarious prey has been demonstrated in many previous works such as Turner & Pitcher (1986), Reluga & Viscido (2005) and Olson et al. (2013), and the causation has been known as the ‘dilution effect’ (Turner & Pitcher, 1986; Krause & Ruxton, 2002), that is, the larger the group an agent is in, the smaller chance it will be the victim of one predatory attack, which is known as the dilution effect.

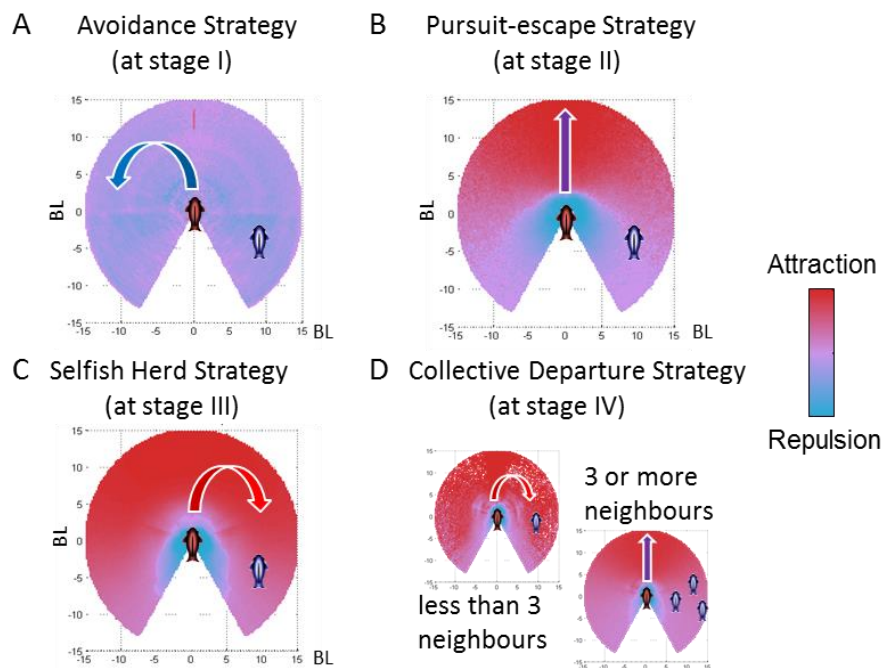


Figure 4.4: Adaptive Strategies in Evolution

The adaptive strategies of prey agents are visualised along the four stages. About the 'collective departure strategy', only the tactic when being on the margin of a swarm (C_m) is displayed, since it is the most important tactic of this strategy. Neighbours in the red range will trigger the focal fish's attraction behaviour, in the blue range will trigger its repulsion behaviour, and hence, in the purple range will cause a parallel movement mediated by repulsion and attraction. The white area is outside the sensory range. These panels are plotted through an input-output mapping of the evolved NEAT networks given $PS=1.8$. The qualitative results given other predator speeds are the same.

The second transition observed in the present simulations is that a swarming pattern will replace a schooling pattern if the marginal prey are available to enter the safe centre (Figure 4.2 and Figure 4.3, from II to III). At the grouping stage, prey agents flock into moving groups by the ‘pursuit-escape strategy’. Under this situation, it is measured that pioneers (P) become more at risk than are followers (Fm and Fc) (Figure 4.5B). Agents thus evolve to reduce their frequencies of being pioneers by the preference of being attracted to the rearward neighbours (from Figure 4.4B to Figure 4.4C). Due to the lack of pioneers, the schooling groups are also converted to disordered swarms (Figure 4.3A), which scenario has been described and considered as the ‘paradox of individuality’ in Parrish & Edelstein-Keshet (1999). Since the centre of these swarms (Cc) is the safest position in the present model (Figure 4.5C), prey agents keep evolving to be attracted to all of its neighbours, except extremely close ones (Figure 4.4C), so that the probability of moving into the interior of a crowd is maximised (Figure 4.6A, from II to III). As a result of this adaptation, prey agents form few huge stationary swarms at the population level, as visualised in Figure 4.2B.

So far, the evolutionary trajectory in the present simulation is consistent to the prediction in Hamilton (1971) and similar to the demonstrations in Viscido et al. (2002), Reluga & Viscido (2005), Olson et al. (2013) and so on. Since this transition has been well known as the ‘selfish herd scenario’ (Hamilton, 1971), the adaptive strategy to cause this transition is termed ‘selfish herd strategy’.

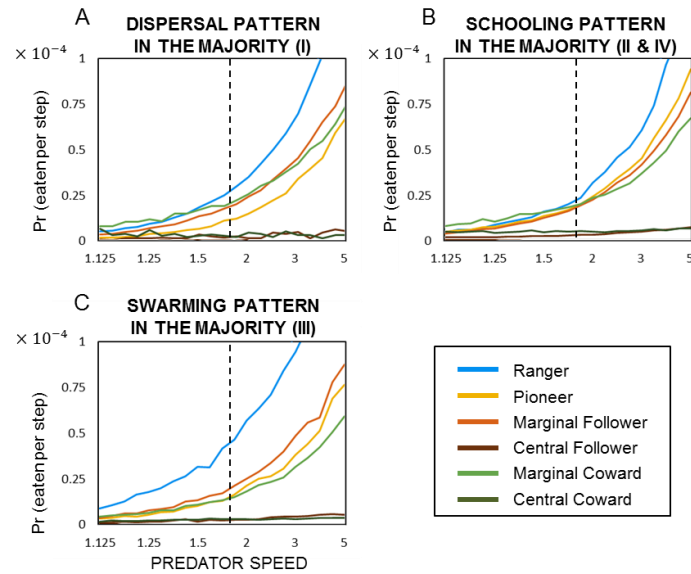


Figure 4.5: Frequency-dependent Risk Distribution

The positional risk, defined as the probability of being eaten per step at a certain position, is frequency-dependent, that is, depending on the frequencies of the six positions (or the three patterns, in general). For example, when schooling is in the majority, that is, the frequency of the schooling pattern exceeds 50%, pioneers are more at risk than marginal followers. However, when the majority is a dispersal pattern or a swarming pattern, the risk of pioneers is less than marginal followers. It is worth mentioning that both schooling and swarming patterns are self-organised. That is to say, the higher the frequency of a schooling pattern, the safer is the marginal position of a school (P and Fm), which phenomenon also exists in the swarming pattern. Additionally, being a lone ranger (R) is always dangerous and being in the protected centre (Fc and Cc) is extremely safe.

Prevalent spread of the ‘selfish herd strategy’ then cause those swarms denser and denser as more agents prefer to occupy the central position (Figure 4.7). In previous models, it will result into a compact swarm where physical overlaps among prey agents are frequent (Olson et al., 2013; Reluga & Viscido, 2005). However, because overlap is specifically forbidden in the present model, the centre of a swarm will finally become too compact for marginal agents to enter. For example, when the average NND (nearest neighbour’s distance) among swarming prey is less than 4 BL in the simulation (Figure 4.7), it is measured that the probability of entering the swarm centre decreases gradually (Figure 4.6A). In this situation, adopting ‘selfish herd strategy’ cannot reduce a marginal agent’s predation risk since entering the centre of a swarm becomes extremely

difficult. Even worse, this agent will keep staying at the periphery of its swarm, bearing the predatory attacks towards the group, and providing those central members a risk-free position (Figure 4.5C).

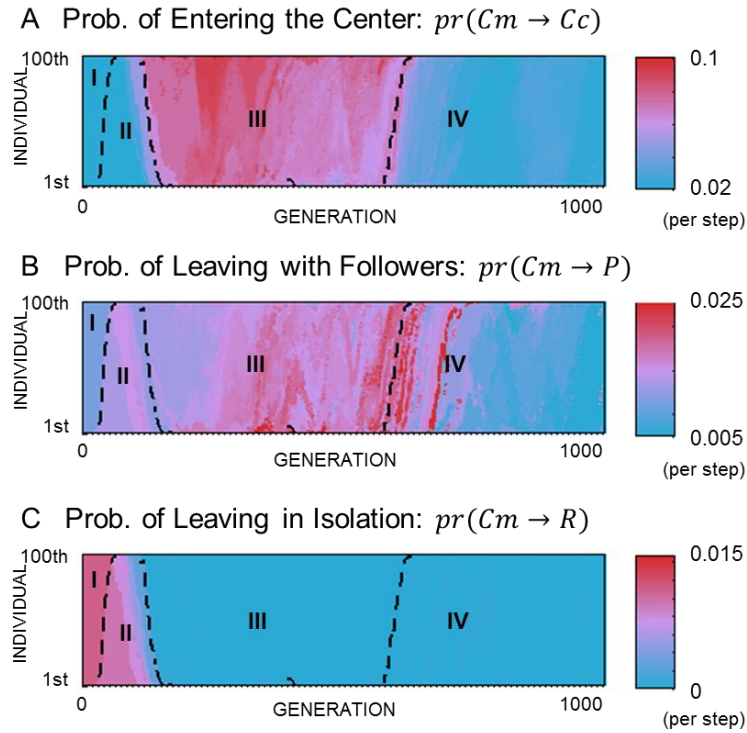


Figure 4.6: Probabilities of Positional Changes

The following three probabilities of positional changes are measured at the individual level. Panel A shows the probability to enter the swarm centre (Cc) from the swarm margin (Cm). Panel B shows the probability to leave the swarm margin as a pioneer with companions. Panel C shows the probability to leave the swarm margin as an isolated ranger. The broken lines divide the evolutionary trajectory into the four stages as shown in Fig 4.2. The probabilities are measured based on a simulation given $PS=1.8$. Similar distributions of these probabilities can be found in other simulations.

At this point, the third evolutionary transition is originally demonstrated by the present work: the schooling pattern will replace the swarming pattern if marginal prey are unavailable to enter the safe centre (Figure 4.2 and Figure 4.3, from III to IV). At the late swarm stage, since the agent on the border of a swarm is difficult to reduce its predation risk by moving into the crowded centre (Figure 4.6A), prey then develop a tricky strategy, as leaving the compact swarm together (Figure 4.6B), to earn relative

fitness by exposing those interior neighbours and sharing the risk with the exposed ones (analysed in the latter subchapter). As the positional change from a marginal coward (Cm) to a ranger (R) seriously aggravates the predation risk (Figure 4.5C), a marginal coward evolves to play this trick only if it has sufficient companions (three in the present model) (Figure 4.4D) to avoid being a long ranger (Figure 4.6C). This adaptive strategy is named 'collective departure strategy'. As more agents adopt this strategy and avoid being on the periphery of a swarm, these swarms will finally be replaced by schooling groups at the population level (Figure 4.2). At the same time, the frequency of central positions decreases to an extremely low level (Figure 4.7).

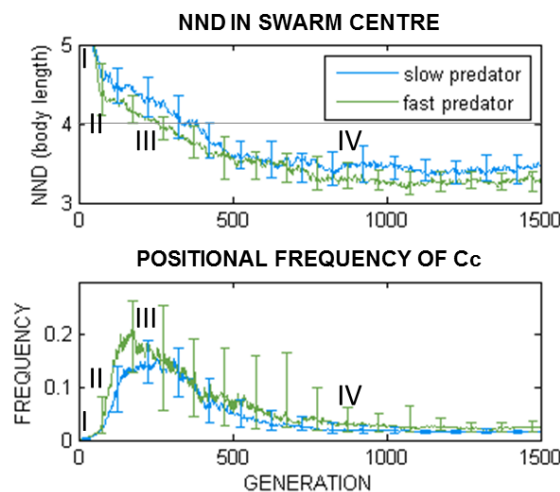


Figure 4.7: Density and Frequency of Swarm Centre

The decrease of NND (the nearest neighbour's distance) shows that the 'selfish herd strategy' is crowding the swarm centre and increasing the level of crowd density in the swarm centre. Then, since a growing number of prey agents develop 'collective departure strategy' to leave the swarm border, the frequency of the 'central coward' position decreases until there is no central position in swarms. In particular, fast predators ($PS > 1.8$) will cause a denser swarm compared to slow predators ($PS < 1.8$).

The 'collective departure strategy' (denoted as CDS) can be sophisticated in order to adapt to different surroundings. As listed in Figure 4.8, the most important tactic is that when a CDS agent is on the periphery of a swarm (Cm), it will leave the border only when a few companions (three or more) are behind. Otherwise, it will turn back to the

swarm border to prevent itself from being isolated. Comparatively, when a CDS agent is on the boundary of a school (P and Fm), it prefers to maintain its position even if the companions are less than three, to prevent itself from falling behind the moving group. When a CDS agent becomes a ranger (R), it is attracted to any apparent neighbours. When being in the protected centre (Fc and Cc), it moves in coordination with neighbours to narrow the distance between itself and adjacent ones.

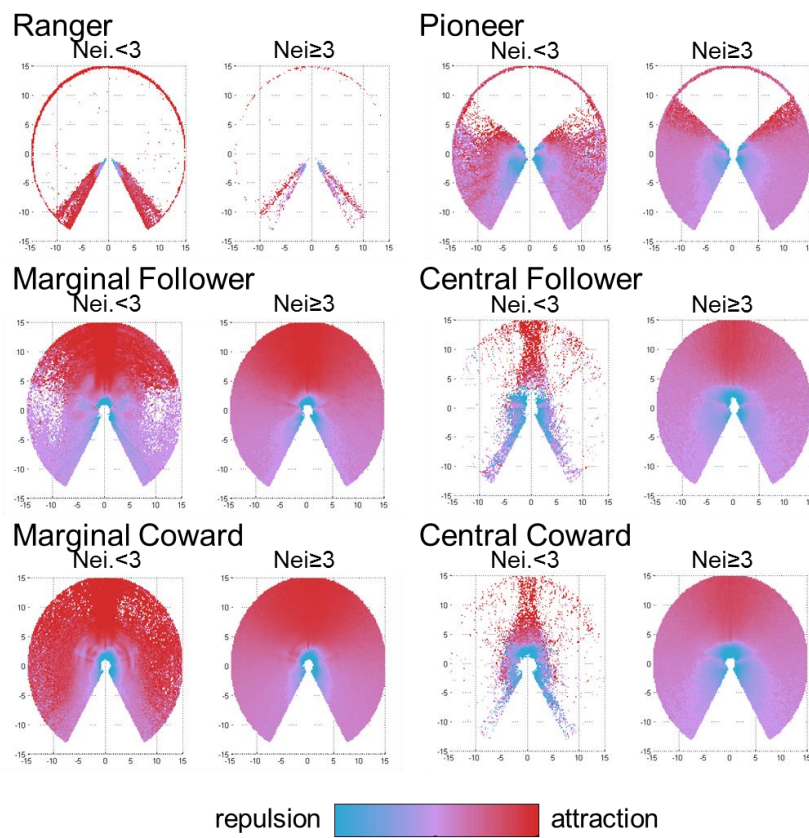


Figure 4.8: CDS's Adaptation to Different Positions

It is observed that the 'collective departure strategy' responds to prey neighbours variously at different positions. For example, when a CDS prey is schooling, it keeps aligning with its neighbours even if they are less than three. Comparatively, a CDS prey at the swarm border only aligns with its neighbours if they are more than three. This strategy has not been reported in previous works and is originally demonstrated by the proposed model with an open-ended search space.

4.4 Analysis

When being on the boundary of a compact swarm, a prey adopting SHS (selfish herd strategy, Figure 4.3C) will keep staying on the periphery, instead of entering the centre. In contrast, a prey adopting CDS (collective departure strategy, Figure 4.3D) will leave the border with sufficient companions. The simulation has demonstrated that CDS can replace SHS and finally reaches the stable school stage (Figure 4.2), which reason has been described as adding predation risk to those exposed neighbours. This issue is investigated here through a game-theoretic analysis, to answer the last two research questions in this chapter.

4.4.1 Collective Departure Scenario

In a population of N prey, given that there are N_S schooling individuals, hence, $N - N_S$ individuals are in disordered swarms. In a swarm, there are two positions, as marginal cowards (Cm) and central cowards (Cc), bearing the predation risk (probability of being eaten per step) X^{Cm} and X^{Cc} , respectively. In a school, three positions were categorised, as pioneers (P), marginal followers (Fm), and central followers (Fc). Here these positions are simplified into one, as pioneers (P), since the risk of marginal followers (Fm) is relatively similar to that of pioneers (P) (Figure 4.5), and the central position (Fc) of the elongated groups is rare (Figure 4.1B). The positional risk of pioneers is denoted as X^P , which represents the risk of being in a school thereafter. It should be noted that a prey's fitness is the survival probability per predatory hunt, which is different from the positional risk.

Given the event that prey i is eaten at a certain step as E_i , the probability of this event, $pr(E_i)$, then depends on this prey's position at this step, which value is the associated

positional risk. Comparatively, the survival probability of prey i can be represented as $1 - pr(E_i|E)$, where E is the event of a successful hunt at a certain step, or equivalently, the event that at least one prey is eaten at a certain step. The probability of event E can be represented by

$$pr(E) = pr(E_1 \cup E_2 \cup \dots \cup E_N). \quad (4.1)$$

Since the predator is set catching one prey per hunt in the present model, the probability of two prey being eaten at the same step is zero, or to say, prey individuals being eaten are mutually exclusive events:

$$\forall i \neq j, pr(E_i \cap E_j) = 0. \quad (4.2)$$

Hence, the probability of a successful hunt at a certain step, $pr(E)$, is a simple summation of all prey's positional risks:

$$pr(E) = \sum_{i=1}^N pr(E_i). \quad (4.3)$$

The survival probability of prey i , as the probability prey i not to be eaten given a successful hunt, then can be represented by

$$u_i = 1 - pr(E_i|E) = 1 - \frac{pr(E_i \cap E)}{pr(E)} = \frac{pr(E_i)}{pr(E)} = \frac{pr(E_i)}{\sum_j pr(E_j)} \quad (4.4)$$

where, based on equations (4.2) and (4.3),

$$\begin{aligned} pr(E_i \cap E) &= pr[E_i \cap (E_1 \cup E_2 \cup \dots \cup E_N)] = pr[(E_i \cap E_1) \cup (E_i \cap E_2) \cup \dots \cup (E_i \cap E_N)] \\ &= pr(E_i \cap E_i) = pr(E_i). \end{aligned}$$

If a peripheral prey of a compact swarm plays SHS, it then keeps its position at the swarm border (Cm) and bears the corresponding predation risk, X^{Cm} . As derived above,

its survival probability is one minus $pr(E_i)$ over $\sum_j pr(E_j)$, where $pr(E_i) = X^{Cm}$ as its positional risk. Since there are N_S schooling prey, the summation of all prey's positional risks is

$$\sum_{j=1}^N pr(E_j) = N_S X^P + M X^{Cm} + (N - N_S - M) X^{Cc} \quad (4.5)$$

where M denotes the number of marginal cowards (Cm), which value will be estimated latter, so that $N - N_S - M$ is the number of central cowards (Cc) (Figure 4.9). Since X^{Cc} is nearly zero (Figure 4.5), the probability can be estimated as

$$pr(E) \cong N_S X^P + M X^{Cm} . \quad (4.6)$$

Hence, the survival fitness of adopting SHS at the swarm periphery is

$$u_{SHS} = 1 - \frac{X^{Cm}}{N_S X^P + M X^{Cm}} . \quad (4.7)$$

To qualitatively set the value of M , as the number of marginal cowards (Cm), it is assumed that the $N - N_S$ swarming prey form a round compact swarm, which area is $N - N_S BL^2$ (Figure 4.9). Hence, the radius of this swarm is

$$\pi r^2 = N - N_S \Rightarrow r = \sqrt{(N - N_S)/\pi} . \quad (4.8)$$

Then, the number of marginal cowards can be calculated through the area of this swarm's margin, which width is $1BL$ (Figure 4.9): $M = \pi r^2 - \pi(r - 1)^2$. Since $r = \sqrt{(N - N_S)/\pi}$, it can be derived that

$$M = \pi r^2 - \pi(r - 1)^2 = 2\pi r - \pi = \sqrt{4\pi(N - N_S)} - \pi . \quad (4.9)$$

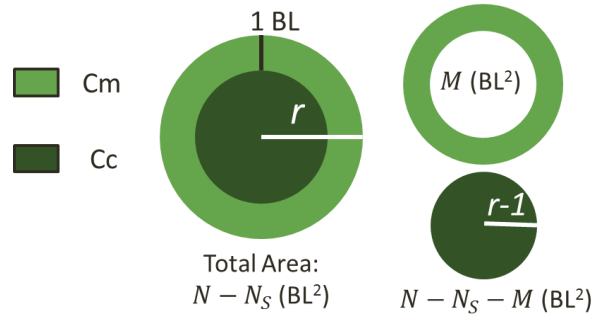


Figure 4.9: An Idealised Circular 2D Swarm

To estimate the number of marginal cowards (Cm) in a swarm, it is assumed that the swarm is an ideal circular group which area is the sum of swarming prey's body sizes, that is, $1BL^2$. Then, given marginal cowards form a margin with the width $1BL$, the amount of prey in this margin can be estimated as in equation (4.9).

Instead of staying on the periphery of a swarm, a marginal prey adopting CDS will leave the swarm and attracts a few followers, which then results in another survival probability: $u_{CDS} = 1 - pr(E'_i) / \sum_j pr(E'_j)$, where $pr(E'_i) = X^P$ as this prey has changed its position from a marginal coward to a pioneer. Given the number of this prey and its companions as n , since n swarming prey, including itself, now become schooling, the new environment consists of $N - N_S - n$ prey in swarms and $N_S + n$ prey in schools, and the summation of all prey's positional risks becomes

$$\sum_j pr(E'_j) = (N_S + n)X^P + M'X^{Cm} + (N - N_S - n - M')X^{Cc} \cong (N_S + n)X^P + M'X^{Cm} \quad (4.10)$$

where, similar to the derivation in equations (4.8) and (4.9),

$$M' = \sqrt{4\pi(N - N_S - n)} - \pi.$$

Therefore, the survival probability of adopting CDS and departing from the swarm periphery is

$$u_{CDS} = 1 - \frac{X^P}{(N_S + n)X^P + M'X^{Cm}}, \quad (4.11)$$

According to equations (4.7) and (4.11), the parameters which affect the values of u_{CDS} and u_{SHS} are N , n , N_S and the X^P/X^{Cm} ratio, where N is 100 by the model setting and n is observed around 8 from the simulation. (The parameter n must be greater than four since a CDS agent only leaves the periphery with three or more companions as shown in Figure 4.4D, and there can be more companions outside its sensory range.) Therefore, as drawn in Figure 4.10A, the relation between u_{CDS} and u_{SHS} only depends on the frequency of schooling pattern (N_S/N , as the x-axis) and the X^P/X^{Cm} ratio in the environment (as the y-axis). When $u_{CDS} > u_{SHS}$, which means adopting CDS can gain better fitness than SHS for a marginal coward (Cm), the evolution should drive more prey to develop CDS with generations and increase the frequency of the schooling pattern at the population level (Figure 4.10A). On the other hand, when $u_{CDS} < u_{SHS}$, adopting CDS and leaving the margin of a swarm is less beneficial, and hence prey should evolve to adopt SHS and lead to the collective swarming pattern (Figure 4.10A).

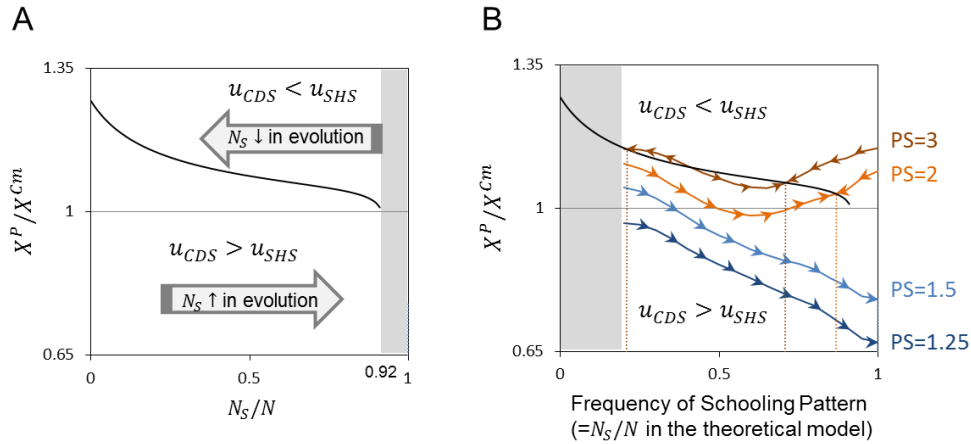


Figure 4.10: Adaptive Dynamic of CDS

The black curve is the theoretical upper bound for CDS to be more adaptive than SHS, by setting $N = 100$ and $n = 8$. Since n is set to 8, the condition that $N_S > 92$, as the grey area in panel A, is neglected. In panel B, the X^P/X^{Cm} ratios measured from the simulation are compared with the theoretical borderline, where there is no experimental data collected in the grey area. Panel B explains the different adaptive dynamics observed in the agent-based simulations. In slow-predator situations ($PS < 1.8$), the environmental ratio is always lower than the upper bound, which implies pure CDS is an evolutionarily stable strategy. In fast-predator situations ($PS > 1.8$), the environmental ratio exceeds the upper bound if the proportion of schooling prey is too large, which implies a mixed strategy of CDS and SHS, to let the frequency of schooling less than 1, is evolutionarily stable.

By comparing the measured X^P/X^{Cm} ratio in the simulations to the theoretical boundary, it is evident that in slow-predator situations ($PS < 1.8$), the environmental X^P/X^{Cm} ratio is always located in the area where $u_{CDS} > u_{SHS}$ (Figure 4.10B). In other words, in slow-predator situations, CDS is always more beneficial than SHS for a marginal prey, despite the frequency of the schooling pattern. Such result indicates that, given a slow predator, CDS dominates SHS, and hence pure CDS is evolutionarily stable. The evolutionary dynamic is that, the frequency of the schooling pattern increases with generations and, theoretically, reaches 100% because CDS is always more beneficial to marginal cowards than SHS.

On the contrary, in fast-predator situations ($PS > 1.8$), the ratio X^P/X^{Cm} can go above the theoretical borderline when the frequency of schooling pattern is extremely high (Figure 4.10B). Prey should evolve to adopt a mixed strategy of CDS and SHS, to decrease the frequency of the schooling pattern and to let the environmental ratio equal the upper bound. This mixed strategy is evolutionarily stable since when the proportion of CDS in the population increases, the frequency of the schooling pattern also increases and the environmental ratio then exceeds the upper bound, which causes CDS inferior to SHS. Similarly, the increasing proportion of SHS in the population also causes SHS inferior to CDS. Compared with the slow-predator situation, where pure CDS is evolutionarily stable, the analysis has well explained why the frequency of the schooling pattern at the final stage decreases gradually when $PS > 1.8$ (Figure 4.1).

4.4.2 Exceptions of Collective Departure Scenario

In contrast to the above collective departure scenario, many species of animals still exhibit ‘selfish herd strategy’ and form disordered swarms in front of predators (Vulinec, 1990). This divergence can be due to the following three conditions.

The first condition is that the environmental X^P/X^{Cm} ratio, as the degree of predators’ preference to hunt schooling groups, is higher than the theoretical bound. In this case, adopting CDS is less beneficial than adopting SHS so that evolution cannot favour CDS and the corresponding schooling pattern (Figure 4.10A). In the present model, where the predator is set always chasing the nearest prey, the X^P/X^{Cm} ratio is observed to increase along the predator speed (Figure 4.10B). Hence, when the predator speed is sufficiently high, the large X^P/X^{Cm} ratio will let the swarming pattern be evolutionarily stable. For example, when $PS = 3$, there can be an evolutionarily stable strategy to cause the swarming pattern in the majority (Figure 4.10B). It should be noted that the above relationship between the predator speed and the risk ratio is just a modelling feature by setting the predator always chasing the nearest prey. The essential factor is the risk ratio distributed by the predator’s feeding preference.

The second condition is that the central position is also dangerous. In this case, leaving the periphery and exposing interior neighbours cannot harm others’ fitness. Similar to the derivation in the previous section, letting $X^{Cc} = X^{Cm}$, the probability of being eaten in a hunt then becomes

$$u_{SHS} = 1 - \frac{X^{Cm}}{N_S X^P + (N - N_S) X^{Cm}}, \quad (4.12)$$

$$u_{CDS} = 1 - \frac{X^P}{(N_S + n)X^P + (N - N_S - n)X^{Cm}} \quad (4.13)$$

where $u_{CDS} > u_{SHS}$ if and only if $X^P/X^{Cm} < 1$. The derivation is that

$$\begin{aligned} u_{CDS} &= 1 - \frac{X^P}{(N_S+n)X^P+(N-N_S-n)X^{Cm}} > u_{SHS} = 1 - \frac{X^{Cm}}{N_S X^P+(N-N_S)X^{Cm}} \\ \Rightarrow X^P [N_S X^P + (N - N_S)X^{Cm}] &< X^{Cm} [(N_S + n)X^P + (N - N_S - n)X^{Cm}] \\ \Rightarrow (X^P - X^{Cm}) [N_S X^P + (N - N_S - n)X^{Cm}] &< 0 \end{aligned}$$

where $N_S X^P \geq 0$, and $(N - N_S - n)X^{Cm} \geq 0$ because $N - N_S - n$ is the number of swarming prey after the departure of a CDS prey and its companions. Hence, $X^P/X^{Cm} < 1$ is derived. As X^P represents the risk of a schooling prey and $X^{Cm} = X^{Cc}$ is the risk of a swarming prey, this condition means when the group benefit of schools is higher than that of swarms.

According to the measured positional risks in fast-predator situations (Figure 4.6, also Figure 4.4C), the X^P/X^{Cm} ratio is greater than 1 when $N_S/N < 50\%$, or to say, when the swarming pattern is in the majority. It implies ‘collective departure strategy’ cannot invade ‘selfish herd strategy’ if there is no biased risk within a swarm. In other words, pure ‘selfish herd strategy’ should be evolutionarily stable in the case of dangerous centres. In nature, central positions may really be unsafe, since natural predators usually consume multiple prey continuously during a hunt (Parrish, 1991), which can indirectly reduce the utility of ‘collective departure strategy’.

The third condition is that squeezing into the centre remains an option. In the present model, a marginal prey cannot enter the centre unless there is enough space to avoid overlaps. It may not be the case of some species, like in a wide variety of insects

(Vulinec, 1990). For those species, a marginal individual is possible to squeeze into the centre by pushing away its neighbours. In this case, the predation risk among swarming members is equal, as pX_{Cm} , where $0 < p < 1$ is the probability of being pushed to the periphery. Similar to the derivation and explanation of the second condition, ‘collective departure strategy’ is more beneficial than ‘selfish herd strategy’ if and only if $X^P / X^{Cm} < p$ and hence pure ‘selfish herd strategy’ should be evolutionarily stable.

The detailed derivation of the above statement is as follows:

$$\begin{aligned}
u_{CDS} &= 1 - \frac{X^P}{(N_S + n)X^P + (N - N_S - n)pX^{Cm}} > u_{SHS} = 1 - \frac{pX_{Cm}}{N_S X^P + (N - N_S)pX_{Cm}} \\
&\Rightarrow X^P [N_S X^P + (N - N_S)pX^{Cm}] < pX^{Cm} [(N_S + n)X^P + (N - N_S - n)pX^{Cm}] \\
&\Rightarrow (X^P - pX^{Cm}) [N_S X^P + (N - N_S - n)pX^{Cm}] < 0 \Rightarrow X^P / X^{Cm} < p < 1. \quad (4.14)
\end{aligned}$$

As explained in the derivation of the second condition, $N - N_S - n \geq 0$ because it is the number of remaining cowards in the swarm after the collective departure of n prey.

4.5 Discussion

The findings of this research reveal that schooling can evolve under a selection pressure at the individual level, through the competition for safer positions within a group. As a complement to the selfish herd story (Hamilton, 1971), it is demonstrated that: when a selfish herd finally becomes too dense to provide refuge to outer prey, ‘collective departure strategy’, as to demolish others’ refuge, will invade ‘selfish herd strategy’ and reach its evolutionary stability. This adaptation then leads to the emergence of schooling pattern, even if the group benefit may decrease. Compared with explanations based on

group benefit, this interpretation may be more consistent with the principle of natural selection.

In nature, schooling fish is observed to form compact groups under predatory threats (Partridge, 1982; Couzin & Krause, 2003), in which the unsuccessful attempt of marginal followers to enter the protected centre is also reported in the early literature (Springer, 1957). It is also informed by Iain D. Couzin that the Atlantic silverside (*Menidia menidia*) and the sunbleak (*Leucaspius delineatus*) exhibit a character similar to the 'collective departure strategy', that fish leaving a group will return if not followed, but if followed by a sufficient number of neighbours will continue to leave. These observations may be evidence to support the collective departure scenario, and leave hints for further inspection on the proposed adaptive strategy of schooling fish.

The analysis shows a potential to predict the equilibrium of other group-living animals in different conditions. However, it should be emphasised that the model simplifies evolution into the competition among prey individuals by the setting that the predator is unbeatable but unable to influence the amount of prey population. It is to describe the situation of gregarious fish in open waters, where predators are much stronger than the prey and the prey is abundant (Parrish, 1991). Regarding other predator-prey interactions, the competition between prey and predators may also play a critical role in their evolutionary dynamic. In this case, further extension of this collective departure scenario may be necessary.

CHAPTER V

COEVOLUTION BETWEEN PREY FISH AND PREDATORS

This chapter addresses the third main research question, about the influence of predators' adaptation to the evolution of schooling, by investigating the four specific research questions:

- How to model the behavioural coevolution between predators and prey?
- Are there evolutionarily stable states in the coevolution system?
- What are the adaptive strategies of predators and prey in a stable state?
- Are predatory fish and cetaceans really cooperative?

Based on the collective departure scenario proposed in Chapter IV, a simplified model is built for the behavioural coevolution between prey fish and their predators. The model demonstrates that this coevolution system contains evolutionarily stable states (also termed 'stable states' or 'ESSs' thereafter). These ESSs are reachable from other states, and once any of these states are attained, no small proportion of predators or prey can gain excess fitness by another strategy. Generally, in a stable state, prey fish form the schooling pattern and predatory fish exhibit the tactic of 'marginal predation'

(Parrish, 1991), that is, feeding those marginal prey rather than the central ones. An exception is that when the predators are much stronger than the prey (which is described in the following sections). In this case, attacking the central prey becomes the adaptive hunting strategy in a stable state, by which prey are more likely to form stationary swarms but the schooling pattern is still in the majority. As discussed in Chapter 5.5, these outputs are consistent to the natural predator-prey interaction in open waters. Therefore, it is inferred that certain features of the hunting tactics adopted by predatory fish and cetaceans can be explained by evolutionary selfishness, or to say, by individual selection without additional mechanisms.

This chapter reveals some novel viewpoints on the behavioural coevolution between prey fish and their predators. First, fish schools can evolve even if their predators' feeding preferences are also adaptive. Secondly, the appearance of marginal predation in a wide range of predatory vertebrates can be an adaptation in evolution. Thirdly, the various hunting strategies of predatory fish and cetaceans in the pelagic ocean can be illustrated by evolutionary selfishness.

5.1 Background

The interaction between gregarious fish and their predators in the open ocean is a striking phenomenon. At the prey side, vigilant fish form a collective schooling pattern in response to the predatory attacks (Magurran & Pitcher, 1987). At the predator side, dramatic hunting strategies have been developed by many species of predatory fish and cetaceans. For example, sailfish and swordfish wield their elongated bills to slash at a prey aggregate (Domenici et al., 2014), thresher sharks lash their tails to whip a fish group (Oliver et al., 2013), dolphins herd prey fish into a milling baitball (Vaughn-

Hirshorn et al, 2013), and humpback whales expel air bubbles to centralise prey fish for its feeding (Wiley et al., 2011).

At present, advanced studies of this interaction are biased to the prey side. For example, self-organising models have explained how the schooling pattern can emerge from fish's local interactions (Aoki, 1982; Couzin et al, 2002). The survival benefit of this formation has also been reported from many aspects, like the dilution effect, confusion effect and information transfer effect (Krause & Ruxton, 2002). About the adaptive dynamic in evolution, the model in Hamilton (1971) has explained the flocking tendency under individual selection. Following this work, various agent-based models have been proposed to demonstrate potential evolutionary trajectories of the collective motion when fish confront a survival hazard (Ward et al., 2001; Wood & Ackland, 2007; Olson et al., 2013).

However, these evolutionary models, as well as the work in Chapter IV, all simulated the evolution of prey agents by a predefined distribution of the predation risk. This distribution is usually drawn by a prey's domain of danger (Hamilton, 1971), or equivalently, by a predator which always chases the nearest prey and only feed one prey per hunt. Although an evolvable predator was designed in Olson et al. (2013), its adaptation is from random walks to chasing the nearest prey. Unfortunately, in the marine world, this generalisation of predation risk is not always suitable (Hamilton, 1971; Parrish, 1991). For example, a wide range of primary predators in the pelagic ocean have developed the preference to attack those prey at the central position (Simila & Ugarte, 1993; Oliver et al., 2013; Domenici et al., 2014). Under this situation, is prey fish's schooling pattern still evolutionarily stable?

Obviously, both the prey and the predators have undergone the selection and adaptation. As predators' feeding preferences should drive the evolution of prey aggregation, prey's collective behaviours should also affect the development of predators' hunting tactics. This reciprocal influence forms a coevolution system of the behavioural strategies. However, related works to simulate this behavioural coevolution are rare at present. Few attempts to model this coevolution system seem to be limited and incomplete due to the considerable difficulty of representing potential hunting strategies. For example, Olson et al. (2016b) simulated the adaptation of predators by evolving the hunting path, which output was only a preference between isolated prey and aggregated prey. These simple tactics carry little information about the sophisticated behaviours of marine predators.

To address this difficulty, this work formulates the predators' hunting strategies from an ex post view. The model abandons mimicking predators' spatial movements. Instead, since all hunting attempts eventually end in feeding, a strategy of predators can be treated as a risk distribution on different positions of a prey aggregate. Two advantages of this mapping are as follows. First, the various hunting behaviours, which seem impossible to be considered comprehensively, are projected to certain distributions of positional risks. Through this projection, the strategy set at the predator side can be well defined and hence, the analysis of evolutionary stability in the system becomes practical. Secondly, the connection between natural hunting strategies and their associated risk distributions, as the most arbitrary part of this mapping, is independent from the theoretical analysis and can be investigated by further ecological experiments.

5.2 Model

The proposed model in this chapter is an extension of the findings in Chapter IV. In other words, this model simulates the adaptations of predators and prey based on the preconceived knowledge: collective departure scenario. The reason that the simplification is made rather than using the spatial-explicit model in Chapter III is because the spatiotemporal simulation cannot withstand the scope of the following experiments, for its computational time.

The model in this chapter can be divided into three components: viz. the adaptation of prey, the emergent pattern through a self-organising mechanism, and the adaptation of predators, where the self-organising part is relatively tedious. For a reader-friendly layout, the explanation of the self-organising mechanism is left in Chapter 5.2.3 for a further interest.

5.2.1 Model Framework

The former chapter has shown that the schooling pattern of prey fish can be evolutionarily stable given that entering the central position is unavailable. It has been demonstrated and analysed that in a wide range of environments, the collective departure strategy, as leaving the periphery of a swarm and being a schooling prey, is more adaptive than the selfish herd strategy, which tactic is equal to staying at the periphery and protecting those central ones. Hence, the swarming pattern is converted to the schooling pattern by the adaptation of collective departure. This dynamic was referred to as the collective departure scenario. (Details are provided in Chapter IV)

However, the influence of the biased risks within a school was omitted in the analysis, because the rule-based predator in the simulation leads to an insignificant difference of the risks on a school's internal positions. This simplification cannot be universal when other distributions of predation risk are drawn. According to the scenario stated in Parrish & Edelstein-Keshet (1999), this model extends the collective departure scenario by an additional transition: schooling prey can be replaced by swarming prey if the predation risk biases to the front position of a school significantly. Under this situation, all schooling prey prefer to be followers so that no one can lead the group. Based on these two scenarios, the self-organising mechanism of the present model is designed. That is to say, moving schools can become stationary herds if every individual shirks from being a pioneer. At the same time, stationary herds can be replaced by moving schools if every individual adopts the collective departure strategy.

In the model, a prey's strategy (c_i) is a set of probabilities of its positional changes, and a predator's strategy (x_j) is the feeding preference among prey's positions. Based on the positional changes in the prey population, the collective pattern, D , emerges through the self-organising mechanism. A prey's survival fitness is reflected from its positional distribution in the collective pattern, and a predator's foraging fitness is linked to its expected feeding amount. In detail, given the feeding preferences of all predators, a prey which appears at the safer positions more frequently is evolutionarily selected. On the other hand, those predators prefer to feed on the more frequent positions of the collective pattern are evolutionarily selected.

According to the definition of evolutionary stability (Smith, 1982), when the emergent pattern, D , is a stable state of this coevolution system, the resident strategies at the prey

and predator sides, termed c_i^{ESS} and x_j^{ESS} , respectively, should satisfy the following two conditions:

$$\forall c_m \neq c_i^{ESS} \text{ and } x_q \neq x_j^{ESS}, \quad \exists \epsilon^* > 0, \forall \epsilon < \epsilon^*$$

$$u\left(c_i^{ESS} | D^{(1-\epsilon)c_i^{ESS} + \epsilon c_m}\right) > u\left(c_m | D^{(1-\epsilon)c_i^{ESS} + \epsilon c_m}\right) \quad (5.1)$$

$$u\left(x_j^{ESS} | D^{(1-\epsilon)x_j^{ESS} + \epsilon x_q}\right) > u\left(x_q | D^{(1-\epsilon)x_j^{ESS} + \epsilon x_q}\right) \quad (5.2)$$

, where $u(s,d)$ is the utility of strategy s at state d , and $D^{(1-\epsilon)s_r + \epsilon s_m}$ is the perturbed state which consists of $1 - \epsilon$ proportion of the resident strategy and ϵ proportion of the invasive one. These two conditions ensure that either for prey or for predators, a small proportion of any other strategy is less beneficial than the resident one. Hence, the invasive strategy will die out in evolution and the state will be restored. (Background information is provided in Chapter 2.5.3)

5.2.2 Selection and Adaptation at the Both Sides

The categorisation of positions in the RPFC metric is simplified based on the findings in Chapter IV. First, since an isolated prey is inferior to an aggregated prey in most cases (Figure 4.4), the ‘ranger’ position in the RPFC metric is not considered. A population of prey fish only consists of moving schools and stationary herds, which refer to either milling or disordered swarms. Subsequently, a moving school is separated into two, rather than three, positions: pioneers, which have no leading neighbour, and followers, which have leading neighbours. Here the centre and the margin of a school are not distinguished and the focus is put on its polarised property. Lastly, a stationary herd is divided into two positions: marginal cowards and central cowards, as in the RPFC metric.

A prey's strategy is a set of three free-willed positional changes, $c_i = \{p_i^{M2P}, p_i^{P2F}, p_i^{F2P}\}$, as the probabilities to move from a given position to the other one at each time step. The first free-willed positional change, p_i^{M2P} , is leaving the margin of a herd with a few followers and being a pioneer of a school, that is, from a marginal coward to a pioneer, as the collective departure strategy reported in Chapter IV. To study the influence of the biased risk within a school, the positional changes between pioneers and followers, as p_i^{P2F} and p_i^{F2P} , are reserved to prey's free wills in the model. These two changes can result from the speed-up and slow-down of a schooling prey, or from the fission and fusion of prey schools. Apart from these three free-willed changes, other changes between two positions are assumed unable to be controlled by prey fish. For example, due to the crowding effect observed in Chapter IV, a marginal prey cannot choose to be a central coward, and vice versa. Also, a schooling prey cannot choose to be in a stationary herd because it cannot force its pioneers to stop. Similarly, a marginal coward cannot choose to be a follower due to the lack of pioneers.

At the predator side, predator j 's hunting strategy is viewed as a risk distribution among the four positions, which can be represented by a vector $\mathbf{x}_j = a_j(x_j^P, x_j^F, x_j^B, x_j^C)$, where $x_j^P + x_j^F + x_j^B + x_j^C = 1$ as a normalisation and hence the scale $a_j > 0$ reflects the predatory capability, that is, the stronger predator has a larger a_j . Hence, the environmental risk on prey aggregation is the sum of all predators' feeding preferences, $\sum \mathbf{x}_j$. Here the assumption is made: prey are attacked by a single species of predators, and the same species of predators have the same a_j . Under this assumption, a_j becomes a constant and can be discarded without any influence to the result. For convenience, a hunting strategy is treated as $\mathbf{x}_j = (x_j^P, x_j^F, x_j^B, x_j^C)$ and the environmental risk $\mathbf{X} =$

(X^P, X^F, X^M, X^C) is set as the average of all \mathbf{x}_j . These representations normalise the sum of the four elements to one, that is, $|\mathbf{x}_j| = |\mathbf{X}| = 1$.

Through the self-organising mechanism outlined in Chapter 5.2.3, the average positional distribution of each prey can emerge from the adopted strategies in the population. This distribution is represented as the vector $\mathbf{D}_i = (P_i, F_i, M_i, C_i)$ for prey i , where $P_i + F_i + M_i + C_i = 1$ are the frequencies of the four corresponding positions. The sum of all prey's positional distributions is equal to that of the whole population, as

$$\mathbf{D} = \sum \mathbf{D}_i = (P, F, M, C). \quad (5.3)$$

The predation risk of a prey is calculated by the inner product of its emergent distribution, \mathbf{D}_i , and the environmental positional risk, \mathbf{X} , that is,

$$P_i X^P + F_i X^F + M_i X^M + C_i X^C. \quad (5.4)$$

The foraging fitness of a predator is defined as the expected level of the feeding amount, affected by an energy cost, as

$$(x_j^P P + x_j^F F) e_j + x_j^M M + x_j^C C, \quad (5.5)$$

where $0 \leq e_j \leq 1$ considers the extra energy cost when predator j chases a moving school. Similar to the assumption on a_j , the parameter e_j is assumed a constant for predators of the same species. This parameter is used to compare the adaptations from larger and stronger predators to smaller and weaker predators in nature.

To simulate the evolutionary trajectory at the prey side, each of the N prey agents is initially assigned three random probabilities to its strategy, $c_i = \{p_i^{M2P}, p_i^{P2F}, p_i^{F2P}\}$, as the three free-willed positional changes described above. In every generation, a prey's

positional distribution, $\mathbf{D}_i = (P_i, F_i, M_i, C_i)$, as the frequencies to appear at these four positions, emerges from the self-organising mechanism of the positional changes in the population. Those prey with higher predation risks are eliminated and replaced by the same amount of the offspring from the well-performed prey. Finally, when all prey share the same predation risk and are less in danger than any small proportion of mutants, an evolutionarily stable state is attained at the prey side.

Parameter settings are as follows. The population size, N , is set 100. The reproduction probability and the replacement rate conform to the setting in Chapter III, as the exponential rank selection with $I^{ER} = 1.16$ and 17%, respectively. Denoting the strategy of a selected parent as $c_p = \{p_p^{B2P}, p_p^{P2F}, p_p^{F2P}\}$, the offspring's strategy is generated by

$$c_o \xleftarrow{\text{assign}} \{p_p^{B2P} + \epsilon, p_p^{P2F} + \epsilon, p_p^{F2P} + \epsilon\}, \quad (5.6)$$

where $\epsilon \sim N(0,0.2)$ simulates the mutation. If any of the probabilities is smaller than 0 or greater than 1, it is adjusted to 0 or 1, respectively.

The simulation of the evolution at the predator side is not by a genetic algorithm. Instead, a game-theoretic approach is applied. First, since the fitness functions of predators are homogeneous, the condition $\mathbf{X}_r = \mathbf{x}_r$ must hold in an evolutionarily stable state. As a simple proof of the above statement, it is wrongly assumed that there is a stable state, where two strategies coexist, termed \mathbf{x}_1 and \mathbf{x}_2 , by the frequencies p and $1 - p$, respectively. Given a small proportion of the invasive strategy $\mathbf{x}_m = q\mathbf{x}_1 + (1 - q)\mathbf{x}_2$, where $q \neq p$, this strategy receives the same fitness as the resident strategies and the state is invaded. Hence, the contradiction happens. Therefore, the property of symmetry in typical evolutionary games (described in Chapter 2.5.3) is also satisfied here.

Now, given a population of homogeneous predators which all adopt the feeding preference \mathbf{x}_r and cause the environmental risk $\mathbf{X}_r = \mathbf{x}_r$, the present state, $\mathbf{D}^{\mathbf{x}_r}$, is evolutionarily stable if and only if $\forall \mathbf{x}_q \neq \mathbf{x}_r, \exists \epsilon^* > 0, \forall \epsilon < \epsilon^*$

$$u(\mathbf{x}_r | \mathbf{D}^{(1-\epsilon)\mathbf{x}_r + \epsilon\mathbf{x}_m}) > u(\mathbf{x}_m | \mathbf{D}^{(1-\epsilon)\mathbf{x}_r + \epsilon\mathbf{x}_m}) \quad (5.7)$$

, where $\mathbf{D}^{(1-\epsilon)\mathbf{x}_r + \epsilon\mathbf{x}_m}$ is the perturbed state with a small proportion of \mathbf{x}_q in the population. Since the utility function has been defined as $(x_j^P P + x_j^F F)e_j + x_j^M M + x_j^C C$, the above condition can be rewritten by a linear combination of the strategies as

$$\begin{aligned} u(\mathbf{x}_r | \mathbf{D}^{(1-\epsilon)\mathbf{x}_r + \epsilon\mathbf{x}_m}) &> (1 - \epsilon)u(\mathbf{x}_r | \mathbf{D}^{(1-\epsilon)\mathbf{x}_r + \epsilon\mathbf{x}_m}) + \epsilon u(\mathbf{x}_m | \mathbf{D}^{(1-\epsilon)\mathbf{x}_r + \epsilon\mathbf{x}_m}) \\ &= u\left(\left((1 - \epsilon)\mathbf{x}_r + \epsilon\mathbf{x}_m\right) | \mathbf{D}^{(1-\epsilon)\mathbf{x}_r + \epsilon\mathbf{x}_m}\right) \\ &\Rightarrow u(\mathbf{x}_r | \mathbf{D}^{Adj}) > u(\mathbf{x}_{Adj} | \mathbf{D}^{Adj}) \end{aligned} \quad (5.8)$$

This equivalent condition shows that a state is evolutionarily stable if and only if its resident strategy can invade the adjacent states. Therefore, by segmenting X^P, X^F, X^M and X^C into sufficiently small grids, an evolutionarily stable state, \mathbf{D}^{ESS} , can be detected through the greater fitness of its resident strategy, \mathbf{x}_r^{ESS} , in any of its $3^4 - 1 = 80$ adjacent states. To depict the evolutionary trajectory of predators, a state is converted to an adjacent state if this state can be invaded by the resident strategy of the nearby one. When there are multiple adjacent states able to cause this transition, the one which strategy gains the largest fitness is chosen since this strategy should receive the highest growth rate.

In the model, each of the four positional risks is divided into 100 segments, from 0 to 1 by 0.01. Each of the 100^4 grids draws a risk distribution, $\mathbf{X} + \epsilon^G$, in the environment, where \mathbf{X} is the average risk distribution in this grid and $\epsilon^G = (\epsilon^P, \epsilon^F, \epsilon^M, \epsilon^C)$, where each

$\epsilon \sim U(-0.005, 0.005)$, simulates the stochasticity inside this grid at each generation. This risk distribution then causes an evolutionarily stable state, \mathbf{D} , at the prey side, which experimental value is computed by the average positional distribution from the 10000th generation to the 15000th generation. Finally, the adaptation at the predator side is simulated through the transition from a given grid to its adjacent grids.

5.2.3 Self-organising Mechanism of Prey

In a population of N prey, there are S prey in moving schools and H prey in stationary herds (Figure 5.1A), where $S + H = N$. Schooling prey can be categorised into pioneers (denoting the number as P) and followers (denoting the number as F). Herding prey are divided into marginal cowards (denoting the number as M) and central cowards (denoting the number as C). To summarise the above model setting, the following three relations always keep at any time step T :

$$N = S^T + H^T, \quad (5.9)$$

$$S^T = P^T + F^T, \quad (5.10)$$

$$H^T = M^T + C^T. \quad (5.11)$$

Ideally, a stationary herd should be in a round shape, and hence the number of marginal cowards can be estimated as

$$M^* = \min(\sqrt{4\pi H}, H), \quad (5.12)$$

through the derivation from $H = \pi r^2$ and $M^* = \min(2\pi r, H)$. Hence, once H is decided, M and C are also decided. It is possible that prey aggregation forms multiple herds in the

environment. In this case, assuming there are k herds with the same size, the number of marginal cowards becomes $M^* = \min(\sqrt{4\pi kH}, H)$, or equivalently,

$$M^*/k = \min(\sqrt{4\pi kH}, H)/k = \min(\sqrt{4\pi(H/k)}, H/k), \quad (5.13)$$

as inspecting a smaller population with the size $N' = N/k$, which consists of a single herd. Without the loss of generality, it is set $k = 1$.

According to the additional scenario, a moving school should become a stationary herd if no individual likes to be the pioneer. For example, the situation that $S > 0$ and $P/F = 0$ must be contradictory. Since there can be multiple schools in the environment, a threshold, w , is used to draw this constraint. It is defined that if at any time step, $P/F < 1/w$, then $F - wP$ schooling followers are converted to herding cowards.

At each time step, six game rules are applied sequentially to simulate the self-organising mechanism. The first three rules illustrate the transition from a school to a herd (Figure 5.1B), as the additional scenario, and the later three rules illustrate the transition from a herd to a school (Figure 5.1C), as the collective departure scenario. The reason for the order is that a schooling pattern usually lasts for a long time before it collapses. During the derivation, a time step, $T+0.5$, is used to mention the intermediate stage between the two transitions.

The first three rules are as follows (Figure 5.1B). Rule 1: a pioneer which decides to be a follower, or a follower which decides to be a pioneer, is triggered. Rule 2: if now $F > wP$, the randomly chosen $F - wP$ followers become marginal cowards. Rule 3: if now $M > M^*$, then the randomly chosen $M - M^*$ marginal cowards become central cowards.

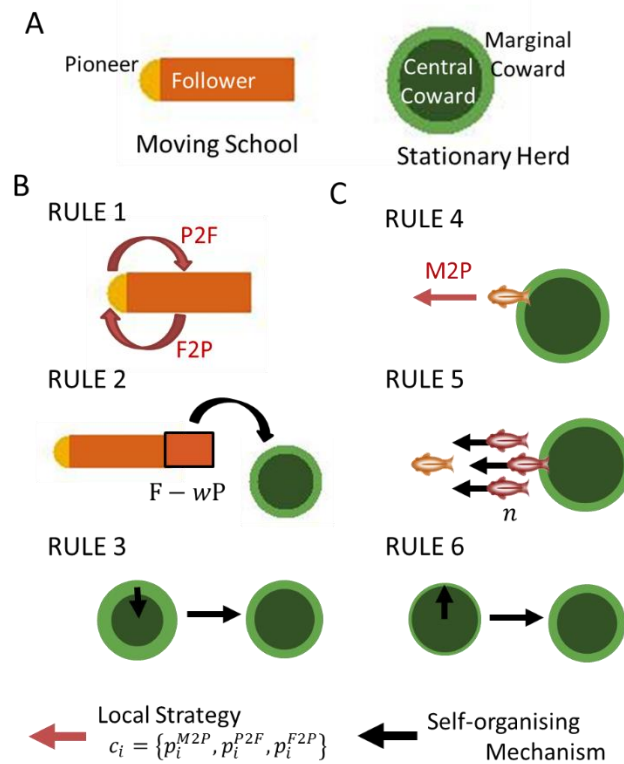


Figure 5.1: Diagram of the Self-organising Mechanism

Subfigure A shows that a prey is defined either in a moving school, as a pioneer or a follower, or in a stationary herd, as a marginal coward or a central coward. Subfigure B shows the three rules which simulate the self-organising mechanism to emerge the swarming pattern. Subfigure C shows the three rules which simulate the self-organising mechanism to emerge the schooling pattern, that is, the collective departure scenario. It is highlighted by the red arrows that a prey can only make decision on three positional changes: from a pioneer to a follower, from a follower to a pioneer, and from a marginal coward to a pioneer (as the collective departure strategy). Other positional changes, drawn by the black arrows, are triggered based on the strategies of all prey individuals.

Instead of simulating prey's positional changes under the above rules by real movements, the expected positional distribution of each prey, \mathbf{D}_i , as well as the whole population, \mathbf{D} , are concerned in the following mathematical expressions. That is to say, taking Rule 1 for example, given a prey which prefers to move from the 'follower' position to the 'pioneer' position with the probability 0.2, that is, $p_i^{F2P} = 0.2$, when this prey is a follower, it will either remain a follower or change to a pioneer at each single movement. However, given a long observation period, its frequency of remaining a

follower is expected to be 80%, and its frequency of changing to a pioneer is expected to be 20%. Therefore, this prey's positional distribution, $\mathbf{D}_i = (P_i, F_i, M_i, C_i)$, is expected to transform from (0,100%,0,0) to (20%,80%,0,0), or generally speaking, from (P_i, F_i, M_i, C_i) to $(P_i + p_i^{F2P} F_i - p_i^{P2F} P_i, F_i - p_i^{F2P} F_i + p_i^{P2F} P_i, M_i, C_i)$ after applying Rule 1, where $p_i^{P2F} P_i$ is the expected frequency of moving from the 'pioneer' position to the 'follower' position. The following expressions are all based on the expected positional frequencies.

Given $\mathbf{D}_i^T = (P_i^T, F_i^T, M_i^T, C_i^T)$, where $P_i^T + F_i^T + M_i^T + C_i^T = 1$, as the distribution of prey i 's positions at time T , the above transition, from schooling to herding, can be formulated at the group level as:

$$P^{T+0.5} = P^T - \sum_j p_j^{P2F} P_j^T + \sum_j p_j^{F2P} F_j^T \quad (5.14)$$

$$F^{T+0.5} = \min(S^T - P^{T+0.5}, wP^{T+0.5}) \quad (5.15)$$

$$S^{T+0.5} = P^{T+0.5} + F^{T+0.5} \quad (5.16)$$

$$H^{T+0.5} = N - S^{T+0.5} \quad (5.17)$$

$$M^{T+0.5} = \min(\sqrt{4\pi H^{T+0.5}}, H^{T+0.5}) \quad (5.18)$$

$$C^{T+0.5} = H^{T+0.5} - M^{T+0.5} \quad (5.19)$$

The first expression calculates the expected number of pioneers at time $T+0.5$ by the number of pioneers at time T minus those from pioneers to followers and plus those from followers to pioneers, as the first rule. The second expression describes the second rule. The third and fourth expressions are the fundamental relations. The latter two

expressions recalculate the proportions of marginal and central cowards, as mentioned in the third rule.

At the individual level, this transition can be formulated as:

$$P_i^{T+0.5} = (1 - p_i^{P2F})P_i^T + p_i^{F2P}F_i^T \quad (5.20)$$

$$F_i^{T+0.5} = F^{T+0.5} \frac{S_i^T - P_i^{T+0.5}}{S^T - P^{T+0.5}} \quad (5.21)$$

$$S_i^{T+0.5} = P_i^{T+0.5} + F_i^{T+0.5} \quad (5.22)$$

$$H_i^{T+0.5} = 1 - S_i^{T+0.5} \quad (5.23)$$

$$M_i^{T+0.5} = M^{T+0.5} \frac{H_i^{T+0.5} - C_i^T}{H^{T+0.5} - C^T} \quad (5.24)$$

$$C_i^{T+0.5} = H_i^{T+0.5} - M_i^{T+0.5} \quad (5.25)$$

About the value of F_i at time $T+0.5$, if the total number of followers does not exceed the threshold, that is, $F^{T+0.5} = S^T - P^{T+0.5}$, prey i 's frequency of being a follower is derived through the fundamental relation $S_i^T - P_i^{T+0.5}$, where $S_i^T = S_i^{T+0.5}$ since no follower is converted to a coward. Otherwise, only a part of followers are kept, which number is $F^{T+0.5} = wP^{T+0.5}$. Since these left followers are randomly chosen, the ratio of a prey's frequency of being a follower over that of the whole population is unchanged. Hence, the value of F_i at time $T+0.5$ is the amount of the kept followers times the ratio. The calculation of the frequency of being a marginal coward follows the same logic.

The latter three rules describe the collective departure scenario (Figure 5.1C). Rule 4: a marginal coward which decides to be a pioneer is triggered. Rule 5: at the same time, it randomly brings n herding prey to be its followers. Rule 6: if now $M < M^*$, the

randomly chosen $M^* - M$ central cowards become marginal cowards. As a note, the condition $M > M^*$ cannot happen at this moment since the size of the herd can only decrease.

Denoting the expected number of marginal cowards which turn to be pioneers as $L = \sum_j p_j^{M2P} M_j^{T+0.5}$, this transition can be formulated at the group level as:

$$P^{T+1} = P^{T+0.5} + L \quad (5.26)$$

$$F^{T+1} = F^{T+0.5} + p^{H2F} (H^{T+0.5} - L) \quad (5.27)$$

$$S^{T+1} = P^{T+1} + F^{T+1} \quad (5.28)$$

$$H^{T+1} = N - S^{T+1} \quad (5.29)$$

$$M^{T+1} = \min(\sqrt{4\pi H^{T+1}}, H^{T+1}) \quad (5.30)$$

$$C^{T+1} = H^{T+1} - M^{T+1} \quad (5.31)$$

The first expression is based on the fourth rule. The second expression describes the fifth rule, where $H^{T+0.5} - L$ is the number of remaining cowards and p^{H2F} is the probability that a remaining coward becomes a follower of some new pioneers, which value is discussed later.

At the individual level, this transition can be formulated as:

$$P_i^{T+1} = P_i^{T+0.5} + p_i^{M2P} M_i^{T+0.5} \quad (5.32)$$

$$F_i^{T+1} = F_i^{T+0.5} + p_i^{H2F} (H_i^{T+0.5} - p_i^{M2P} M_i^{T+0.5}) \quad (5.33)$$

$$S_i^{T+1} = P_i^{T+1} + F_i^{T+1} \quad (5.34)$$

$$H_i^{T+1} = 1 - S_i^{T+1} \quad (5.35)$$

$$C_i^{T+1} = C^{T+1} \frac{(1 - p_i^{H2F})C_i^{T+0.5}}{\sum_j [(1 - p_j^{H2F})C_j^{T+0.5}]} \quad (5.36)$$

$$M_i^{T+1} = H_i^{T+1} - C_i^{T+1} \quad (5.37)$$

where $p_i^{M2P} M_i^{T+0.5}$ is the frequency of being a new pioneer from a marginal coward, and p_i^{H2F} is the probability that prey i becomes a follower of a new pioneer, given that prey i is herding. Hence, the calculation of F_i^{T+1} is the frequency of being a remaining coward times p_i^{H2F} and finally plus the original frequency of being a follower. The calculation of C_i^{T+1} is related to the sixth rule, explained as follows. After randomly caught by the new pioneers and being their followers, prey i 's frequency of being a central coward becomes the numerator part, and the denominator portion is the addition of these frequencies in the population. When some central cowards are randomly chosen to be the marginal ones, as the sixth rule, this ratio is unchanged. Hence, the final frequency of being a central coward is the amount of central cowards times the ratio.

At the group level, the probability p^{H2F} is supposed to be nL (the number of remaining cowards going to be brought by the L new pioneers) over $H^{T+0.5} - L$ (the number of remaining cowards), or one if $nL \geq H^{T+0.5} - L$. However, the derivation of the associated probability at the individual level, p_i^{H2F} , then becomes difficult. Since a prey cannot follow itself, this probability at the individual level should be negatively correlated to p_i^{M2P} . Here it is estimated in the model by

$$p_i^{H2F} = \min \left[\frac{n(L - p_i^{M2P} M_i^{T+0.5})}{H^{T+0.5} - L}, 1 \right]. \quad (5.38)$$

To coordinate with p_i^{H2F} , the probability p^{H2F} is derived as

$$p^{H2F} = \frac{\sum_j [p_j^{H2F} (H_j^{T+0.5} - p_j^{M2P} M_j^{T+0.5})]}{H^{T+0.5} - L}, \quad (5.39)$$

which is the expected amount of being followers from cowards over the expected amount of cowards.

So far, the explanation of the self-organising mechanism has been completed. To solve this discrete Markov process, one method is to derive the final state by letting $\mathbf{D}_i^T = \mathbf{D}_i^{T+1}$, and the other is to approach this state by a computer. Generally, a process of this self-organising mechanism converges in less than 10 time steps, so the second method is chosen due to its simplicity. In the following experiments, the average positional distribution of each prey, \mathbf{D}_i , and that of the population, \mathbf{D} , are set by the outputs at the 60th time step. In addition, the population size (N) is set at 100, the maximal F/P ratio (w) is set at 8 and the number of followers brought by a departure pioneer (n) is set at 8.

As a compliment, the above self-organising mechanism is referred to as a Markov process since the individual positional distributions at time $T+1$ only depends on those distributions at time T , regardless of the preceding distributions or the time stamp, as the Markov property of ‘memorylessness’, or to say, time independence (Karlin, 2014). However, this mechanism is unsuitable to be represented by typical transition matrices or transition functions for two reasons. The first one is that each prey’s positional distribution at time $T+1$ depends not only on its strategy and its distribution at time T , but also on other $N-1$ prey’s strategies and distributions at time T , that is, $D_i^{T+1} = f(c_i, D_i^T, c_0, D_0^T, c_1, D_1^T, \dots, c_N, D_N^T)$, given f is the transition function. Hence, the expression by an equivalent transition function becomes tedious and difficult to be understood. The second reason is that this mechanism contains ‘if-else’ branches, like the condition “if there is no pioneer in a school, the followers become cowards” (Rule

2). These ‘if-else’ branches block the usage of those analytical tools derived from a transition function, like the Jacobian ratio or the Chapman–Kolmogorov equation (Bharucha-Reid, 2012), and hence reduces the significance to represent the above mechanism by typical transition matrices or transition functions.

5.3 Result

5.3.1 Adaptation of Prey

In the previous chapter, it has been demonstrated and analysed that under a slow-predator situation, the X^P/X^M ratio (referred to as X^P/X^{Cm}) is less than one and the schooling pattern is expected to emerge in the evolutionarily stable state. In contrast, under a fast-predator situation, the X^P/X^M ratio is greater than one, and given this ratio is not too high, the schooling pattern is still in the majority due to the adaptive tactic of the collective departure. In the both cases, generally, the followers are slightly less at risk than the pioneers and the central cowards bear no risk. These findings are duplicated by the model.

Given $\mathbf{X} = (X^P, 0.9X^P, X^M, 0)$, as a similar risk distribution to that in the spatial-explicit agent-based simulation, the evolutionarily stable states in the present model are displayed in Figure 5.2. It shows the frequency of the emergent schooling pattern, as the sum of pioneers (P_i) and followers (F_i), decreases when the X^P/X^M ratio increases. There is a threshold of the ratio that when $X^P/X^M > 1.28$, the swarming pattern emerges and the schooling pattern disappears. However, when $1.14 < X^P/X^M < 1.28$, both schooling and swarming patterns can be the emergent state depending on the initial strategies in the population. These findings were predicted in Chapter 4.5 as an exceptional environment where the swarming pattern can be evolutionarily stable.

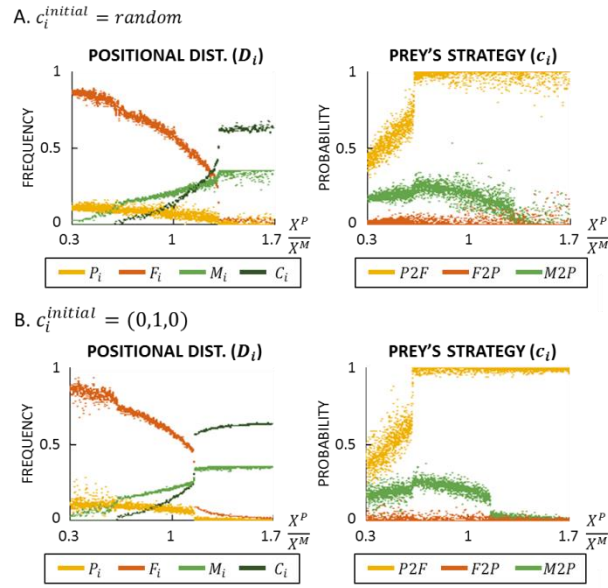


Figure 5.2: Prey's Adaptation under $\mathbf{X} = (X^P, 0.9X^P, X^M, 0)$

The simulated adaptation of prey fish and their emergent patterns in the previous chapter can be duplicated by setting a similar environmental risk $\mathbf{X} = (X^P, 0.9X^P, X^M, 0)$, where $|\mathbf{X}|=1$. Subfigure A displays the evolutionarily stable states under different X^P/X^M ratios given the initial strategies are randomly assigned. It is observed that schooling can emerge when $X^P/X^M < 1.28$. Subfigure B shows there are two potential evolutionarily stable states in the range $1.14 < X^P/X^M < 1.28$, depending on the setting of initial strategies. These outputs are consistent with the demonstrations and analyses in Chapter IV. The discontinuous changes among collective patterns display the non-linear structure of the self-organising mechanism, for example, the 'if-else' conditions.

In the range of schooling patterns, a marginal coward evolves a probability of around 0.13 to exhibit the collective departure strategy, that is, p_i^{M2P} . This small probability is because although leaving the boundary is beneficial to marginal cowards, the best situation of a departure is being brought by other leaving pioneers to acquire the positional risk $X^F = 0.9X^P$. This advantage of being free riders leads to a remaining herd even in a slow-predator situation ($X^P/X^M < 1$), which phenomenon is also observed in the spatial-explicit simulation (Figure 4.1). When the X^P/X^M ratio is less than around 0.6, the pioneers are more hesitant about changing to the follower position since this action implies a possibility to convert itself to a herding coward.

The analysis in Chapter 4.5 predicted that the swarming pattern can emerge in the three conditions: first, the risk on a school is extremely high; secondly, the central position is not safe; thirdly, prey can squeeze into the centre, which is equal to the second condition from the view of the risk distribution. The first condition has been supported in Figure 5.2. About the second condition, as well as the third condition, it was derived that when $X^C = X^M$ and $X^P/X^M > 1$, the swarming pattern is evolutionarily stable. Given $\mathbf{X} = (X^P, 0.9X^P, X^M, X^M)$, this prediction is also supported by the present model (Figure 5.3A).

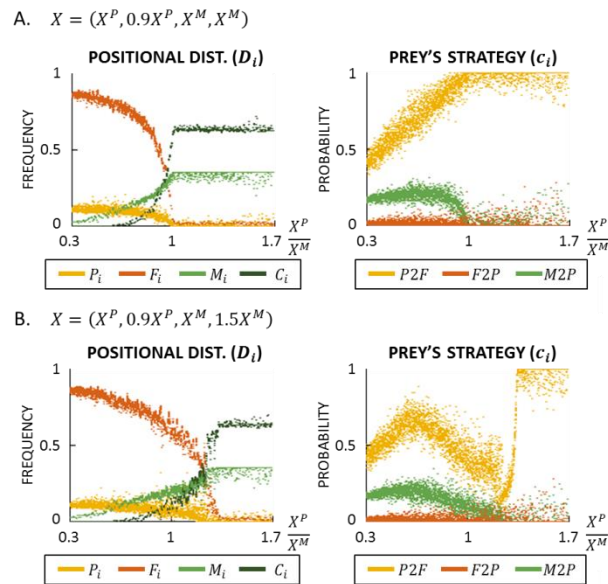


Figure 5.3: Prey's Adaptation given a Dangerous Centre

When the central position of a herd is as dangerous as the margin, schooling can only emerge in a smaller range of the X^P/X^M ratio compared to the case that the centre is risk-free. However, when the risk of the central position keeps increasing, the range where schooling can emerge expands again. It should be noted that the case $X^C > X^M$ may conflict the precondition of the model.

When the central position becomes more dangerous than the margin (Figure 5.3B), the schooling pattern is more likely to emerge compared to the case $X^C = X^M$ (Figure 5.3A). In this kind of schools, a pioneer reduces its tendency to change its position due to the avoidance of being buried into the centre of a stationary herd. However, it is

questionable whether this risk distribution accords with the precondition of the model. As an extension from the simulation outputs in Chapter IV, this model assumes that prey groups are compact, which can be explained by the selfish herd scenario when $X^C \leq X^M$, where $X^C = X^M$ draws the bound. When $X^C > X^M$, the precondition to cause compact groups may not be satisfied.

Apart from the schooling pattern and the swarming pattern, a stable state which usually appears in the model is that all prey become pioneers. This pattern can emerge when $X^P < X^F$, under which condition, all followers are more beneficial by leaving their leading neighbours and being pioneers themselves. This appearance can be linked to the dispersal pattern in Chapter IV, which is composed of isolated prey. However, to avoid unnecessary ambiguity, this pattern is termed the line abreast formation.

5.3.2 The Emergent Patterns

By computing prey's adaptive dynamics in the full range of risk distributions, all possible emergent patterns can be plotted as a map in Figure 5.4. It is implemented by dividing each of the four positional risks into 100 segments, and then simulating prey's adaptation given the predation risk $X + \epsilon^G$ in each of the 100^4 grids, where X is the average risk distribution in a grid and ϵ^G provides stochasticity to the distribution in every generation. In general, the emergent pattern in each grid is evolutionarily stable at the prey side, since it is demonstrated that any small proportion of different positional changes cannot perturb the state.

Three primary types of emergent patterns in the map are as follows (Figure 5.4A). The first type is the line abreast formation, which only consists of pioneers. This state can emerge when the risk of pioneers is less than that of followers. The second type is the

swarming pattern, which consists of cowards in a herd. This state can be observed when the risk of pioneers is much higher than the others. The third type is the schooling pattern, where a few pioneers, many followers and few cowards are present. It happens when the risk of pioneers is slightly higher than that of followers, at the same time lower or slightly higher than the risk of cowards.

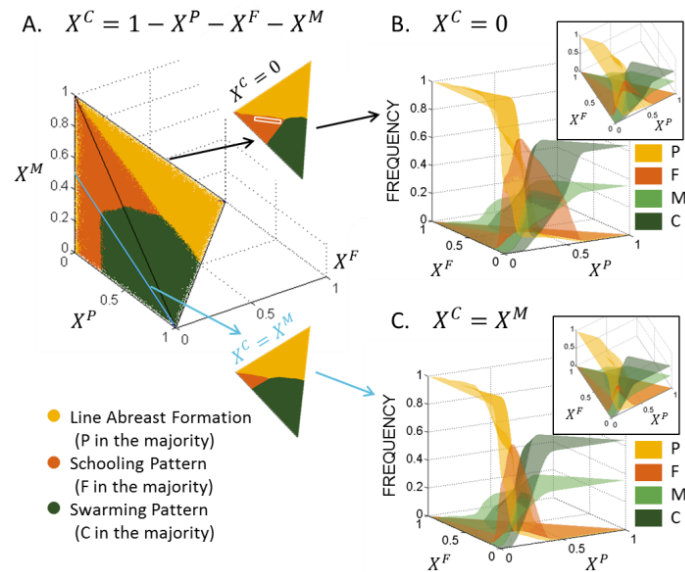


Figure 5.4: Full-range Map of Emergent Patterns

The emergent patterns of prey aggregation under all possible risk distributions are displayed. To plot these states in a 3-D panel, the major position in a state is used to represent the general type, as in subfigure A. If the pioneers are in the majority, the state is a line abreast formation. If the followers are in the majority, it is a schooling pattern. Lastly, if central cowards are in the majority, it is a swarming pattern. Subfigure B provides complete information of the positional frequencies when $X^C=0$, which is the surface slice in subfigure A. Subfigure B shows the case when $X^C=X^M$, which is the blue slice in subfigure A. The white rectangle on the $X^C=0$ slice marks the experimental range in Chapter IV.

The boundary between the line abreast formation and the other types is generally fixed on the surface $X^P = X^F$. In contrast, the boundary between the schooling pattern and the swarming pattern shifts when the risk of central cowards alters. When this risk equals that of marginal cowards (Figure 5.4C), the range of schooling patterns shrinks to the minimum. As noted in the previous section, the stable states in the area $X^C > X^M$ can be

less reasonable considering that the prey group cannot become compact through the selfish herd scenario.

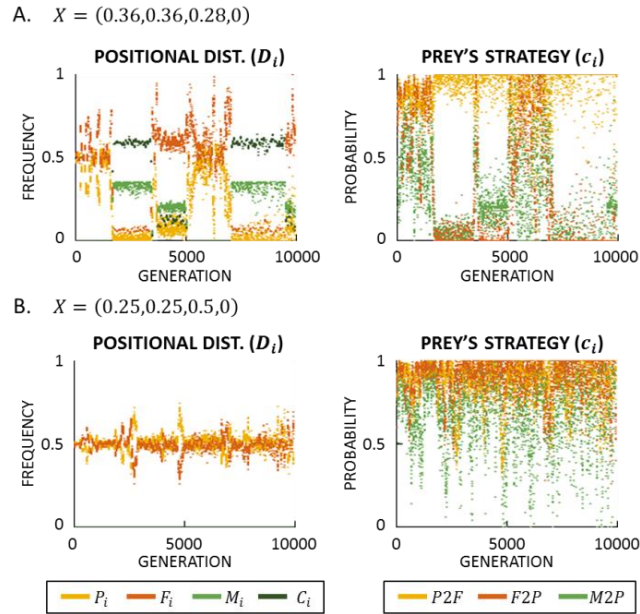


Figure 5.5: Two Specific Risk Distributions

The risk distribution, $\mathbf{X} + \epsilon^G$, of those grids on the junction of the three types cannot lead to an evolutionarily stable state, as subfigure A. It is because the noise, ϵ^G , randomly converts the expected stable state from one to another, which is an error due to the discretisation. Subfigure B shows a special type of the emergent pattern when $X^P = X^F$. Under this condition, a prey with even frequencies to be a pioneer and a follower can average the noise from ϵ^G and avoid being eliminated.

The adaptive strategy, c_i , of all prey in a line abreast formation is $\{p_i^{M2P}, p_i^{P2F}, p_i^{F2P}\} = \{1, 0, 1\}$ due to the avoidance of being a follower. In a swarming pattern, since being a pioneer is highly in danger, the typical strategy of all prey is $c_i = \{0, 1, 0\}$. The adaptive strategy to cause a schooling pattern contains two features. One is that the probability to turn from a marginal coward to a pioneer, p_i^{M2P} , is small (around 0.13), even if the risk of marginal cowards is much higher than that of pioneers. As explained in the former section, it is because being brought as a follower is more beneficial than being a pioneer itself. The other feature is that the probability to turn from a follower to a pioneer, p_i^{F2P} , is always zero and the opposite probability, p_i^{P2F} , is significantly greater than zero. This

adaptation leads to a behavioural dynamic similar to the natural fish, which often form a temporary milling herd, that is, a stationary aggregate where individuals move around the centre, during their collective movement.

There is a group of grids which evolutionarily stable states cannot be computed, as those fall on the junction of the three types, for example, $\mathbf{X} = (0.36, 0.36, 0.28, 0)$ in Figure 5.5A. In these grids, prey's adaptive strategies cannot be converged permanently because the noise to the positional risk, ϵ^G , converts the evolutionarily stable state from one type to another with generations. This is a phenomenon caused by the error of discretisation, and if further segments are applied, these grids are actually composed of three types of evolutionarily stable states. The expected states of these grids are estimated by averaging the positional distributions from the 10000th generation to the 15000th generation. Another special case happens on the boundary of the line abreast formation. The noise ϵ^G in this kind of grids creates a subtle type of stable states, as $\mathbf{D} = (50, 50, 0, 0)$ (Figure 5.5B). It is because a prey with even frequencies of being a pioneer and a follower can average the noises at the two positions, and hence is less likely to be the worst-performed ones (as well as the best-performed ones). In addition, on the boundary of the swarming pattern, there can be multiple evolutionarily stable states (Figure 5.2). These states are averaged based on their frequencies of being reached by simulations, which does not influence the adaptation at the predator side, as analysed in Chapter 5.4.

5.3.3 Adaptation of Predators

The adaptation of predators' feeding preference is simulated through the transition from a state to its adjacent state in the full-range map. In the previous sections, \mathbf{X} is

considered as the risk distribution in the environment from the view at the prey side. Here, from the view at the predator side, $\mathbf{X} = \mathbf{x}$ is treated as the feeding preference adopted by a homogeneous population of predators, which leads to its associated state, \mathbf{D} . Therefore, the evolution of predators should convert a state to an adjacent one if the resident strategy of the nearby state is more adaptive than the original tactic.

The adaptive dynamic of predators is largely influenced by the energy cost, e_j . For example, assuming that the central position is always risk-free (Figure 5.6A), the evolutionarily stable states of the strongest predators ($e_j = 1$) fall around the junction of the three emergent types. The junction is not directly attained because of the errors brought by a computational simulation. On average, the adaptive strategy is $\mathbf{X} = (0.37, 0.35, 0.28, 0)$, or $\mathbf{X} = (1.32X^M, 1.25X^M, X^M, 0)$, which can be linked to the risk distribution of fast-predator situations in Chapter IV. In contrast, when predators are weaker ($e_j < 1$), that is, their energy costs of chasing a moving school is higher than the costs of attacking a stationary herd, the evolutionarily stable state shifts along the boundary of school patterns and line abreast formations (Figure 5.6). For example, when $e_j = 0.1$, the average feeding preference is $\mathbf{X} = (0.2, 0.19, 0.61, 0)$ or equivalently, $(0.33X^M, 0.31X^M, X^M, 0)$, similar to the slow-predator situations in the previous chapter. This kind of adaptive dynamics can be observed in any $X^C = kX^M$ situation, even if $k > 1$. The adaptation of predators given $X^C = X^M$ is shown in Figure 5.6B as another example.

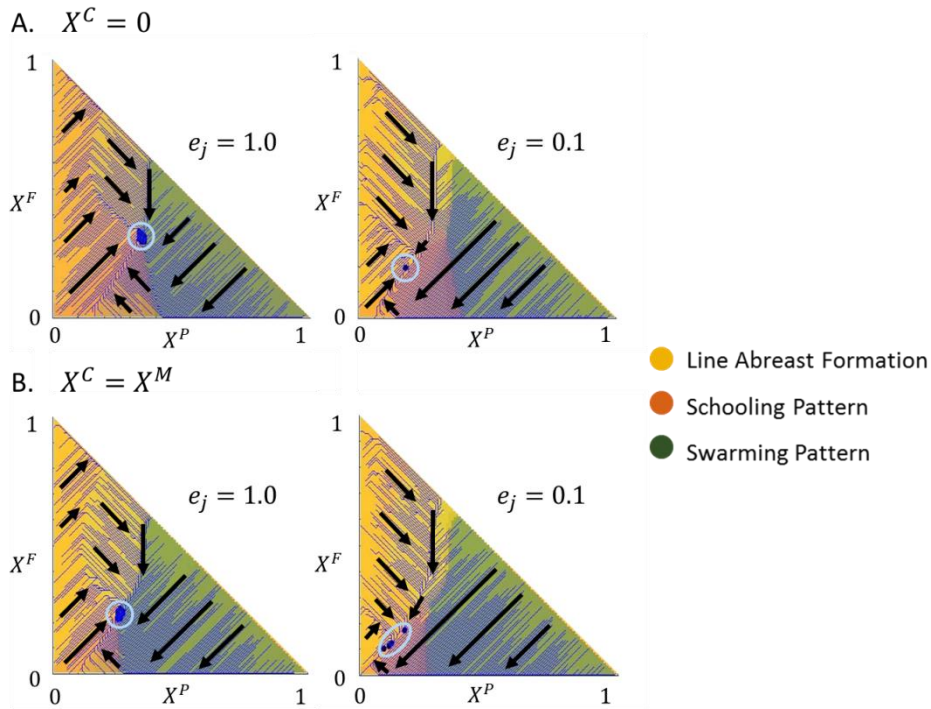


Figure 5.6: Adaptive Dynamic of Predators

The adaptation of predators causes the transition of states, as plotted by the grey paths and the black arrows. Given the environment where X^C is fixed to zero, as in subfigure A, these paths are toward to the junction of the three emergent types when $e_j = 1$. It is an evolutionarily stable state in the coevolution system. When $e_j < 1$, for example, $e_j = 0.1$, the equilibrium shifts towards the zero point. Subfigure B shows the case of $X^C = X^M$.

When predators can evolve their feeding preferences freely, those weaker predators ($e_j < 0.8$) still evolve the preference of marginal predation, that is, $X^C = 0$ (Figure 5.7 & Figure 5.8). However, the extremely strong predators which $e_j > 0.8$ lead to different evolutionarily stable states which resident strategies are $X = (0.23, 0.19, 0.16, 0.42)$ on average (Figure 5.7 & Figure 5.8), or $X = (0.27, 0.24, 0.25, 0.25)$ subject to $X^C \leq X^M$. Since these final states of predators' adaptation have been evolutionarily stable at the prey side, they are the evolutionarily stable states in the coevolution system. It is observed that the coevolution of predators and prey can only drive extremely strong predators to hunt the central position of fish aggregation. In contrast, the weaker predators should evolve to feed on marginal prey of a stationary herd based on

evolutionary selfishness. On the other hand, prey evolve into the schooling pattern, composed of pioneers and followers equally, in front of any predators (Figure 5.7).

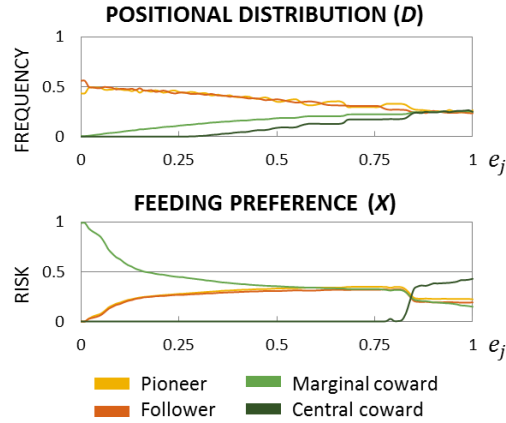


Figure 5.7: Evolutionarily Stable States

Given a group of predators, which energy difference is e_j , and a group of prey, the evolutionarily stable state of their behavioural adaptations is plotted. In a stable state, prey generally form a schooling pattern with an equal amount of pioneers and followers, and the frequency of herding prey increases when e_j becomes larger. On the other hand, only those extremely strong predators ($e_j > 0.8$) can adopt the preference to hunt the central position of a prey group. The preference to hunt the margin of a stationary herd is enhanced when e_j decreases.

For those extremely strong predators ($e_j > 0.8$), the feeding preference in an evolutionarily stable state can lead to the maximal foraging benefit, which is defined as $(x_j^P P + x_j^F F)e_j + x_j^M M + x_j^C C$, among almost all strategies in their emergent states (Figure 5.8A). However, the adaptive strategies of weaker predators are not the optimal ones to the population (Figure 5.8B), which situation becomes worse with the decrease of e_j (Figure 5.8C & Figure 5.8D). If cooperation is allowed in evolution, a species of group-hunting predators should add risk on the central cowards unselfishly so that they can gain better fitness from the emergent swarming pattern (Figure 5.8). Another possibility to reach these optimal states in evolution is when a species of predators have evolved to hunt alone. In this case, a predator's feeding preference is directly equal to

the risk distribution on prey aggregation, so that it can add risk on the central positions without the worry of selfish predators.

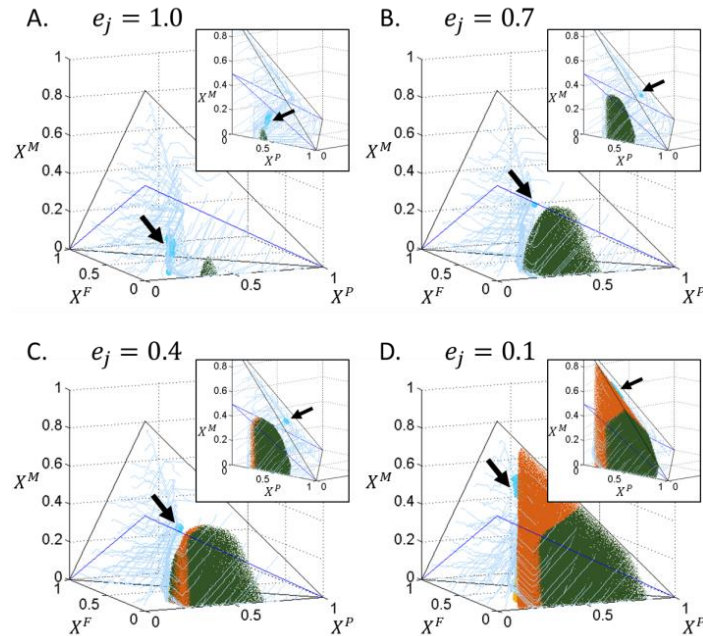


Figure 5.8: ESSs versus Optimal States

The azure paths draw the adaptive dynamic when predators evolve freely, which move towards the evolutionarily stable states pointed by the black arrows. These evolutionarily stable states can be different from the optimal states where the predator population receives the maximal foraging fitness. Those states which provide higher group benefit to the predator population are plotted in the figure, which colours are based on their types, as green for swarming patterns and orange for schooling patterns.

5.4 Analysis

The computational simulation has demonstrated all possibilities of adaptations between predators and prey in their coevolution. In this subchapter, theoretical analyses are provided to validate the experimental outputs. These derivations are partly based on the knowledge acquired from the simulation, so the analysis and the simulation are complements to each other.

5.4.1 Deriving ESSs at the Prey Side

The simulation of prey's adaptation has shown that the emergent pattern can be a line abreast formation, a schooling pattern or a swarming pattern. The boundaries of these three types have been drawn by experiments. Here these boundaries are derived theoretically.

Considering the case $X^C = kX^M$, where $k \geq 0$, if the ideal swarming pattern, $\mathbf{D}^{Sw} = (0, 0, \sqrt{4\pi N}, N - \sqrt{4\pi N})$, is evolutionarily stable, the adaptive probability to turn from a marginal coward to a pioneer, p_i^{M2P} , must be zero. From the aspect of evolution, it implies that this positional change should harm the survival benefit of a prey in the state \mathbf{D}^{Sw} . That is to say, if a marginal coward in the ideal swarming pattern chooses to be a pioneer with n followers, the probability of being caught during a predatory hunt should be greater than the original status, as

$$\frac{X^M}{MX^M + CkX^M} < \frac{X^P}{X^P + nX^F + M'X^M + C'kX^M}, \quad (5.40)$$

$$\text{where } M' = \sqrt{4\pi(N - n - 1)} \text{ and } C' = N - n - 1 - M'.$$

Similar to the analysis in Chapter 4.4, the numerator parts are the probabilities of being caught per step (X^M for stay and X^P for departure) at the same time there is a successful hunt, which is inevitable if the former event holds. The denominator parts are the probabilities of a successful hunt per step, which is the addition of all prey's positional risks. As a note, there is no pioneer and follower in the ideal swarming pattern before a departure, and if a prey decides to leave, there is one pioneer, as itself, and n followers. When a departure happens, the size of the herd becomes $N - n - 1$ and the amounts of

marginal cowards and central cowards are recalculated as M' and C' , respectively. This condition draws the area where an ideal swarming pattern is evolutionarily stable.

Considering the ideal line abreast formation $D^{La} = (N, 0, 0, 0)$, if it is evolutionarily stable, becoming a follower from a pioneer must increase the probability of being eaten per hunt. Mathematically to say, the condition to ensure $p_i^{P2F} = 0$ is

$$\frac{X^P}{NX^P} < \frac{X^F}{X^F + (N-1)X^P}, \quad (5.41)$$

which is equivalent to $X^P < X^F$, through the derivation

$$\begin{aligned} \frac{X^P}{NX^P} = \frac{1}{N} < \frac{X^F}{X^F + (N-1)X^P} &\Rightarrow X^F + (N-1)X^P < NX^P \Rightarrow (N-1)X^P < (N-1)X^F \\ &\Rightarrow X^P < X^F. \end{aligned}$$

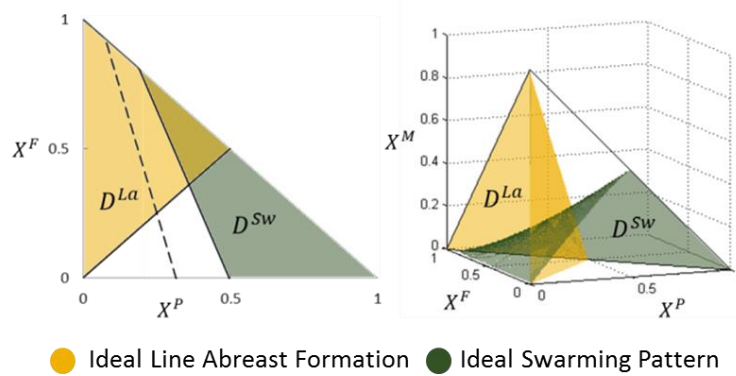


Figure 5.9: ESSs at the Prey Side

The subfigure at the left hand side plots the two boundaries given $X^C = kX^M$, where the solid borderline of the ideal swarming pattern is when $X^C = 0$ and the dashed line is its boundary when $X^C = X^M$, which shows the area where the ideal swarming pattern can be evolutionarily stable is extended. The subfigure at the right hand side plots the two areas in a full-range map.

As plotted in Figure 5.9, there is an area where both the ideal line abreast formation and the ideal swarming pattern cannot be evolutionarily stable. The stable states in this area are observed as schooling patterns from the simulation. Furthermore, there is an area

where both the two patterns are evolutionarily stable. It means evolution can drive prey into any of these two types. However, the probability for a stable state to be attained is not considered in the game-theoretic analysis. In the simulation, the line abreast formation is more likely to emerge given prey's initial strategies are randomly assigned.

5.4.2 Deriving ESSs at the Predator Side

When the adaptive strategy of predators causes a swarming pattern, evolution should drive the predator population to add risk on cowards. Similarly, when a line abreast formation is present, the risk on pioneers should rise through the adaptation at the predator side. Lastly, when the emergent pattern is schooling, predators' preference to hunt followers should be enhanced in evolution. By observing these adaptive dynamics of the three emergent types on the map (Figure 5.10A), it is expected that the evolutionarily stable state should fall on the junction of the three types given $X^C = kX^M$ and $e_j = 1$. The apparent states in the overlap area of line abreast formations and swarming patterns may influence the adaptive path, but cannot change the tendency to reach the junction in evolution.

For each $X^C = kX^M$ situation, this junction can be derived from the equations of the two borderlines. Since the junctions of all $X^C = kX^M$ situations are the turning points of the three emergent types, it is assumed that their emergent states consist of an equal amount of pioneers, followers and central cowards, as the corresponding major positions of the three types. Mathematically to say, the states on the junction are estimated by $\mathbf{D}^J = (d, d, M, d)$, where $|\mathbf{D}^J| = N$, as the population size, and the amount of marginal cowards can be derived from the definition $M = \sqrt{4\pi(M + C)}$. It implies that the emergent states of these turning points are set identical. Hence, the feeding preference which gains

better fitness in D^J should be selected in evolution, which is $X = (0.33, 0.33, 0.29, 0.05)$ theoretically (Figure 5.10B). The derived risk on central cowards is much smaller than the simulation output. It is because in this analysis, the schooling pattern is simplified to the formation of followers. However, in the simulation, the amount of cowards increases in a schooling pattern when the risk distribution is close to the border of the swarming pattern (Figure 5.2). Given that the emergent state on the junction contains slightly more cowards, as $D^J = (d, d, M, td)$, where t is slightly greater than one, the adaptive strategy on the junction then put much more risk on the central position (Figure 5.10C).

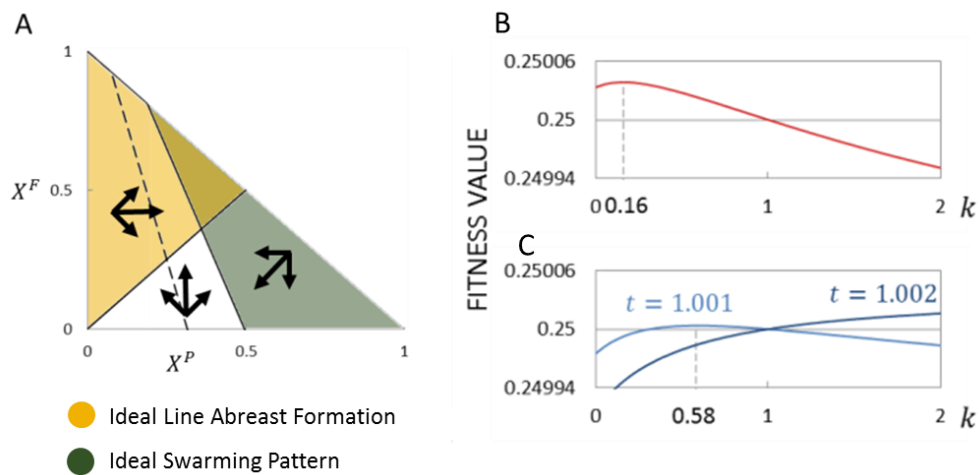


Figure 5.10: ESSs at the Predator Side

Subfigure A shows the expected directions during the transition of states in every $X^C = kX^M$ situation, where the dashed line draws the boundary of the ideal swarming pattern when $k = 1$, as explained in Figure 5.9. Assuming the state on the junction is the same in any $X^C = kX^M$ situation, where there is an equal amount of pioneers, followers and central cowards, the fittest feeding preference happens when $X^C = 0.16X^M$, as in subfigure B, which shows that the marginal predation is not adaptive for the strongest predator ($e_j = 1$). Subfigure C shows that if the state on the junction contains slightly more central cowards, the fittest strategy largely increases the risk on the central prey.

When $e_j < 1$, the payoff of X^M is weighted. As a reminder, a schooling pattern usually contains an obvious frequency of marginal cowards due to the expectation of being a free rider during a collective departure (Figure 5.2 & Figure 5.4). Hence, the stable state

in each $X^C = kX^M$ situation should shift from the junction toward to the zero point because the increase of X^M is proportional to the decrease of $X^P + X^F$. This shifting causes the stable state away from the boundary of the swarming pattern, which implies the frequency of central cowards in the state should be zero or extremely small. Therefore, reducing the risk on central cowards must earn excess short-term fitness and the adaptation of predators should lead to the $X^C = 0$ situation.

5.5 Discussion

The findings in this research infer that when gregarious fish are under predation risk, their schooling pattern can be evolutionarily stable even if the feeding preference of predators is also adaptive. In the stable states of this coevolution system, prey fish always form moving schools, in which the amounts of pioneers and followers are equal. In contrast, the adaptive strategies at the predator side are various, depending on the level of the extra energy cost when chasing the schooling prey. If the extra energy cost is smaller than a threshold, predators should evolve to hunt the central position of prey aggregates. Otherwise, predators adopt the marginal predation, that is, attacking the margin of stationary prey herds and keeping the prey at the central position secure. This tendency is enhanced when the extra energy cost is getting larger.

It has been observed that when a group of dusky dolphins (*Lagenorhynchus obscurus*) hunt prey fish, they exhibit this marginal predation behaviour (Vaughn-Hirshorn et al., 2013). In contrast, when a group of killer whales (*Clupea harengus*) (around 10 times larger than typical dolphins) hunt prey fish, they attack the central positions by their tails (Simila & Ugarte, 1993). For those smaller predators in fresh waters, like bass (*Micropterus salmoides*), goldfish (*Carassius auratus*), and bullgill (*Lepomis*

macrochirus), the strong preference of marginal predation has been reported (Romey et al., 2008; Ioannou et al., 2012). Although these predatory fish do not exhibit a coordinative hunting behaviour like the cetaceans, they are still group-hunting predators since they are group-living fish themselves. These observations all accord with the prediction of the model.

Ecological fieldworks usually mentioned the cetaceans as ‘cooperative’ predators due to the appearance of coordinative hunting behaviours. However, from the evolutionary point of view (Nowak, 2006; Hammerstein & Selten, 1994), it is not answered whether these organised behaviours really deviate from the equilibrium of short-term selfishness. The findings of this work infer that some features of group-hunting predators in the open ocean can be explained by short-term selfishness. Moreover, these adaptations are not mutually beneficial, since they usually decrease the individual fitness. For example, although the best strategy for predators is to attack the centre of prey aggregates, dolphins still evolve into the marginal predation behaviour as the prediction based on evolutionary selfishness. From the opposite aspect, when predators hunt in isolation, it is predicted that they should attack the central prey due to the excess benefit compared to the marginal predation. This adaptation has been observed from swordfish (*Xiphias gladius*), sailfish (*Istiophorus albicans*) and thresher sharks (*Alopias pelagicus*), which are isolated hunters and have evolved tactics to attack the centre of a prey group (Oliver et al., 2013; Domenici et al., 2014).

To connect the findings with other predator-prey systems, the precondition of this model should be noted. In this work, the competition between predators and prey, as the evolution of their population sizes, is not considered. It implies that a prey only competes with other prey, and a predator only competes with other predators. This

setting is due to the fact that, in the marine world, the predators are much stronger than the prey and the prey are abundant. If extinction is a possibility of the adaptation, the equilibrium of a predator-prey system may deviate from the prediction of this work.

CHAPTER VI

CONCLUSION

This thesis aims to propose a holistic answer to the pending question, that is, why fish have evolved into schooling behaviour. To investigate this scientific issue systematically, three main research questions have been studied from Chapter III to Chapter V sequentially: viz., whether a model can be built with less preconceived bias on the setting, whether the evolution of schooling can be simulated under individual selection, and whether schooling can be evolutionarily stable in the predator-prey coevolution. The works in the thesis have resulted in fruitful findings by which the proposed main research questions were addressed to a significant extent. Through the efforts step by step, this thesis has proposed a novel explanation for the schooling behaviour when fish are in danger of predation.

In the following section, the works to address the three research questions are reviewed and summarised. The contribution of these efforts, then, is evaluated in Chapter 6.2. Lastly, the limitations and future works are discussed in Chapter 6.3.

6.1 Summation of Research Works

The research works in this thesis were all aimed to solve the question why fish evolve to form collective schooling behaviour when facing predators. As reviewed in Chapter 2.3.2, the traditional explanations of this question, which were based on the group benefit, cannot completely satisfy the principle of natural evolution, that is, individual selection and adaptation. However, the explanations which took individual selection into account, such as the individual difference and the evolutionary trade-off, have not been widely accepted due to the significant conflicts with empirical data (reviewed in Chapter 2.3.3). To discover the mechanism by which fish evolve into coordinated schools, the spatial-explicit agent-based models, which were widely used to simulate the self-organising mechanism of animal collective behaviour (reviewed in Chapter 2.4.1), have been adopted to demonstrate the behavioural adaptation of a prey population and infer the evolutionary dynamic of fish schools (reviewed in Chapter 2.4.2). However, the various simulation outputs based on different model designs have caused concerns and criticisms on the validity of an ecological model and its inference (reviewed in Chapter 2.5.1).

To investigate the ‘why’ question of fish schools based on an agent-based simulation, the first research question in this thesis is how to reduce the bias of model setting so that the simulation outputs can be more informative for the understanding of fish’s adaptation in evolution. The works in Chapter III addressed this question from the following two aspects. One is that the predesignated set of potential strategies (for prey agents to adopt in evolution) in most of the previous works was replaced by an open-ended solution space. Since the outcome of an evolutionary simulation is crucially

affected by the candidate strategies which are chosen for agents to adopt, the proposed model was designed to include all possible strategies (mappings from local information to elementary behaviours), whether known or unknown at present, by introducing the NEAT algorithm (Stanley & Miikkulainen, 2002). This algorithm can increase the complexity of its neural networks during an evolutionary process, without an upper bound of the number of nodes and links. Hence, a profitable strategy, regardless of its complexity, can be generated automatically without the necessity of being designed in advance. These works are in Chapter 3.2. The other aspect of the efforts to reduce modelling biases is to adjust and validate the proposed model based on the big concerns in the ecological domain, which are the accordance of model settings and the empirical data (analysed in Chapter 3.4), the robustness of a model against noises and the sensitivity of parameters (analysed in Chapter 3.5). By heeding these concerns, the proposed model has avoided many biases present in previous works. Therefore, the simulation outputs can be more persuasive.

Then, the next research question, about whether the evolution of fish's schooling behaviour can be simulated and explained reasonably, was proposed and addressed in Chapter IV. It is worth mentioning that although few previous works had proposed inspiring findings on this research question, those explanations may be not as complete due to the significant conflict between their agent designs and the real fish, which will be discussed in Chapter 6.2.1. In Chapter IV, based on the proposed model in Chapter III, the evolutionary trajectory from isolated prey agents to the schooling pattern was observed and reported in Chapter 4.3. The simulation demonstrated that under individual selection, these fish-like agents with local sensors and local responses evolve along the transitions from being isolated, via the formation of swarms, to the formation

of schools. While the dynamic of the transition from isolated individuals to cohesive swarms have been widely understood as the selfish herd scenario, the proposed model in this thesis originally demonstrated that, in the swarming stage, fish agents will evolve to leave the boundary of a tightly packed swarm if it is followed by a number of nearby agents (3 or more in the simulation). When this ‘collective departure strategy’ is widely adopted in the population, the transition from the swarming pattern to the schooling pattern emerges. Through the game-theoretic analysis in Chapter 4.4, it was derived that this ‘collective departure strategy’, which has not been noticed and proposed in previous models, can be evolutionarily stable in a considerable range of the risk distributions among positions. The simulation and analysis revealed that schooling can be self-organised by the ‘collective departure strategy’, and the ‘collective departure’ can be evolutionarily stable in a wide range of the risk distribution among positions.

Since the positional risk distribution is affected by the feeding preference at the predator side, the follow-up research question is whether the ‘collective departure strategy’ and its emerged schooling pattern can still be evolutionarily stable given predators are also adaptive. To address this issue, an extensive agent-based model was built in Chapter 5.2 to simulate the coevolution between predators and prey. The simulations in Chapter 5.3 and analyses in Chapter 5.4 demonstrated that there are evolutionarily stable states in this behavioural coevolutionary system. In these stable states, prey agents always adopt the collective departure strategy and lead to the emergence of a schooling pattern. In contrast, the adaptive hunting strategies can be varied depending on the strength of the predators. If predators are extremely strong so that the energy cost has no difference between chasing a moving school and chasing a stationary swarm, they evolve to hunt the central position of a prey aggregate. Otherwise, they exhibit the ‘marginal predation’

behaviour, which means hunting those on the boundary of a prey group. Moreover, the game-theoretic analysis implied that marginal predation is no longer evolutionarily stable when predators evolve to hunt in isolation. In this case, hunting the central position should be evolutionarily stable regardless of the strength of a predator. As discussed in Chapter 5.5, the significant consistency between these theoretical predictions and the observed behaviours of predatory fish and prey fish in the marine world has largely highlighted the validity of this study.

6.2 Contribution

Through the systematic experiments and analyses, this thesis has brought a unique viewpoint on the behavioural evolution of prey fish as well as their predators. It is evaluated that these findings have considerably revealed the essence of fish's schooling adaptation, which had provoked disputes for decades. Here three points of this thesis's contributions are indicated, from the major ones to the minor ones sequentially.

6.2.1 The Proposed Collective Departure Strategy

The collective departure strategy, that is, leaving the swarm periphery together to expose the central prey and share the predation risk, was originally observed from the spatial-explicit agent-based simulations in Chapter IV. The game-theoretic analysis in Chapter IV has shown that given prey groups are too crowded to be entered, this strategy can invade the well-known 'selfish herd scenario' (Hamilton, 1971), where prey individuals always attempt to get into the centre of a group. Through this invasion, a stationary swarm then converts into moving schools and reaches the evolutionary stability. As being at the front edge of a school can be slightly more at risk than being a

follower, Chapter 5.3.1 further demonstrated how the collective departure scenario reaches its evolutionary stability under this kind of risk distribution.

Previous explanations of the evolution of fish schools are mainly from the two aspects. One is that the higher predation risk of being at the front edge of a school could be balanced by the better foraging opportunity, which implies fish are more likely to exhibit schooling behaviour at the foraging stage (Krause, 1992; Krause, 1993; DeBlois & Rose, 1996). As not favoured by the empirical data (Hoare et al., 2004; Tien et al., 2004), this explanation has been less proposed in recent works. The other explanation is that the individual difference may drive a sub-group of fish to lead the other ones, which implies there is leadership in fish schools (Krause et al., 2000). There have been many modelling works to demonstrate this kind of 'leader-follower' movement can be self-organised (Couzin et al., 2005; Conradt et al., 2009; Couzin et al., 2011) or evolved (Conradt & Roper, 2009; Guttal & Couzin, 2010; Eshel et al., 2011) by heterogeneous prey agents. As supportive evidence, some empirical data showed that fish do have leaders at the foraging stage (Krause et al., 1992; Couzin et al., 2011). However, the schooling pattern under predation risk has long been considered composed of relatively homogeneous fish individuals (Partridge, 1980; Ward et al., 2001; Ioannou et al., 2012). Therefore, the originally proposed 'collective departure scenario', which is purely based on the survival benefit of homogeneous prey, may be a more reasonable explanation of fish's schooling behaviour in danger.

Although few modelling works, like Oboshi et al. (2003), Wood & Ackland (2007) and Ioannou et al. (2012), have demonstrated that relatively homogeneous prey agents can evolve into the schooling behaviour, the agents in these works were all designed without sensors to detect the environmental information. In other words, an agent is

constrained to exhibit the same response at different positions in these works. However, the different response based on the acquisition of local information is essential to the evolution of collective animal behaviour (Hamilton, 1971; Krause et al., 1998; Parrish & Edelstein-Keshet, 1999). Also, it has been reported that the schooling behaviour of real fish is maintained by a fish's eyes and lateral lines (Partridge, 1982; Faucher et al., 2010). Nevertheless, previous modelling works which allowed their agents (with identical endowments) to make decisions based on their local surroundings have not demonstrated the evolution of schooling behaviour. Instead, these works usually demonstrated an evolutionary trajectory from isolated prey to stationary swarms (Viscido et al., 2002; Reluga & Viscido, 2005; Olson et al. 2013).

An important reason that the previous works did not demonstrate the collective departure scenario is the neglect of body overlaps among agents. In the proposed model, physical overlaps between two agent's bodies were strictly forbidden through a hard penalty on the fitness value, which setting avoids an agent's attempt to enter a compact group. However, almost all of previous works in this domain, like all the above mentioned works, allowed overlaps. As analysed in Chapter 4.5.2, if outer agents can squeeze into the centre of a group, the condition to let the collective departure scenario evolutionarily stable can no longer exist.

6.2.2 The ESS in Predator-Prey Coevolution

There have been few modelling works which simulated the behavioural coevolution between the predator(s) and the prey aggregation (Ward et al., 2001; Olson et al., 2016b). So far, the findings from these works are rarely considered an informative analogy to the adaptations of natural predators and prey. For example, Olson et al.

(2016b) demonstrated that when prey evolve into a cohesive swarm, the predator will evolve to attack large groups. Prey then evolve to form a dispersal pattern, which drives the predator evolves to attack the nearest prey and the prey evolve into a cohesive swarm again. This simulation output seems difficult to be linked to the natural predator-prey coevolution.

In these works, the evolution of predators' hunting strategies depended on the development of a geometric movement in a virtual arena. That is to say, these works expected that the predator agent, which made its decision based on simple environmental information, can evolve into a hunting movement similar to that of some natural predators. Considering the sophisticated hunting behaviours exhibited by natural predators, like the 'marginal predation' by bass and the 'herding pass' by dolphins (reviewed in Chapter 2.2.2), the attempt to evolve a predator agent into such kind of movement would be difficult to succeed.

As mentioned in Chapter V, an original breakthrough by the proposed coevolutionary model was to project predators' hunting strategies into the feeding preferences among different positions. Since a feeding preference can be represented by a vector, the adaptation at the predator side then can be easily simulated. Through the literature search by the author, there are no related works which proposed a similar idea to formulate the predator's hunting behaviour. By connecting the feeding preferences of predators to the positional risks at the prey side, the coevolutionary system, as the interaction between predators' adaptation and prey's adaptation, can be built, which details are in Chapter 5.2.

As summarised in Chapter 6.1, this coevolutionary model illustrated a comprehensive framework to explain various predatory behaviours in the marine world. Compared to previous related works, such as Ward et al. (2001), Olson (2016a) and Olson (2016b), the findings of the present work provided a more realistic analogy to the behaviours of predatory fish and cetaceans. Moreover, the game-theoretic analysis in Chapter 5.4 also originally explained how these adaptive strategies in the predator-prey coevolution can be evolutionarily stable. These contributions have highlighted the significance of the works in Chapter V.

6.2.3 The Adjustments to Reduce Modelling Biases

It is obvious that those model settings which may let the simulation deviate from the targeted system should be avoided. However, whether a design is a reasonable simplification or a modelling bias has been a difficult question in ecological modelling. At the same time introducing many model settings developed in previous works, this thesis also highlights a few modifications which significantly increase the validity of a model.

The most significant modification is to provide an open-ended solution space to the evolution of prey agents' strategies. Although techniques to search solutions in an open-ended space have already been developed in Computer Science for a long time (Ficici & Pollack, 1998; Stanley & Miikkulainen, 2002), introducing this kind of algorithms into the ecological modelling domain is still an excellent contribution. As demonstrated in Chapter IV, this modification allowed prey agents to adopt beneficial strategies even if they were unknown in advance. This advantage makes the proposed model distinct from previous related works, like Reluga & Viscido (2005), Wood & Ackland (2007),

Ioannou et al. (2012) and Olson (2016b). The agents in these works can only adopt strategies among the predesignated candidates. Once a beneficial strategy is neglected by the model designer, the simulation output then deviates from the real system.

A simple but important modification is to forbid body overlaps strictly. The influence of physical overlaps between two prey agents' bodies has long been ignored in previous evolutionary and coevolutionary models, such as Viscido et al. (2002), Oboshi et al. (2003), Reluga & Viscido (2005), Wood & Ackland (2007), Ioannou et al. (2012), Olson et al. (2013), Olson et al. (2016a) and Olson et al. (2016b). Although some of these works, like Wood & Ackland (2007) and Ioannou et al. (2012), forced an agent to repulse from those extremely close neighbours to reduce the level of overlapping, this smooth control is far from enough to forbid agents to adopt the unrealistic strategy as entering a crowded group by passing through others' bodies. The present work has originally shown that when entering a group with body overlaps is strictly forbidden, the schooling pattern can replace the swarming pattern through the collective departure scenario.

The individual paralleling behaviour was widely adopted in related agent-based models (reviewed in Chapter 2.4). However, this setting has been criticised due to the inconsistency with the empirical data (reviewed in Chapter 2.5.1). Romanczuk et al. (2009) and Strombom (2011) have demonstrated how a collective motion can be self-organised only by individual attraction and repulsion. Based on the knowledge from these works, the proposed model further demonstrated that the evolution of schooling behaviour can be well simulated without the design of individual paralleling behaviour.

6.3 Limitations and Future Works

The present works in this thesis have proposed fruitful findings to the topic why fish adopt the schooling behaviour in evolution. However, these works also contain limitations which are waiting for further investigations and studies. As discussed in Chapter 3.6, there were few potentially influential factors of the model setting which have not been experimented in the proposed spatial-explicit agent-based model, such as the adaptation of fish's speed and the influence of fish's body shape. Besides, the collective departure scenario proposed in Chapter IV can be more significant if biological evidence from the empirical data is reported. Lastly, the research outputs have revealed a potential to explain the evolution of collective behaviour in other animals or even in human society. It is expected that through more experiments and validations, further models based on this thesis can discover the evolutionary reasons of more collective behaviours. These future works are discussed sequentially in the following sub-sections.

6.3.1 Influence of Other Factors to the Simulation

The proposed spatial-explicit agent-based model in this thesis followed most of the popular simplifications in previous works, at the same time modifying some previous settings which may cause the bias of simulation. For example, one significant modification is to forbid the body overlaps. However, two simplifications in the present model, which were also adopted by most of the related modelling works, are evaluated worthy of further experiments. One is the fixed speed of prey agents, and the other is the round body shape of an agent.

The moving speed of an agent was fixed as a constant in the proposed model and many other works (Schellinck & White, 2011). However, in Couzin et al. (2002) and Wood & Ackland (2007), the influence of speed on schooling behaviour has been demonstrated. In fact, the schooling behaviour of natural fish also involves coordinated changes of speeds (Magurran & Pitcher, 1987). Therefore, one future work is to investigate whether the involvement of speed adaptation can affect the collective departure scenario.

The other potentially influential factor is the setting of agents' body shape. A fish agent is usually designed with a round shape (Schellinck & White, 2011), even though many species of schooling fish are in an elongated shape. It may be because the demonstrated self-organising mechanisms are qualitatively the same compared with the agents with elongated body shapes. However, according to the findings in this thesis, the body shape may be influential when simulating the adaptation of schooling fish in evolution. It is because a longer body shape may imply a longer schooling group, which could affect the distribution of positional risks and hence affect the behavioural adaptation.

6.3.2 Evidence of Collective Departure Scenario in Fish

As the collective departure strategy is originally proposed in this thesis, the empirical data to validate whether fish exhibit this tactic are scant. Although it was informed by a biologist, Iain D. Couzin, that some species of fish do exhibit the collective departure behaviour, more biological experiments are still needed to know whether the proposed theoretical scenario exactly explains the adaptation of fish's schooling behaviour.

Additionally, the coevolutionary model in Chapter V has predicted various evolutionarily stable strategies at the predator side given different conditions. Although

supportive evidence has been presented in Chapter 5.6 through a literature search by the author, a more detailed investigation with the cooperation of biological experts will be helpful to construct a complete validation of these theoretical predations.

6.3.3 Analogy of Collective Departure Scenario to Other Animals

The research works in this thesis were all carefully focused on fish which are under predation risk. However, it is obvious that some findings have revealed a potential to explain other group-living animals, for example, the collective motion of a herd of sheep or a flock of birds. For two reasons the research domain of this thesis was strictly put on gregarious prey fish. One is that the evolutionary mechanisms to drive different animal individuals into the collective motion can be various. For example, the coordinated movement of locust has been reported due to the cannibalism phenomenon (Romanczuk et al., 2009; Guttal et al., 2012). The other reason is that a generalised inference and analogy to other animals may reduce the authority of the model design. For example, some species of ungulates have been observed to make decisions based on their social roles (Leuthold, 2012). To maintain the authenticity of the model design and findings, the thesis only considered the schooling behaviour of prey fish.

Nevertheless, the findings in Chapter IV and Chapter V, as the collective departure scenario and its extension under the predator-prey coevolution, would be more significant if these demonstrations and derivations can be compared with a wider range of animal behaviour. It can be expected that some cluster of organisms may better fit the theoretical analysis as prey fish, and some others may be the exceptions. By analysing these differences, meaningful adjustments of the model can be made, so that a more

convincing framework could be constructed to explain the evolution of collective behaviours in animals.

Furthermore, an ambition remained in the future work is to extend the evolutionary model and its inferences into the human social dynamics, which is a domain about the self-organising phenomenon in human society. As intimated by the name of the proposed RPF metric (abbreviations of 'ranger', 'pioneer', 'follower' and 'coward') in Chapter 3.5, it has been noticed that the proposed scenario of fish, as an unfair group may collapse due to the collective departure of suffering individuals, could be linked to some features in human society. It will be studied whether certain adaptations of human social roles can be explained by an extension of the collective departure scenario.

REFERENCES

- Angeline, P. J., & Pollack, J. B. (1993). Competitive Environments Evolve Better Solutions for Complex Tasks. In ICGA (pp. 264-270).
- Aoki, I. (1982). A simulation study on the schooling mechanism in fish. *Bulletin of the Japanese Society of Scientific Fisheries*, 48.
- Atz, J. W. (1953, February). Orientation in schooling fishes. In *Proc. Conf. Orientation Anim. Off. Nav. Res* (pp. 103-130).
- Baker, J. E. (1987, July). Reducing bias and inefficiency in the selection algorithm. In *Proceedings of the second international conference on genetic algorithms* (pp. 14-21).
- Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., ... & Zdravkovic, V. (2008). Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proceedings of the National Academy of Sciences*, 105(4), 1232-1237.
- Beasley, D., Martin, R. R., & Bull, D. R. (1993). An overview of genetic algorithms: Part 1. *Fundamentals. University computing*, 15, 58-58.
- Benda, M. (1985). On optimal cooperation of knowledge sources. Technical Report BCS-G2010-28.
- Benoit-Bird, K. J., & Au, W. W. (2009). Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *The Journal of the Acoustical Society of America*, 125(1), 125-137.
- Bharucha-Reid, A. T. (2012). *Elements of the Theory of Markov Processes and their Applications*. Courier Corporation.
- Blickle, T., & Thiele, L. (1995). A comparison of selection schemes used in genetic algorithms.
- Bonabeau, E., Dorigo, M., & Theraulaz, G. (1999). *Swarm intelligence: from natural to artificial systems* (No. 1). Oxford university press.
- Bouffanais, R. (2016). *Design and Control of Swarm Dynamics*. Springer.
- Breckling, B., Middelhoff, U., & Reuter, H. (2006). Individual-based models as tools for ecological theory and application: understanding the emergence of organisational properties in ecological systems. *Ecological Modelling*, 194(1), 102-113.
- Breder, C. M. (1967). On the survival value of fish schools. *Zoologica*, 52(2), 25-40.
- Bumann, D., Krause, J., & Rubenstein, D. (1997). Mortality risk of spatial positions in animal groups: the danger of being in the front. *Behaviour*, 1063-1076.
- Carlson, S. E. (1995). A general method for handling constraints in genetic algorithms. In *Proceedings of the second annual joint conference on information science* (pp. 663-667).
- Cliff, D., & Miller, G. F. (1995). Co-evolution of pursuit and evasion II: Simulation methods and results.

- Clua, É., & Grosvalet, F. (2001). Mixed-species feeding aggregation of dolphins, large tunas and seabirds in the Azores. *Aquatic Living Resources*, 14(1), 11-18.
- Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist*, 661-696.
- Conradt, L. (2011). Collective behaviour: when it pays to share decisions. *Nature*, 471(7336), 40-41.
- Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology & Evolution*, 20(8), 449-456.
- Conradt, L., & Roper, T. J. (2009). Conflicts of interest and the evolution of decision sharing. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 364(1518), 807-819.
- Conradt, L., Krause, J., Couzin, I. D., & Roper, T. J. (2009). "Leading According to Need" in Self-Organizing Groups. *The American Naturalist*, 173(3), 304-312.
- Couzin, I. D., & Krause, J. (2003). Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior*, 32(1).
- Couzin, I. D., Krause, J., James, R., Ruxton, G. D., & Franks, N. R. (2002). Collective memory and spatial sorting in animal groups. *Journal of theoretical biology*, 218(1), 1-11.
- Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, 433(7025), 513-516.
- Couzin, I. D., Ioannou, C. C., Demirel, G., Gross, T., Torney, C. J., Hartnett, A., ... & Leonard, N. E. (2011). Uninformed individuals promote democratic consensus in animal groups. *science*, 334(6062), 1578-1580.
- Davis, L. (1991). *Handbook of Genetic Algorithms*. Van Nostrand. New York.
- Dawkins, R. (1976). *The selfish gene*. Oxford university press. (2006 edition)
- De Vos, A., & O'Riain, M. J. (2010). Sharks shape the geometry of a selfish seal herd: experimental evidence from seal decoys. *Biology Letters*, 6(1), 48-50.
- DeAngelis, D. L., & Grimm, V. (2013). Individual-based models in ecology after four decades. *F1000prime reports*, 6, 39-39.
- Deb, K., Pratap, A., Agarwal, S., & Meyarivan, T. A. M. T. (2002). A fast and elitist multiobjective genetic algorithm: NSGA-II. *Evolutionary Computation, IEEE Transactions on*, 6(2), 182-197.
- DeBlois, E. M., & Rose, G. A. (1996). Cross-shoal variability in the feeding habits of migrating Atlantic cod (*Gadus morhua*). *Oecologia*, 108(1), 192-196.
- Delcourt, J., & Poncin, P. (2012). Shoals and schools: back to the heuristic definitions and quantitative references. *Reviews in Fish Biology and Fisheries*, 22(3), 595-619.
- Deutsch, A., Theraulaz, G., & Vicsek, T. (2012). Collective motion in biological systems. *Interface Focus*, rsfs20120048.
- Domenici, P. (2001). The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 131(1), 169-182.

- Domenici, P., & Blake, R. (1997). The kinematics and performance of fish fast-start swimming. *Journal of Experimental Biology*, 200(8), 1165-1178.
- Domenici, P., Wilson, A. D. M., Kurvers, R. H. J. M., Marras, S., Herbert-Read, J. E., Steffensen, J. F., ... & Krause, J. (2014). How sailfish use their bills to capture schooling prey. *Proceedings of the Royal Society of London B: Biological Sciences*, 281(1784), 20140444.
- Eshel, I., Sansone, E., & Shaked, A. (2011). On the evolution of group-escape strategies of selfish prey. *Theoretical population biology*, 80(2), 150-157.
- Faucher, K., Parmentier, E., Becco, C., Vandewalle, N., & Vandewalle, P. (2010). Fish lateral system is required for accurate control of shoaling behaviour. *Animal Behaviour*, 79(3), 679-687.
- Ficici, S. G., & Pollack, J. B. (1998). Challenges in coevolutionary learning: Arms-race dynamics, open-endedness, and mediocre stable states. In *Proceedings of the sixth international conference on Artificial life* (pp. 238-247).
- Foster, W. A., & Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect.
- Giardina, I. (2008). Collective behavior in animal groups: theoretical models and empirical studies. *HFSP journal*, 2(4), 205-219.
- Goh, C. K., & Tan, K. C. (2009). A competitive-cooperative coevolutionary paradigm for dynamic multiobjective optimization. *Evolutionary Computation, IEEE Transactions on*, 13(1), 103-127.
- Goldberg, D. E. (1989). *Genetic algorithms in search optimization and machine learning* (Vol. 412). Reading Menlo Park: Addison-wesley.
- Goldberg, D. E., & Deb, K. (1991). A comparative analysis of selection schemes used in genetic algorithms. *Foundations of genetic algorithms*, 1, 69-93.
- Grégoire, G., Chaté, H., & Tu, Y. (2003). Moving and staying together without a leader. *Physica D: Nonlinear Phenomena*, 181(3), 157-170.
- Grimm, V., & Railsback, S. F. (2012). Pattern-oriented modelling: a 'multi-scope' for predictive systems ecology. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 367(1586), 298-310.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., ... & DeAngelis, D. L. (2005). Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *science*, 310(5750), 987-991.
- Guttal, V., & Couzin, I. D. (2010). Social interactions, information use, and the evolution of collective migration. *Proceedings of the National Academy of Sciences*, 107(37), 16172-16177.
- Guttal, V., Romanczuk, P., Simpson, S. J., Sword, G. A., & Couzin, I. D. (2012). Cannibalism can drive the evolution of behavioural phase polyphenism in locusts. *Ecology letters*, 15(10), 1158-1166.
- Hall, S. J., Wardle, C. S., & MacLennan, D. N. (1986). Predator evasion in a fish school: test of a model for the fountain effect. *Marine biology*, 91(1), 143-148.
- Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of theoretical Biology*, 31(2), 295-311.
- Hammerstein, P., & Selten, R. (1994). Game theory and evolutionary biology. *Handbook of game theory*

with economic applications, 2, 929-993.

Handegard, N. O., Boswell, K. M., Ioannou, C. C., Leblanc, S. P., Tjøstheim, D. B., & Couzin, I. D. (2012). The dynamics of coordinated group hunting and collective information transfer among schooling prey. *Current Biology*.

Haupt, R. L., & Haupt, S. E. (2004). *Practical genetic algorithms*. John Wiley & Sons.

Hauser, L., Carvalho, G. R., & Pitcher, T. J. (1998). Genetic population structure in the Lake Tanganyika sardine *Limnothrissa miodon*. *Journal of Fish Biology*, 53(sA), 413-429.

Herbert-Read, J. E., Perna, A., Mann, R. P., Schaerf, T. M., Sumpter, D. J., & Ward, A. J. (2011). Inferring the rules of interaction of shoaling fish. *Proceedings of the National Academy of Sciences*, 108(46), 18726-18731.

Hillis, W. D. (1990). Co-evolving parasites improve simulated evolution as an optimization procedure. *Physica D: Nonlinear Phenomena*, 42(1), 228-234.

Hirsch, B. T., & Morrell, L. J. (2011). Measuring marginal predation in animal groups. *Behavioral Ecology*, 22(3), 648-656.

Hoare, D. J., Couzin, I. D., Godin, J. G., & Krause, J. (2004). Context-dependent group size choice in fish. *Animal Behaviour*, 67(1), 155-164.

Holland, J. H. (1975). *Adaptation in natural and artificial systems: an introductory analysis with applications to biology, control, and artificial intelligence*. U Michigan Press.

Horn, J., Nafpliotis, N., & Goldberg, D. E. (1994, June). A niched Pareto genetic algorithm for multiobjective optimization. In *Evolutionary Computation, 1994. IEEE World Congress on Computational Intelligence., Proceedings of the First IEEE Conference on* (pp. 82-87). Ieee.

Huth, A., & Wissel, C. (1994). The simulation of fish schools in comparison with experimental data. *Ecological modelling*, 75, 135-146.

Inada, Y., & Kawachi, K. (2002). Order and flexibility in the motion of fish schools. *Journal of theoretical Biology*, 214(3), 371-387.

Ingber, L., & Rosen, B. (1992). Genetic algorithms and very fast simulated reannealing: A comparison. *Mathematical and computer modelling*, 16(11), 87-100.

Ioannou, C. C., Guttal, V., & Couzin, I. D. (2012). Predatory fish select for coordinated collective motion in virtual prey. *Science*, 337(6099), 1212-1215.

Jadaan, O. A. Rajamani, L., Rao, C. R. (2005). Improved Selection Operator for GA. *Journal of Theoretical and Applied Information Technology*.

James, R., Bennett, P. G., & Krause, J. (2004). Geometry for mutualistic and selfish herds: the limited domain of danger. *Journal of Theoretical Biology*, 228(1), 107-113.

Joines, J. A., & Houck, C. R. (1994, June). On the use of non-stationary penalty functions to solve nonlinear constrained optimization problems with GA's. In *Evolutionary Computation, 1994. IEEE World Congress on Computational Intelligence., Proceedings of the First IEEE Conference on* (pp. 579-584). IEEE.

- Karlin, S. (2014). *A first course in stochastic processes*. Academic press.
- Katz, Y., Tunstrøm, K., Ioannou, C. C., Huepe, C., & Couzin, I. D. (2011). Inferring the structure and dynamics of interactions in schooling fish. *Proceedings of the National Academy of Sciences*, 108(46), 18720-18725.
- King, A. J., & Cowlshaw, G. (2007). When to use social information: the advantage of large group size in individual decision making. *Biology Letters*, 3(2), 137-139.
- Krause, J. (1993). The influence of hunger on shoal size choice by three-spined sticklebacks, *Gasterosteus aculeatus*. *Journal of Fish Biology*, 43(5), 775-780.
- Krause, J. (1994). Differential fitness returns in relation to spatial position in groups. *Biological Reviews*, 69(2), 187-206.
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.
- Krause, J., Bumann, D., & Todt, D. (1992). Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (*Rutilus rutilus*). *Behavioral Ecology and Sociobiology*, 30(3-4), 177-180.
- Krause, J., Ruxton, G. D., & Rubenstein, D. (1998). Is there always an influence of shoal size on predator hunting success?. *Journal of Fish Biology*, 52(3), 494-501.
- Krause, J., Hoare, D., Krause, S., Hemelrijk, C. K., & Rubenstein, D. I. (2000). Leadership in fish shoals. *Fish and Fisheries*, 1(1), 82-89.
- Krause, J., Hoare, D. J., Croft, D., Lawrence, J., Ward, A., Ruxton, G. D., ... & James, R. (2000). Fish shoal composition: mechanisms and constraints. *Proceedings of the Royal Society of London B: Biological Sciences*, 267(1456), 2011-2017.
- Křivan, V. (1998). Effects of optimal antipredator behavior of prey on predator-prey dynamics: the role of refuges. *Theoretical population biology*, 53(2), 131-142.
- Lee, S. H., Pak, H. K., & Chon, T. S. (2006). Dynamics of prey-flock escaping behavior in response to predator's attack. *Journal of theoretical biology*, 240(2), 250-259.
- Leuthold, W. (2012). *African ungulates: a comparative review of their ethology and behavioral ecology* (Vol. 8). Springer Science & Business Media.
- Lima, S. L. (1995). Collective detection of predatory attack by social foragers: fraught with ambiguity?. *Animal Behaviour*, 50(4), 1097-1108.
- Magurran, A. E. (1990). The adaptive significance of schooling as an anti-predator defense in fish. *Ann. Zool. Fennici*, 27, 51-66.
- Magurran, A. E., & Pitcher, T. J. (1987). Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. *Proceedings of the Royal society of London. Series B. Biological sciences*, 229(1257), 439-465.
- Michalewicz, Z. (1995). A Survey of Constraint Handling Techniques in Evolutionary Computation Methods. *Evolutionary Programming*, 4, 135-155.
- Michalewicz, Z., & Attia, N. (1994, February). Evolutionary optimization of constrained problems.

In Proceedings of the 3rd annual conference on evolutionary programming (pp. 98-108). World Scientific Publishing, River Edge, NJ.

Milinski, M., & Heller, R. (1978). Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.).

Miller, J. H. (1996). The coevolution of automata in the repeated prisoner's dilemma. *Journal of Economic Behavior & Organization*, 29(1), 87-112.

Mooney, H. A., & Cleland, E. E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, 98(10), 5446-5451.

Mooring, M. S., & Hart, B. L. (1992). Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour*, 123(3), 173-193.

Morgan, M. J., & Godin, J. G. J. (1985). Antipredator benefits of schooling behaviour in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus*). *Zeitschrift für Tierpsychologie*, 70(3), 236-246.

Naish, K. A., Carvalho, G. R., & Pitcher, T. J. (1993). The genetic structure and microdistribution of shoals of *Phoxinus phoxinus*, the European minnow. *Journal of Fish Biology*, 43(sA), 75-89.

Nolfi, S., & Floreano, D. (1998). Coevolving predator and prey robots: do "arms races" arise in artificial evolution?. *Artificial life*, 4(4), 311-335.

Noraini, M. R., & Geraghty, J. (2011). Genetic algorithm performance with different selection strategies in solving TSP. *Proc. World Congress Engineering*, 2.

Nowak, M. A. (2006). Five rules for the evolution of cooperation. *science*, 314(5805), 1560-1563.

Nowak, M. A., & Sigmund, K. (2004). Evolutionary dynamics of biological games. *science*, 303(5659), 793-799.

O'Donoghue, S. H., Drapeau, L., Dudley, S. F., & Peddemors, V. M. (2010). The KwaZulu-Natal sardine run: shoal distribution in relation to nearshore environmental conditions, 1997–2007. *African Journal of Marine Science*, 32(2), 293-307.

Oboshi, T., Kato, S., Mutoh, A., & Itoh, H. (2003). Collective or scattering: Evolving schooling behaviors to escape from predator. In *Proceedings of the 8th International Conference on the Simulation and Synthesis of Living Systems: Artificial Life (Vol. 8, pp. 386-389)*.

Olson, R. S., Hintze, A., Dyer, F. C., Knoester, D. B., & Adami, C. (2013). Predator confusion is sufficient to evolve swarming behaviour. *Journal of The Royal Society Interface*, 10(85), 20130305.

Olson, R. S., Haley, P. B., Dyer, F. C., & Adami, C. (2015). Exploring the evolution of a trade-off between vigilance and foraging in group-living organisms. *Royal Society open science*, 2(9), 150135.

Olson, R. S., Knoester, D. B., & Adami, C. (2016a). Evolution of swarming behavior is shaped by how predators attack. *Artificial life*.

Olson, R. S., Hintze, A., Dyer, F. C., Moore, J. H., & Adami, C. (2016b). Exploring the coevolution of predator and prey morphology and behavior. *arXiv preprint arXiv:1602.08802*.
Olst, J. C. V., & Hunter, J. R. (1970). Some aspects of the organization of fish schools. *Journal of the Fisheries Board of Canada*, 27(7), 1225-1238.

- Osborne, M. J., & Rubinstein, A. (1994). *A course in game theory*. MIT press.
- Paredis, J. (1995). Coevolutionary computation. *Artificial life*, 2(4), 355-375.
- Parr, A. E. (1927). A contribution to the theoretical analysis of the schooling behaviour of fishes. *Occas. Pap. Bingham Oceanogr. Coll.*, 1.
- Parrish, J. K. (1991). Do predators' shape fish schools: interactions between predators and their schooling prey. *Netherlands Journal of Zoology*, 42(2), 358-370.
- Parrish, J. K., & Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science*, 284(5411), 99-101.
- Parrish, J. K., Viscido, S. V., & Grünbaum, D. (2002). Self-organized fish schools: an examination of emergent properties. *The biological bulletin*, 202(3), 296-305.
- Partridge, B. L. (1980). The effect of school size on the structure and dynamics of minnow schools. *Animal Behaviour*, 28(1), 68-IN3.
- Partridge, B. L. (1982). The structure and function of fish schools. *Scientific American*, 246(6), 114-123.
- Powell, G. V. N. (1974). Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour*, 22(2), 501-505.
- Reeves, C. (2003). Genetic algorithms. In *Handbook of metaheuristics* (pp. 55-82). Springer US.
- Reluga, T. C., & Viscido, S. (2005). Simulated evolution of selfish herd behavior. *Journal of Theoretical Biology*, 234(2), 213-225.
- Reynolds, C. W. (1993). An evolved, vision-based behavioral model of coordinated group motion. *From animals to animats*, 2, 384-392.
- Richardson, J. T., Palmer, M. R., Liepins, G. E., & Hilliard, M. (1989, December). Some guidelines for genetic algorithms with penalty functions. In *Proceedings of the third international conference on Genetic algorithms* (pp. 191-197). Morgan Kaufmann Publishers Inc..
- Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal behaviour*, 51(5), 1077-1086.
- Romanczuk, P., Couzin, I. D., & Schimansky-Geier, L. (2009). Collective motion due to individual escape and pursuit response. *Physical Review Letters*, 102(1), 010602.
- Romey, W. L., Walston, A. R., & Watt, P. J. (2008). Do 3-D predators attack the margins of 2-D selfish herds?. *Behavioral Ecology*, 19(1), 74-78.
- Schellinck, J., & White, T. (2011). A review of attraction and repulsion models of aggregation: Methods, findings and a discussion of model validation. *Ecological Modelling*, 222(11), 1897-1911.
- Seghers, B. H. (1974). Schooling behavior in the guppy (*Poecilia reticulata*): an evolutionary response to predation. *Evolution*, 486-489.
- Shaw, E. (1978). Schooling fishes: the school, a truly egalitarian form of organization in which all members of the group are alike in influence, offers substantial benefits to its participants. *American Scientist*, 166-175.

- Similä, T., & Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, 71(8), 1494-1499.
- Sinervo, B., & Lively, C. M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, 380(6571), 240-243.
- Smith, J. M. (1982). *Evolution and the Theory of Games*. Cambridge University Press, Cambridge, UK.
- Smith, M. F., & Warburton, K. (1992). Predator shoaling moderates the confusion effect in blue-green chromis, *Chromis viridis*. *Behavioral ecology and Sociobiology*, 30(2), 103-107.
- Springer, S. (1957). Some observations of the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. *Ecology*, 38(1), 166-171.
- Stanley, K. O., & Miikkulainen, R. (2002). Evolving neural networks through augmenting topologies. *Evolutionary computation*, 10(2), 99-127.
- Stanley, K. O., & Miikkulainen, R. (2004). Competitive coevolution through evolutionary complexification. *J. Artif. Intell. Res.(JAIR)*, 21, 63-100.
- Storn, R., & Price, K. (1997). Differential evolution—a simple and efficient heuristic for global optimization over continuous spaces. *Journal of global optimization*, 11(4), 341-359.
- Strandburg-Peshkin, A., Twomey, C. R., Bode, N. W., Kao, A. B., Katz, Y., Ioannou, C. C., ... & Couzin, I. D. (2013). Visual sensory networks and effective information transfer in animal groups. *Current Biology*, 23(17), R709-R711.
- Strombom, D. (2011). Collective motion from local attraction. *Journal of theoretical biology*, 283(1), 145-151.
- Sumpter, D. J. (2006). The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361(1465), 5-22.
- Sumpter, D. J. (2009). Group behaviour: leadership by those in need. *Current Biology*, 19(8), R325-R327.
- Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., ... & Hails, R. S. (2013). Identification of 100 fundamental ecological questions. *Journal of ecology*, 101(1), 58-67.
- Syswerda, G. (1991). A study of reproduction in generational and steady state genetic algorithms. *Foundations of genetic algorithms*, 2, 94-101.
- Thompson, J. N. (1989). Concepts of coevolution. *Trends in Ecology & Evolution*, 4(6), 179-183.
- Tien, J. H., Levin, S. A., & Rubenstein, D. I. (2004). Dynamics of fish shoals: identifying key decision rules. *Evolutionary Ecology Research*, 6(4), 555-565.
- Tunstrøm, K., Katz, Y., Ioannou, C. C., Huepe, C., Lutz, M. J., & Couzin, I. D. (2013). Collective states, multistability and transitional behavior in schooling fish. *PLoS Comput Biol*, 9(2), e1002915.
- Turner, G. F., & Pitcher, T. J. (1986). Attack abatement: a model for group protection by combined avoidance and dilution. *American Naturalist*, 228-240.
- Van Valen, L. (1973). A new evolutionary law. *Evolutionary theory*, 1, 1-30.

- Vaughn-Hirshorn, R. L., Muzi, E., Richardson, J. L., Fox, G. J., Hansen, L. N., Salley, A. M., ... & Würsig, B. (2013). Dolphin underwater bait-balling behaviors in relation to group and prey ball sizes. *Behavioural processes*, 98, 1-8.
- Vavak, F., & Fogarty, T. C. (1996, May). Comparison of steady state and generational genetic algorithms for use in nonstationary environments. In *Evolutionary Computation, 1996., Proceedings of IEEE International Conference on* (pp. 192-195). IEEE.
- Viscido, S. V., & Wethey, D. S. (2002). Quantitative analysis of fiddler crab flock movement: evidence for 'selfish herd' behaviour. *Animal behaviour*, 63(4), 735-741.
- Viscido, S. V., Miller, M., & Wethey, D. S. (2001). The response of a selfish herd to an attack from outside the group perimeter. *Journal of Theoretical Biology*, 208(3), 315-328.
- Viscido, S. V., Miller, M., & Wethey, D. S. (2002). The dilemma of the selfish herd: the search for a realistic movement rule. *Journal of Theoretical Biology*, 217(2), 183-194.
- Vulinec, K. (1990). Collective security: aggregation by insects as a defense. *Insect defenses*, 251-288.
- Ward, C. R., Gobet, F., & Kendall, G. (2001). Evolving collective behavior in an artificial ecology. *Artificial life*, 7(2), 191-209.
- Ward, A. J., Sumpter, D. J., Couzin, I. D., Hart, P. J., & Krause, J. (2008). Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences*, 105(19), 6948-6953.
- Watson, R. A., & Pollack, J. B. (2001). Coevolutionary dynamics in a minimal substrate. In *Proceedings of the Genetic and Evolutionary Computation Conference (GECCO 2001)* (pp. 702-709). Morgan Kaufmann.
- Webb, P. W. (1976). The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator-prey interactions. *The Journal of experimental biology*, 65(1), 157-177.
- Webb, P. W., & De Buffrénil, V. (1990). Locomotion in the biology of large aquatic vertebrates. *Transactions of the American Fisheries Society*, 119(4), 629-641.
- Werner, G. M., & Dyer, M. G. (1993). Evolution of herding behavior in artificial animals. In *From Animals to Animats 2: Proceedings of the Second International Conference on Simulation of Adaptive Behavior* (Vol. 2, p. 393). MIT Press.
- Whitley, L. D. (1989, December). The GENITOR Algorithm and Selection Pressure: Why Rank-Based Allocation of Reproductive Trials is Best. *In ICGA* (Vol. 89, pp. 116-123).
- Wiegand, T., Jeltsch, F., Hanski, I., & Grimm, V. (2003). Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. *Oikos*, 100(2), 209-222.
- Wieland, A. P. (1991, July). Evolving neural network controllers for unstable systems. In *Neural Networks, 1991., IJCNN-91-Seattle International Joint Conference on* (Vol. 2, pp. 667-673). IEEE.
- Wiley, D., Ware, C., Bocconcelli, A., Cholewiak, D., Friedlaender, A., Thompson, M., & Weinrich, M. (2011). Underwater components of humpback whale bubble-net feeding behaviour. *Behaviour*, 148(5), 575-602.

Williams, G. C. (1966). *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press.(2008 edition)

Wood, A. J., & Ackland, G. J. (2007). Evolving the selfish herd: emergence of distinct aggregating strategies in an individual-based model. *Proceedings of the Royal Society B: Biological Sciences*, 274(1618), 1637-1642.

Zheng, M., Kashimori, Y., Hoshino, O., Fujita, K., & Kambara, T. (2005). Behavior pattern (innate action) of individuals in fish schools generating efficient collective evasion from predation. *Journal of theoretical biology*, 235(2), 153-167.