

## Dynamics of fish shoals: identifying key decision rules

Joseph H. Tien,<sup>1,2</sup> Simon A. Levin<sup>2</sup> and Daniel I. Rubenstein<sup>2\*</sup>

<sup>1</sup>Center for Applied Mathematics, Cornell University, Ithaca, NY 14853 and <sup>2</sup>Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, USA

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### ABSTRACT

Social aggregations of fish are extremely common in nature. Pitcher (1983) defines a social aggregation of fish as a shoal, with a highly polarized shoal constituting a school. The ultimate causes of fish shoaling have been extensively studied and are well established, with the main causes being protection from predators and enhanced foraging ability. The proximate mechanisms by which groups are maintained are less well understood. Several models exist that examine these decision rules. A common theme to these models is the existence of a region at large nearest-neighbour distances (NND), where an individual will move towards its nearest neighbour, and a region of repulsion at small NND, where the individual will move away from its nearest neighbour. Recent models (Gueron *et al.*, 1996; Couzin and Krause, 2003) suggest that shoaling decisions may not be instantaneous, instead being hierarchical as fish assess the presence or absence of one or more neighbours in zones of attraction, repulsion and neutrality. Here a mixed shoal of creek chubs (*Semotilus atromaculatus*) and blacknose dace (*Rhinichthys atratulus*) was examined in the field through video recording and digitization of images. Shoal dynamics were examined both under normal, undisturbed conditions, and in the presence of a simulated predator. By tracking the movements of individual fish over time, we find evidence for both attraction and repulsion zones. But three other novel features emerge as well. First, between regions where focal fish are attracted to, or are repulsed by, neighbours, there appears to be a 'neutral zone', where no consistent response occurs. Second, changes in NND at far distances, more so than at close distances, are affected not only by the position of nearest neighbours, but by the orientation of their velocity vectors as well. Third, the effect of increased fear level of fish induced by the appearance of simulated predators is a decrease in both the average NND and the sizes of the stress, attraction and neutral behavioural zones.

*Keywords:* decision making, field study, fish shoal, model, proximate mechanisms, schooling.

### INTRODUCTION

Groups of fish have been the focus of many different behavioural, ecological and evolutionary studies. Pitcher (1983) defines a shoal as a social aggregation of fish, with a school referring to a synchronized, polarized shoal. The ultimate mechanisms for shoaling have been extensively studied, with the primary benefits being protection from predators

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\* Author to whom all correspondence should be addressed. e-mail: dir@princeton.edu  
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and enhanced foraging ability. Protection from predators can result from a number of different mechanisms, such as dilution of risk, the confusion effect (Landeau and Terborgh, 1986; Pitcher and Parrish, 1993), early detection of predators (Godin *et al.*, 1988) and coordinated evasive manoeuvres (Magurran and Pitcher, 1987). Shoaling can also enhance foraging ability through the transfer of information if food items are patchily distributed (Pitcher *et al.*, 1982; Ranta and Juvonen, 1993). The proximate mechanisms that govern internal shoal dynamics and maintain shoal cohesion are less well studied. Both abiotic factors, such as temperature (Flierl *et al.*, 1999), current and oxygen levels (McFarland and Moss, 1967), and biotic factors (i.e. social interaction) have a role in shaping shoal structure (Couzin and Krause, 2003). Abiotic factors often affect aggregations of animals on a large scale, whereas social interactions become more important on small scales (Levin, 1997; Flierl *et al.*, 1999). A few models have been constructed that examine biotic factors through simulation of the movement of fish shoals and schools (Aoki, 1982; Huth and Wissel, 1992, 1994). These models are similar in several respects to models of group behaviour for other taxa, such as ungulates (Gueron *et al.*, 1996; Chao and Levin, 1999; Couzin *et al.*, 2002). A common theme to these models is that these groups are leaderless and arise out of local social interactions governed by a few simple rules. The aims of this study were to determine: (1) how accurate are the *assumptions* of these models by tracking the movements of individual shoal members in the field over time; and (2) how closely the observed behaviour of focal fish match the outcomes of decision making *predicted* by the models.

From the early models of Breder (1954) to the recent models of Aoki (1982), Huth and Wissel (1992, 1994), Gueron *et al.* (1996), Flierl *et al.* (1999) and Couzin *et al.* (2002), groups of organisms are maintained through a balance between attractive and repulsive forces acting on individuals. For each individual, there is a focus of attraction/repulsion. In the simplest case, this focus of attraction is the individual's nearest neighbour. Other models have the focus of attraction/repulsion as the weighted average of more than one neighbour, or use more complicated non-linear rules. Still other models consider neighbourhoods ranging from a few close neighbours (Aoki, 1982; Huth and Wissel, 1992, 1994) to the centroid of the entire group (Parrish and Turchin, 1997). In these types of models, repulsion is stronger than attraction at close distances, and the individual is programmed to move away from the focus of repulsion, thereby preventing collisions between group members. At large distances, attraction is stronger than repulsion, and the individual is programmed to move towards the focus of attraction.

These models assume, however, that the 'pushes' and 'pulls' of neighbours act simultaneously. If decision making were based on hierarchical assessments of the presence or absence of neighbours, however, then the mere presence of only one neighbour in zones ranging from close to far would govern an individual's response. As in the models assuming continuous assessment of neighbours and their distances, models employing zones and hierarchical decision making have zones of repulsion and attraction. But they also contain a zone of 'neutrality' where a fish is free to express its natural inclinations. In this zone, an individual will continue moving at whatever velocity (speed and direction) it had previously (Gueron *et al.*, 1996), or, in the case of highly polarized fish schools, it may undertake parallel orientation (Aoki, 1982; Huth and Wissel, 1992, 1994; Couzin *et al.*, 2002). Simulations show that the existence of a neutral zone increases the economic efficiency of moving within a group, since individuals accelerate and decelerate less often in response to neighbours (Gueron *et al.*, 1996). In these hierarchically structured models, at distances greater than where attraction occurs, spacing is so great that the individual no longer can

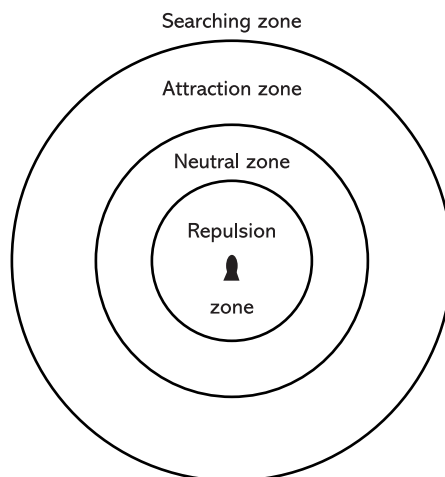
perceive the locations of its nearest neighbours. In effect, it has become separated from the group, and is thought to speed up or slow down while continuing to move in its intrinsically determined direction, searching for another group member. These four different zones of qualitatively different behaviour are called the 'stress', 'neutral', 'attraction' and 'searching' zones, respectively, and are depicted in Fig. 1.

The exact manner in which an individual moves in the different zones varies from model to model. Stochasticity may be introduced to the direction of motion chosen by the focal individual (e.g. Huth and Wissel, 1992). If more than one nearest neighbour affects the focal individual, the relative weightings of the influence of the different neighbours, and how the focal individual acts upon this information, varies among models (Huth and Wissel, 1992).

The first question we address in this study, then, is whether fish utilize hierarchical decision making. Do they use zones as a 'rule of thumb' to govern spacing decisions? Since attractive and repulsive forces are common to all models, identifying the existence of a 'neutral' zone will be critical to determining whether or not fish respond continuously to neighbours or make assessments as if the mere presence or absence of neighbours in zones matters. Only in hierarchical models will there be a region where focal fish are neither attracted nor repulsed in a consistent manner. If such zones exist, then the second question we address is do the sizes of the zones and the behaviour of the fish in them change when fear level is increased? Manipulating fear by simulating the presence of a predator and measuring what effect this has upon the behaviour of focal fish probes both the ultimate and proximate causes for shoaling.

## MATERIALS AND METHODS

Fieldwork was conducted from May to July 1997 at Princeton University's Stony Ford Ecological Research Center, in Cleveland Brook. Cleveland Brook is a small first-order stream. The fish shoal in question resided in a pool 240 cm wide, with a maximal depth



**Fig. 1.** Schematic representation of the different zones of behaviour described by Lagrangian models of animal aggregations. The shapes of the zones are not always circular in the different models, and some models may have a blind spot behind the individual. After Huth and Wissel (1994).

of 12 cm. Current speed was slow, with an average surface speed of  $0.15 \text{ m} \cdot \text{s}^{-1}$ , and not strongly directional (i.e. the pool was more or less an eddy).

The fish shoal was composed of at least two species of fish, *Semotilus atromaculatus* (creek chubs) and *Rhinichthys atratulus* (blacknose dace). Specimens were removed by hand-netting for identification purposes. The fish were juveniles, with an average body length of 2.7 cm. The shoal was not a compact, polarized school, making estimates of the number of fish within the shoal difficult. Approximately 40 fish were present in the pool, as estimated from video stills of the shoal when a predator was being simulated (which made the shoal much more compact, making estimation easier).

Video recording was done by positioning a camcorder directly over the shoal. The camcorder was mounted on a tripod, which stood in the water. The camera pointed straight down, as close to perpendicular to the stream bottom as possible. Glare off the water was a persistent problem throughout the summer. Only on completely clear days with a brilliant sun were recordings clear and glare-free. Because of this problem, replicates from only one day of recording are presented.

The fish quickly habituated to the presence of the tripod. Analysis of the shoal in their normal, undisturbed condition comes from a 5-min stretch, approximately 40 min after the tripod was first put into place.

To examine the effect of increased fear level on shoal structure, a predator was simulated by human approach. A person would walk in the stream up to the shoal and stand there for 2 min, occasionally wiggling a foot to maintain fear by the fish. Analysis of the shoal under the presence of a simulated predator comes from such time periods.

Videotapes were time-coded and images from the relevant parts of the videotape were digitized using Apple Video Player and Adobe Premier version 4.2. Images were grabbed every 1/6 of a second in greyscale. The images were then stored on a recordable compact disc.

Analysis of the images was done by means of a software package called Tracker, written by Robert Klimek and Ted Wright of NASA Lewis Research Center. The package was designed for tracking particles, and has features permitting automated tracking. However, automated tracking could not be used for this study, because the background was too irregular and the contrast between the fish and stream bed not sufficiently sharp. Manual tracking was done instead. Tracker does, however, have the ability to do image arithmetic. This was useful, in that the streambed background with all of its small rocks and cracks could be subtracted away from images, leaving only the fish. The image that was subtracted away was one in which all fish were erased (made the same colour as the stream bed) using Paint Shop Pro. Images resulting from subtraction were fuzzy due to the movement of water in the stream. This motion produced constant fluctuations between the image backgrounds. Nevertheless, this method still facilitated the identification of fish in the images.

Motion was analysed in two dimensions only. The height of the fishes above the streambed was ignored, and tracking was done by following the fishes' shadows. The study site was shallow enough that fish were generally close to the streambed, and instances where one fish passed beneath another were extremely rare. Focal fish were picked randomly. Nine fish were tracked for both the simulated predator-absent and simulated predator-present condition. The focal fish and the fish closest to it were tracked continuously. In this way, it was ensured that the position of the focal fish's nearest neighbour would be known. All neighbours that possibly could have been the focal fish's nearest neighbour for a given

image were tracked at the next image as well, even if they had moved far away from the focal fish. This allowed comparisons of the speeds and velocities of the focal fish and its nearest neighbour, and the determination of when the identity of the nearest neighbour changed.

For the first four sequences tracked in the predator-absent condition, the focal fish were followed for up to 100 images, or approximately 17 s. In subsequent sequences, focal fish were followed for only an average of 20 images. A total of 372 frames were tracked. For the latter sequences, the time at which the sequence started was picked randomly, but the focal fish was selected randomly only from those fish that were initially far apart (nearest neighbour distance [NND] > 4.5 body lengths) from their nearest neighbour. This was done because at that point there were few data points for fish with large NND.

For the predator-present condition, the focal fish in the first five sequences were also selected randomly, and for latter sequences the focal fish was chosen randomly from those fish that were far apart (here, far apart meaning NND > 1.5 body lengths). However, for all sequences tracking took place over 30 frames or less, with the average length of a tracked sequence being 16 frames. A total of 146 frames were examined.

Tracker produced a text file containing the coordinates of all the fish tracked. A simple program was written to read in these coordinates and determine the identity, position and speed of the nearest neighbour for each frame.

Two movement measures were computed. One measured the *overall* change in distance among nearest neighbours. Any increase, decrease or lack of change in distance could result from the movement of the focal fish, its nearest neighbour or both. Therefore, movement of the focal fish was also measured by determining its actual movement *direction*. An imaginary vector pointing directly from the focal fish to the flank of its nearest neighbour was used to generate a new, and individually specific, x-axis for each focal fish. Then, if the actual velocity vector of the focal fish had a positive component when projected onto the x-axis, it was assessed as approaching its neighbour; if the vector had a negative component, it was assessed as separating. Determination of the change in overall NND and the direction of the velocity vector for each focal fish and its nearest neighbour were calculated with the use of templates in Excel. Only instances where the position of the nearest neighbour was known for certain were included in the analysis. If the focal fish was closer to the edge of the field of view than it was to its observed nearest neighbour, for example, the data were excluded, as it was difficult to know if there was a fish just off the edge of the screen that was the true nearest neighbour.

A rough estimate of polarization, defined by Huth and Wissel (1992) as the average deviation of each fish's orientation from the average direction in which the shoal is pointing, was also computed by randomly selecting four frames from the predator-absent condition and three frames from the predator-present condition, and recording the orientation of every fish in these frames. Here, distances are presented as multiples of body lengths, and consistency of behaviour was determined by comparing outcomes to binomial estimates of random behaviour. As a visual guide, consistency was highlighted when over two-thirds of the sample of focal fish showed biased movements towards or away from nearest neighbours.

## RESULTS

### Basic shoal parameters

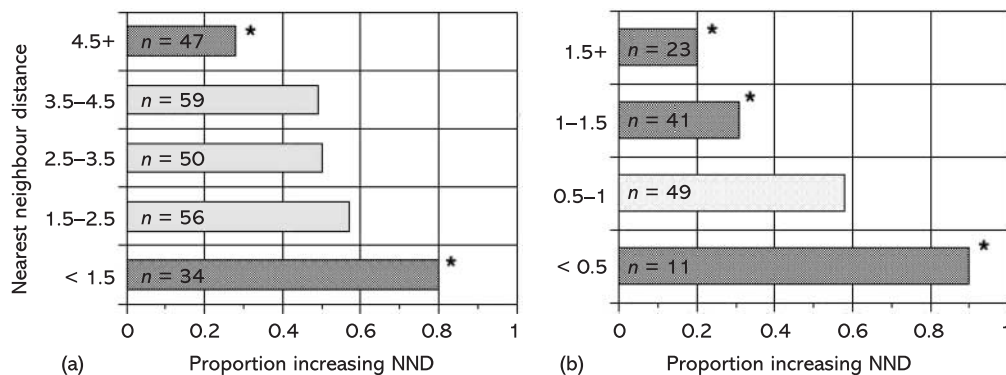
In the absence of the simulated predator, the shoal was neither very cohesive nor highly polarized. Average NND was 2.8 body lengths (BL). Polarization was  $63^\circ$ , with zero degrees describing maximal polarization and  $90^\circ$  maximal confusion. The average speed of a fish was  $1.5 \text{ BL} \cdot \text{s}^{-1}$ . The distribution of speeds is consistent with the heavy upper-tailed distribution typical of fish schools (unpublished data), and may be fit by a gamma distribution (Aoki, 1982; Huth and Wissel, 1992).

In the presence of the simulated predator, cohesion increased as average NND decreased to 0.9 body lengths. Polarization was  $57^\circ$  and fish were moving at an average speed of  $3.1 \text{ BL} \cdot \text{s}^{-1}$ . The shape of the speed distribution with the simulated predator present is similar to that in the predator-absent condition (unpublished data).

### Change in movements in relation to nearest neighbour distance

Figure 2 illustrates the changes in distance of focal fish to nearest neighbours as a function of a focal fish's initial distance to those neighbours. Under normal conditions in the absence of a simulated predator, Fig. 2a shows that only at small NNDs ( $< 1.5 \text{ BL}$ ) do over two-thirds of focal fish increase their distances from such neighbours. At large distances ( $> 4.5 \text{ BL}$ ) over two-thirds of focal fish decrease their NND. Only at intermediate distances (1.5–4.5 BL) are distances to nearest neighbours equally likely to increase or decrease.

Figure 2b shows that the same overall pattern emerges for replicates with simulated predators present. At small NND ( $< 0.5 \text{ BL}$ ) the distances among most focal fish and their nearest neighbours increase, whereas at large NND distances ( $> 1 \text{ BL}$ ) the distances between focal fish and their nearest neighbours decrease. Only at intermediate NND (0.5–1 BL) are distances among focal fish and their nearest neighbours not changing systematically. The

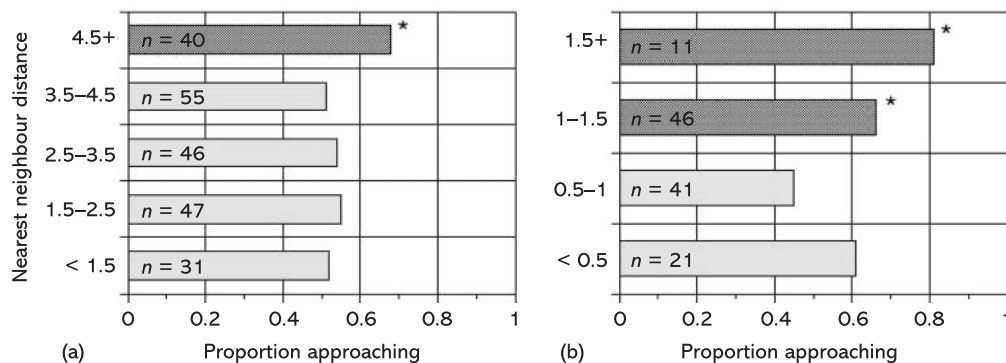


**Fig. 2.** Proportion of pairs of focal fish and a nearest neighbour increasing spacing between times  $t$  and  $t + 1$  versus the initial distance between nearest neighbours at time  $t$ , under conditions (a) without a simulated predator present and (b) with a simulated predator present. Darkened bars indicate initial distances at which more than two-thirds of the sample show similar directionality in distance change. Asterisks denote proportions that differ significantly from random patterns of change at the 0.05 level. Sample sizes indicated by  $n$ .

only difference between the treatments is that all the critical distances are smaller when simulated predators were present. When tested against the null hypothesis that the change in distance would be equally likely to increase or decrease if both the focal fish and its nearest neighbour moved independently of one another at the same speed and in random directions, only at small and large NND are changes in distance different from random at the 0.06 level.

To discern how these changes in NND are accomplished, the direction in which a focal fish moved relative to its nearest neighbour was examined. By considering the positive or negative component of the focal fish's actual velocity vector as projected on an imaginary one pointing from a focal fish's position to that of its nearest neighbour, it appears that only when a focal fish is relatively far away from a neighbour does its behaviour *alone* account for changes in distance to a nearest neighbour (Fig. 3). If a focal fish was responding randomly to its NND, then half the time it would approach its nearest neighbour while half the time it would move away. Under normal conditions when simulated predators are absent, the velocity vector of over two-thirds of the focal fish points towards nearest neighbours only when focal fish are almost 5 body lengths away (Fig. 2a). At other distances, the directional response to NND by focal fish is random.

With simulated predators present, the same overall pattern occurs. The critical distance, however, when more than two-thirds of the response vectors of focal fish point towards a nearest neighbour shrinks to within only one body length. Thus under stress, the responsive actions of individual fish on their own operate over a larger range of distances than when simulated predators are absent. Such enhanced responsiveness appears to increase the cohesion of schools when risk is heightened. Regardless of predator context, however, consistent directionality is not shown by focal fish when neighbours are close ( $< 1$  BL). This suggests that the observation that fish tend to repel each other when close together as illustrated in Fig. 2 emerges from the simultaneous action of both a focal fish and its nearest neighbour.



**Fig. 3.** Change in proportion of focal fish approaching its nearest neighbour between times  $t$  and  $t + 1$  versus the initial distance between nearest neighbours at time  $t$ , under conditions (a) without a simulated predator present and (b) with a simulated predator present. Darkened bars indicate initial distances at which more than two-thirds of the sample show similar directionality in distance change. Asterisks denote proportions that differ significantly from random patterns of change at the 0.05 level. Sample sizes indicated by  $n$ .

## DISCUSSION

Several results emerging from this field study are of interest. One is that increasing the fear level of the fish by simulating the appearance of a predator greatly increases the cohesiveness of the shoal. This has also been seen in studies of minnows, *Phoxinus phoxinus* (Krause, 1993), and is consistent with the selfish-herd concept put forth by Hamilton (1971), which predicts group members will move closer to one another, or even over each other into the centre of a group, to avoid being on the group's more exposed periphery. By individuals behaving in this way, the group will contract as occurred in this study. Fish with large NND may also be more vulnerable to predation by standing out from the rest of the shoal. Fish with unusual appearance or behaviour suffer much higher predation risk unless they are in relatively large shoals (Landeau and Terborgh, 1986).

Becoming separated from a shoal should be avoided as lone fish will lose these and other anti-predator advantages associated with group living (Bertram, 1978; Rubenstein, 1978). Our results suggest that when a simulated predator is present, the risk of being eaten takes precedence over possible adverse consequences of increased cohesiveness associated with interference while swimming or feeding (*sensu* the 'life-dinner' principle [Dawkins and Krebs, 1979]). Not surprisingly, fish in our study reduce average NND in the presence of a simulated predator as predicted by other analyses (Partridge, 1980; Pitcher and Parrish, 1993; Hoare *et al.*, 2000). But more interestingly, focal fish also reduce the distances at which they initiate 'attraction', 'repulsion' and 'neutral' behaviour. When fear levels are normal, all detection zones are large. The attraction zone, for example, begins close to 4.5 body lengths from the focal fish, reflecting the normally non-polarized, loose nature of the shoal. Apparently anti-predator selection pressure has not been strong enough to induce juvenile creek chubs and blacknose dace to form cohesive, polarized schools when not explicitly threatened by predators. Diatoms, desmids, other planktonic organisms and aquatic insect larvae eaten by juvenile chubs and dace are not particularly abundant, nor are they highly aggregated in patches (Scott and Crossman, 1973). Under these conditions close packing, while either swimming or feeding, could lead to interference. If all fish in the shoal emulated the behaviour of our focal fish, then increasing each distance threshold would in turn generate shoals with large NND and low polarization. Our findings illustrate the emergence of an interaction between overall change in spacing and changes in threshold detection distances induced by changes in risk sensitivity or foraging motivation. The outcome of such an interaction will affect the effectiveness of information transfer among shoal mates. Since the average speed of movement in our study also increased in the presence of simulated predators, the ability to transfer information and coordinate movement will impact the adaptive value of forming cohesive shoals.

A second novel finding of our study is that fish appear to react to the presence of only one neighbour and its position relative to boundaries of discrete detection zones as assumed by hierarchical structured models of grouping dynamics. Fish close together tend to increase NND (Fig. 1), mostly by mutual repulsion (Fig. 2). That the consistency with which individuals move apart ceases at a critical distance – a distance that changes with risk – supports the proposition that animals react to nearest neighbours as if they occupy positions in discrete zones. From a critical distance (the boundary of 'stress' and 'neutral' zones; Fig. 1) outwards to another critical distance (the boundary between the 'neutral' and 'attraction' zones; Fig. 1), focal fish express individualistic tendencies and are equally likely to move away or towards a nearest neighbour. Yet again at this second critical distance



the behaviour becomes more structured as focal fish show consistent tendencies to reduce distances between themselves and nearest neighbours. Interestingly, past this critical distance actions by focal fish alone appear to be sufficient to reduce separation and maintain shoal cohesion, as we find no evidence for the 'searching' zone as predicted by Gueron *et al.* (1996) and depicted in Fig. 1.

These results are striking. They are the first to demonstrate the existence of a 'neutral' zone. In both the predator-present and predator-free conditions, regions existed where fish moved about randomly and showed no tendency to approach or move away from nearest neighbours. As Gueron *et al.* (1996) note, an organism in this zone should exhibit individualistic tendencies. Fish ignoring neighbours when in neutral zones will be buffered from having to respond continuously to repulsive or attractive forces, thus saving energy.

The results also illustrate that the assumption underlying most Lagrangian models of group dynamics concerning 'who is responding to whom', and the outcomes from doing so, needs further empirical scrutiny. In virtually all models, the direction in which an individual moves depends upon the positions of one or at most a few other group members (but see Okubo, 1980, p. 124; Flierl *et al.*, 1999). The exact details, however, vary among models. For example, in the model of Gueron *et al.* (1996) the focal individual moves to or from the position of the nearest neighbour entering a particular detection zone. In other models, the response by focal fish is either perpendicular to an imaginary line connecting the positions of two individuals (Huth and Wissel, 1992, 1994) or the centroid of the location of a few nearby fish (Parrish and Turchin, 1997; Couzin *et al.*, 2002). While our results demonstrate that such an assumption can account for the behaviour of focal fish when their closest neighbour is located relatively far away in the 'zone of attraction', the assumption fails to accurately account for the behaviour of focal fish when the closest neighbour is nearby in the 'stress zone'. At great distances, focal fish consistently move towards a nearest neighbour and successfully reduce separation by their own actions alone. Perhaps at larger distances, maintaining contact with the rest of the shoal becomes the dominant concern warranting active movement. Perhaps selection may favour focal fish not waiting for, or relying on, actions of a nearest neighbour to reduce NND. Instead, focal fish are selected to do what they can to reduce NND on their own. For focal fish whose close neighbours appear in stress zones, however, the direction of the velocity vectors of such fish are not detectably different from random. Thus increases in NND appear dependent upon both the location and the movements of the fish's nearest neighbour. Rather than just considering the position of the nearest neighbour when initiating movement, focal fish responding to 'stress' also appear to rely on the movements of their nearest neighbour to ensure increased spacing.

As noted above, this analysis considers responses of focal fish to the single nearest neighbour only and therefore corresponds to the hierarchical version of Gueron and colleagues' (1996) model. However, other studies suggest that fish may be reacting to more of the shoal than this (Aoki, 1982; Huth and Wissel, 1992, 1994; Parrish and Turchin, 1997). In our study, this was unlikely. If a focal fish and its nearest neighbour were both reacting to other fish, such as the centroid of the shoal (*sensu* Parrish and Turchin, 1997), both fish would be predicted to head in the same qualitative direction (positive or negative on the x-axis). Instead, at relatively close distances we observe movement directions no different from random. Also, when the simulated predator is absent, focal fish very rarely change nearest neighbours, suggesting that focal fish move in ways that keep the same nearest neighbours. To completely resolve this problem of how many neighbours are used as

cues, recordings must be made of the positions over time of all the fish in the school – a problem that requires a wider field of view in the video recording and automated tracking of fish – which was not possible in this study.

The study of how complex patterns arise in nature raises fundamental questions pertaining to mechanisms. Social aggregations provide an excellent opportunity to study these proximate mechanisms of causation (Parrish and Edelstein-Keshet, 1999) that balance self-organizing actions with directed forces imposed by the physical environment. While the basic prediction of increasing NND when in the stress zone, and decreasing NND in the attraction zone, is a robust feature common to models covering a range of taxa and is observed in this study, many other details emerging for the first time need further study to substantiate their generality. One is the extent to which changes in the size of detection zones are shaped by interactions between internal state and environmental context. This relationship is likely to be quite complicated, since individuals are likely to differ in many ways. Another is the extent to which a focal individual's actions alone or in conjunction with a neighbour are required to effect spacing that increases fitness. And yet another is the extent to which neighbours other than the nearest one influence the behaviour of focal individuals. In this regard, our results show that considering only the single nearest neighbour provides a reasonable fit to the predictions of a hierarchical decision-making model (Gueron *et al.*, 1996). Other features associated with hierarchical models, such as the existence of a 'searching zone', where individuals lost from the group radically change their behaviour, the actual shapes of detection zones and the existence of blind spots (Huth and Wissel, 1992; Gueron *et al.*, 1996) were not explicitly examined. By determining empirically how these considerations also shape individual behaviour, a more complete understanding of how social groups self-organize will emerge.

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