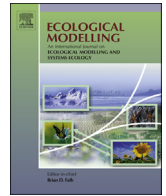




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Evolutionary trends in fish schools in heterogeneous environments

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ABSTRACT

Individual-based modelling has contributed substantially to the understanding of fish schooling behaviour. Schooling is considered to grant several advantages, such as increased defense against predators and increased foraging success. Whereas the former has been well studied with empirical investigations and different modelling approaches, the latter has not received as much attention. Foraging success is considerably influenced by the emergent property of schools to locate and exploit heterogeneously distributed resources more efficiently than solitary fish. However, successful resource exploitation depends on individual fish properties as well as properties of the school in relation to patch size and spatial distribution of resources. Thus, schooling will be favourable in specific environmental conditions and less efficient in others.

We use an individual-based model to assess the foraging efficiency of schooling compared to individual food search under different spatio-temporal distributions of food resources in a dynamic environment. Allowing agents' behaviour to evolve either towards schooling or towards individualism, we demonstrate the adaptation of population characteristics to a particular spatial and temporal distribution of food patches.

With our model we show that the environmental configuration of food patches is crucial for schooling fish to be more efficient in foraging. Moreover, patch size must be considerably larger than the extent of the school but small enough for patch boundaries to take effect. The model contributes to a better understanding of the relationships among spatial dynamics and the driving forces behind behavioural adaptation of trophic strategies in schooling fish.

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1. Introduction

The formation of fish schools is a frequently studied self-organisation phenomenon. Despite the various observational, experimental and modelling studies (see e.g. Hemelrijk and Hildenbrandt, 2012; Lopez et al., 2012 for an overview) there are still important questions concerning the role of schooling behaviour. In particular: how does schooling relate to, and emerge, in an ecological context? Here, we describe a model to analyse structural environmental configurations that would give rise to advantages of schooling, and how schooling and solitary behaviour achieve a balance in a heterogeneous environment.

Several ecological advantages of schooling have been discussed and they include: the defence against predators through confusion effect and the spread of individual risk (e.g. Landeau and Terborgh,

1986; Magurran, 1990; Ioannou et al., 2012), hydrodynamic effects reducing energy cost for swimming (Couzin and Krause, 2003), an increase of foraging efficiency (Pitcher et al., 1982; Packer and Ruttan, 1988), and also the ability to follow gradients more easily (Kils, 1986). Schooling, however, is not always an advantage otherwise solitary fish would be marginalised in the course of evolution. In fact, the grouping of individuals involves ecological trade-offs that assume additional costs that do not always pay off. For instance, schooling requires higher co-ordination efforts and involves competition for resources while increasing survival in particular environments and ecological conditions (Robinson et al., 1996; Packer and Ruttan, 1988; Amarasekare, 2003).

Numerous modelling approaches describe schooling as a distance-dependent shift between three behavioural modes: attraction, alignment and repulsion. These are described for either discrete zones around a fish (Huth and Wissel, 1992; Hoare et al., 2004; Viscido et al., 2007; Hemelrijk and Hildenbrandt, 2007) or for a continuous transition between these modes (Reuter and Breckling, 1994; Breckling et al., 1997; Mirabet et al., 2008). These models address a variety of ecological processes relevant

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to schooling and also, the reaction of the school to the environment. Vabø and Skaret (2008), for instance, focus on schooling in relation to varying spawning events in herring. Couzin et al. (2002) present a more general model on swarming, investigating collective memory associated with these aggregations, whereas Hemelrijk and Kunz (2005) deal with spatial configurations for different sorting and risk avoiding strategies. Viscido et al. (2007) analyse different behavioural modes (e.g. forms of attraction, repulsion and alignment) and derive a set of rules for effective schooling behaviour. Kolpas et al. (2013) analyse how different neighbourhood relations (either purely distance-related or based on Voronoi-neighbourhoods) affect information transfer in schools. Hemelrijk and Hildenbrandt (2012) provide a review of swarm models representing schooling fish and flocking birds with a focus on the internal structure and relationships.

Simulation models contributed considerably to the understanding of schooling phenomena, in particular the individual-based approach (IBM, Huston et al., 1988). The ability of IBMs to represent individual behaviour allows for the testing of behavioural processes (Aoki, 1982) which lead to the formation of fish schools (e.g. Huth and Wissel, 1992). Furthermore, IBMs elucidate structural implications for individual variability and stochastic processes, as well as clarifying how the specific reactions of individuals to other school members contribute to the formation of highly aligned fish schools.

Unresolved are questions about how schooling behaviour is embedded in different ecological interacting networks of lower and higher levels of organisation (e.g. Holling, 2001). These studies often relate to higher trophic levels and study the response of fish schools to attacks by predators with different modelling approaches (Tu and Sayed, 2011; Lett et al., 2014; Chen and Kolokolnikov, 2014). By investigating the emergence of collective decisions, Huse et al. (2002) and Mirabet et al. (2008) showed that only a small fraction of individuals need to focus on a certain direction, or goal, to influence the entire school. This property was also confirmed by empirical experiments (Stienessen and Parrish, 2013). However, plankton patches are inherently patchy yet important for fish at intermediate trophic levels. The explicit reaction of fish schools to patchy resources, has yet to be studied within a modelling framework. Grünbaum (1998) demonstrated that social taxis may enhance the selective advantage of schooling fish feeding on heterogeneously distributed resources (plankton patches). According to simulations with an IBM, schools and fish with only individual orientation use the resources in a spatially heterogeneous environment with differing success (Breckling et al., 1997).

Here, we investigate bottom-up effects of trophic interactions in a context of spatial heterogeneity, quantifying to what extent the feeding efficiency of a fish school depends on the size of food patches and on the temporal frequency of changes in their spatial pattern. As a direct implication, we can show that an adaptation to a particularly structured environment either awards or penalises schooling behaviour.

We put forward the hypothesis that, along a gradient of environmental heterogeneity, the optimal behaviour depends on the scale of fish movement in relation to the spatio-temporal dynamics of food patches.

2. Modelling approach

Our fish school model consists of two basic components; the description of individual fish and a description of the heterogeneous environment. The main focus is on the emergent behaviour of schools and how these differ from individual fish in reaction to size and update frequency of food patches. Fish are implemented in the model with distinct movement behaviours using an individual-based approach. The environment is based on a cellular automaton.

2.1. Technical background and implementation

The model was based on a previous IBM, which considers the distance between neighbouring individuals to adjust the speed and the direction of their movements (for a full model description see Reuter and Breckling, 1994). To facilitate repeated runs and to benefit from an advanced graphical user interface, the model was re-programmed in Java using the MASON Framework (Luke et al., 2005, <http://cs.gmu.edu/~eclab/projects/mason/>), and was run on a Linux-cluster. The model can be run either as a graphical output application or as a batch job in the background. Individual fish move according to a basic movement algorithm, and they may react to food patches by performing autonomous individual movement or by forming a school, as specified by the model's parameters. To investigate potential evolution of schooling behaviour, a simple reproduction process with inheritance of schooling probabilities was implemented (Fig. 1). The parameter specification of the model was built to represent typical schooling fish (e.g. herrings (Clupeidae) or anchovies (Engraulidae)), feeding on plankton patches which vary considerably in space and time (patch size and update frequency). Fish size, i.e. the body length (BL) of each fish, was set to 20 units, the standard cruising speed was one BL per s (time step) and the nearest neighbour distance was below one BL. See Appendix Tables A1–A3 for a full list of parameters.

2.2. Solitary fish: autonomous movement

Following Reuter and Breckling (1994), an individual fish is represented with basic properties of movement. The fish is able to sense neighbouring fish and it has knowledge of the co-ordinates of the current patch that it is within. Movement is described by a vector determined by the current direction (Φ) and a step size. Both of these parameters may vary independently according to the availability of food in the sensed environment. When acting solitarily, the fish performs a directed random walk by randomly choosing a new direction from a Gaussian distribution centred on the former direction with the standard deviation *angDirChgDeg*.¹ The new speed is also chosen from a Gaussian distribution centred on the former speed and the parameter *speedVariance* as the standard deviation. Fish accelerate in regions where food is scarce and slow in regions where food is abundant. In food-free locations acceleration occurs every time-step until the cruising speed (*speedHigh*) has been reached. Otherwise, the fish slows to minimum speed (*speedLow*) while staying on food patches to mimic feeding. The rate of speed change is given by the parameter *acceleration*.

2.3. Schooling behaviour and neighbourhood orientation

In contrast to solitary individuals, schooling fish perform a distance- and density-dependent position adjustment to neighbouring fish (Partridge and Pitcher, 1980; Partridge et al., 1980). Each fish considers neighbouring fish, i.e. those individuals located in *sightRange*, up to a specified maximum number (*maxConsideredNeighbors*). The three behavioural modes a fish can adopt are: (1) attraction (if neighbouring fish are far away but still in *sightRange*), (2) alignment (if neighbouring fish fall into the preferred distance) and (3) repulsion (if a neighbour is too close), with a blind angle (*angBlindBehindDeg*) behind the fish in which neighbours are not considered. The change of behavioural modes is distance-dependent and has been implemented to change continuously (Fig. 2). We assume that the influence of neighbours on

¹ Model parameters are in italics and courier.

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