

## Leadership in fish shoals

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### Abstract

Leadership is not an inherent quality of animal groups that show directional locomotion. However, there are other factors that may be responsible for the occurrence of leadership in fish shoals, such as individual differences in nutritional state between group members. It appears that front fish have a strong influence on directional shoal movements and that individuals that occupy such positions are often characterised by larger body lengths and lower nutritional state. Potential interactions between the two factors and their importance for positioning within shoals need further attention. Initiation of directional movement in stationary shoals and position preferences in mobile shoals need to be addressed separately because they are potentially subject to different constraints. Individuals that initiate a swimming direction may not necessarily be capable of the sustained high swimming performance required to keep the front position or have the motivation to do so, for that matter. More empirical and theoretical work is necessary to look at the factors controlling positioning behaviour within shoals, as well as overall shoal shape and structure. Tracking of marked individuals whose positioning behaviour is monitored over extended time periods of hours or days would be useful. There is an indication that shoal positions are rotated by individuals according to their nutritional needs, with hungry fish occupying front positions only for as long as necessary to regain their nutritional balance. This suggests that shoal members effectively take turns at being leaders. There is a need for three-dimensional recordings of shoaling behaviour using high-speed video systems that allow a detailed analysis of information transfer in shoals of different size. The relationship between leadership and shoal size might provide an interesting field for future research. Most studies to date have been restricted to shoals of small and medium size and more information on larger shoals would be useful.

**Keywords** directional locomotion, fish schools, front fish, nutritional state, schooling, shoal leadership, swimming direction

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### Introduction

Fish shoals were traditionally thought to be leaderless and egalitarian systems (Breder 1951; Shaw 1962). In more recent studies on the mechanisms of shoaling, the question of leadership has been the subject of debate and is closely linked with the issue

of information transfer and individual positioning behaviour within groups (Huth and Wissel 1992, 1994; Bumann and Krause 1993; Pitcher and Parrish 1993; Niwa 1994; Reuter and Breckling 1994). There is agreement that two of the most important sensory channels involved in shoaling behaviour in general are vision and the lateral line

(Pitcher and Parrish 1993). Both of these allow for the rapid exchange of information, which is important for the high-speed co-ordinated manoeuvres observed in many species. In this article we will give an overview of the evidence for leadership behaviour (as defined below) in fish shoals followed by a discussion of its mechanisms and functions.

We define leadership as the initiation of new directions of locomotion by one or more individuals which are then readily followed by other group members. This means that we will restrict our discussion to the issues of (i) whether shoal members have a differential influence on directional decisions of the shoal as a whole, and (ii) what potentially gives individuals this influence. The latter could be related to inherent qualities of an individual (such as size, sex and age) or to the spatial position it occupies in the shoal, which may predispose it to having a strong influence on the general swimming direction of the group. In this paper we are not concerned with leadership in connection with social dominance, which is usually the outcome of some form of contest between group members. Social hierarchies require group membership to be stable over extended time periods of weeks or months, a situation that is rarely the case in fish shoals (an exception is some species of coral reef fish, see Krause *et al.* 2000 for a review) where rapid turnover of individuals is the norm (Hilborn 1991; Hoare *et al.* 2000).

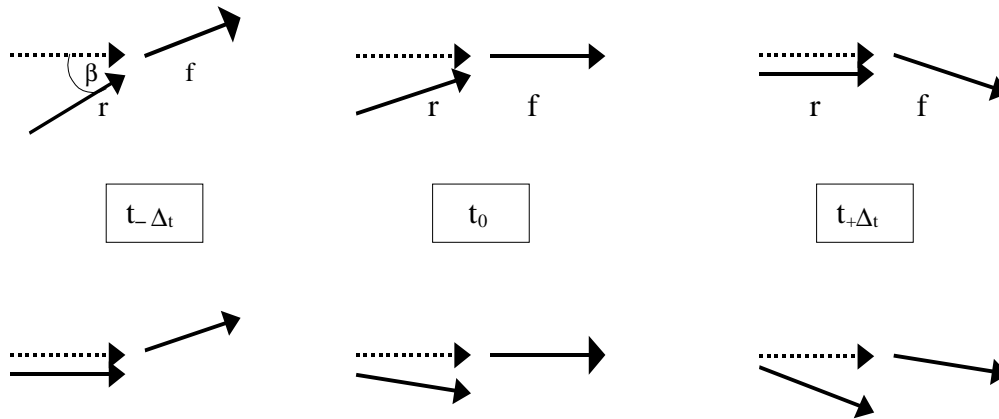
To identify whether some individuals have a stronger influence on the swimming direction than others we can use cross-correlation. This technique can be used to compare the influence of different individuals within shoals on the general swimming direction. It can also be used to compare different parts of a shoal. Bumann and Krause (1993) tested for leadership in shoals of roach, *Rutilus rutilus* (Cyprinidae), by comparing the front part and the rear part of a shoal. For a given moment in time,  $t_0$ , the average direction of the front fish was compared to that of the rear fish up to 400 m earlier and 400 m later than  $t_0$ . If rear fish are followers and front fish leaders, then we should expect that a direction that was initiated by front fish at  $t_0$  is copied by rear fish at  $t_{+\Delta t}$  (Fig. 1). This method allows us to determine which fish lead and which fish follow, and to measure the time lag between the initiation of a new direction and it being copied. The coefficient of the correlation between directional movements of the leader and the follower can be used as an indicator of the strength of leadership.

## Models of fish shoals

In recent years, a number of researchers have developed individual-based models of fish shoaling behaviour to investigate which movement rules are required to produce cohesive shoals capable of directional movement (Huth and Wissel 1992, 1994; Niwa 1994; Reuter and Breckling 1994). In these models a fish's decision regarding its swimming speed and direction is influenced by a small fixed number of near neighbours (Huth and Wissel 1992) or by all visible fish with individuals at greater distances having a decreasing influence. The consensus of these models is that a general swimming direction of the shoal arises from local interactions of shoal members in a self-organised fashion. Thus, leadership (as defined above as the greater influence of one or several individuals on directional decisions of the shoal as a whole) does not appear to be a prerequisite of directional movements of a shoal. However, this does not necessarily mean that leadership could not have evolved for other reasons. It is, for instance, possible that some group members have information regarding the spatial or temporal occurrence of food sources that others do not possess (Reebs 2000). Following the individuals that 'know' would then be beneficial. Likewise, following could be advantageous because it requires a lower degree of environmental awareness (i.e. followers can concentrate on foraging behaviour and/or social interactions) compared to leaders which have to find a path that is free of obstacles and predators (Table 1). Leadership could also result from differential trade-offs between foraging efficiency and predation risk. Well fed individuals should prioritise safety in numbers (and thus be unwilling to separate from the shoal), whereas hungry ones may be more willing to separate (to avoid competition). If a conflict of interest over swimming directions arises, we would expect individuals to relent if they potentially lose more by separating from the group.

## Empirical observations of leadership

Evidence for leadership behaviour has been found in a number of species (*Caranx speciosus*, Carangidae, Yamagishi 1978; *Seriola quinqueradiata*, Yamagishi *et al.* 1978; *Phoxinus phoxinus* (Cyprinidae), but only for pairs of fish, Partridge 1980; *Gasterosteus aculeatus* (Gasterosteidae) and *Rutilus rutilus*, Bumann and Krause 1993; *Aphyicharax erithrurus*,



**Figure 1** Initiation of new swimming directions in fish shoals. The average direction of the front (f) and the rear (r) part of a fish shoal are shown at three different time instants ( $t_{-\Delta t}$ ,  $t_0$  and  $t_{+\Delta t}$ ). The rear direction is compared to the front direction at  $t_0$  (dashed lines) for all three time instants. In the upper panel, the front part initiates a turn and its direction is copied by the rear fish at  $t_{+\Delta t}$ . In the lower panel, the rear part leads and the direction of the rear part at time  $t_{-\Delta t}$  is copied by the front part at  $t_0$  (modified after Bumann and Krause 1993). The angle  $\beta$  between the average direction of front fish at  $t_0$  and that of rear fish at  $t_{-\Delta t}$  and  $t_{+\Delta t}$  can be used as a criterion for leadership.

Levin 1996). Pitcher *et al.* (1982) observed position preferences in mackerel, *Scomber scombrus* (Scombridae), with the largest fish taking up the front position most often, although no direct tests on leadership were carried out. Partridge (1980), however, reported that no leadership was observed in minnow shoals (with more than two members) and in schools of saithe, *Pollachius virens* (Gadidae). Although species' differences cannot be excluded, the discrepancy between these studies is more likely to be due to methodological differences. Bumann and Krause (1993) used a higher time resolution for their analysis than Partridge (1980). Furthermore

Bumann and Krause compared the front half with the rear half of the shoal, which makes it easier to pick up information transfer than a comparison made between individual neighbouring fish. In a second experiment, Bumann and Krause (1993) manipulated the swimming direction of the front part of the shoal and demonstrated that even a single individual can have a strong influence on the entire shoal (16 fish in total) when it is at the front of the shoal.

Empirical measurements of information transfer in roach shoals indicated that directional movements of the front part of the shoal were repeated

Leading	Following
<b>Benefits</b>	
*Reduced probability of conflict between individual's directional choice and that of the group	Reduced energetic expenditure
High food intake	*More time for foraging and social interaction
Access to high quality food	Low predation risk
Access to high-risk areas in the safety of a group	*Increased access to information on temporal and/or spatial occurrence of food sources
<b>Costs</b>	
High predation risk	Low food intake
High energy expenditure	Reduced access to high quality food
*Less time for foraging and social interaction	*Potential conflict between individual's directional choice and that of the group

**Table 1** Potential costs and benefits of leading and following in fish shoals. Here we make the assumption that leaders are in front positions and followers in the centre or rear of the shoal. The costs and benefits which are independent of positional effects are indicated with an asterisk.

250 m later by the rear part (Bumann and Krause 1993). Given the dimensions of the shoal in that study, this meant that the information flow was faster than the swimming speed of the fish, and thus initiated a change of direction in the rear part of the shoal before it reached the point where the front part of the shoal had turned. This has two interesting implications. First, it rules out the possibility that the front and rear parts had performed a turn in the same direction at the same perturbation point in space (in which case there would be no 'leader-follower' relationship but an independent response to the same external cues). Second, rear fish could potentially save energy by following directly because this might cut short the loops that front fish swim while searching for food.

All information at present supports the idea that fish become leaders as a result of occupying a front position in a shoal. There is no conclusive evidence of inherent characteristics of individuals (such as body length or sex) that give leadership potential independent of shoal position. Because of this link between shoal position and leadership, the last section of this review deals exclusively with the positioning behaviour of fish in shoals.

### Mechanisms of leadership behaviour

The mechanism underlying leadership is probably based on some form of distance-regulation between fish. Fish normally keep a distance of about 0.5 to 1 body length to other shoal members (Pitcher and Parrish 1993). If the nearest neighbour is much further away this will result in approach behaviour. Hungry fish have been shown to be more spread out than well fed fish; the function of which is likely to be avoidance of competition for food (Keenleyside 1955). If the threshold distance at which an approach is triggered is indeed larger in hungry fish compared to well fed ones, then this could have important implications for leadership. Hungry fish could potentially out-swim the threshold distance of a well-fed shoal member, in response to which the well fed neighbour would approach (i.e. follow); this could thus lead to the initiation of a new swimming direction of the shoal. This mechanism would explain why hungry fish are often found in front positions of shoals and remain there for some time. In a shoal of well fed conspecifics, food-deprived fish have been shown to adopt front positions and the proportion of time spent at the front was positively correlated with the duration of the food deprivation

(Krause *et al.* 1992, laboratory experiments with roach, *R. rutilus*; Krause 1993, field experiments with roach). Wieser *et al.*'s (1988) study on the effects of food deprivation on small cyprinids illustrated that the duration of food deprivation and swimming speed follow an optimum curve. At the beginning of a deprivation period, fish showed a greatly increased swimming activity. Over time, speed returns to normal activity levels and in cases of prolonged deprivation, fish become relatively inactive. Obviously, differences in the nutritional state between individuals would only be of a temporary nature and, accordingly, Krause (1993) found that such positioning differences disappeared one day after normal feeding had been resumed.

More permanent differences in positioning behaviour could potentially occur due to individual differences in metabolic rates (as reported by Krause *et al.* 1998a) for similar sized sticklebacks, *Gasterosteus aculeatus* in the context of refuge use and/or body length. The latter is known to be positively correlated with swimming performance (Beamish 1978) and could explain differential positioning without invoking any position preferences (DeBlois and Rose 1996; Gueron *et al.* 1996; see Hemelrijk 1998 for a simulation model).

An interesting case of leadership has been reported by Reeb (2000 and personal communication) who conducted experiments in which only a small proportion of the shoal members had information about the location of a temporary food source. Golden shiners, *Notemigonus crysoleucas* (Cyprinidae), normally preferred the darker half of an experimental tank and would only come to forage in the lighter half during a particular time of day when food was provided there. Fish were trained over several weeks to expect food at a certain time of day after which trained and naive fish were mixed, with trained fish making up the smaller proportion of the shoal, down to a single trained fish in a shoal of 11 naive ones. The experiments showed that even single trained fish were capable of leading an entire shoal into the lighter tank area at about the time when they expected food, even if none was provided. This study demonstrates elegantly the strong potential influence that a single individual can have over a group provided that the motivation to do so is strong enough. The mechanism by which the trained (informed) fish manages to lead the shoal is not known, but it could follow the same principle of distance regulation as described above. The

willingness to out-swim the comfort zone of 0.5 to 1 body length would presumably be greater in the trained fish (due to the expectation of food), which would eventually initiate a swimming direction towards the anticipated food source. This experiment illustrates some of the benefits of leadership and followership. The leader manages to forage in the safety of a social group and the followers get access to a food source they may not otherwise have found. Many food sources in the environment are only temporary and mixing between fish that have information on food locations and ones that are naive can be beneficial for both leaders and followers.

### Costs and benefits of front positions

In the previous sections we have presented empirical evidence that front fish can have a greater influence on swimming directions of the shoal than fish in other positions. Here we will discuss which group members take up front positions, why they do this and for how long.

Hamilton's (1971) selfish herd model predicted higher predation risks for peripheral group positions and strong empirical evidence in support of his model has been accumulated over the last three decades (Krause 1994). Hamilton's model, however, was designed to describe stationary groups and there has been some debate over how it can be extended for mobile animal groups (Bumann *et al.* 1997; Parrish and Edelstein-Keshet 1999). In particular, Parrish (1989) questioned whether some of the assumptions of Hamilton's original model are applicable to mobile groups. The selfish herd concept was based on the idea that a predator is positioned randomly with respect to a prey group and that it would always attack the nearest prey in space. Parrish (1989; Parrish *et al.* 1989) argued that given the high attack speed of some pelagic predators (such as tuna) this may not necessarily be the case as these predators may be able to strike even at central positions within schools. A problem with empirical tests of such arguments is that definitions of school positions are difficult to apply to pelagic fish shoals because of their large dimensions.

Bumann *et al.* (1997) developed a model that adopted Hamilton's stated assumptions and quantified the predation risk of different shoal positions for mobile animal groups that are attacked by both mobile and stationary predators. Front positions were clearly identified as more risky than any other

group position, in particular in the case of a mobile prey group and a stationary predator. The predictions of the latter model were subsequently supported by data on a shoal of chub (*Semotilus atromaculatus*) and a rock bass (*Ambloplites rupestris*). The front half of the shoal suffered considerably higher predation risks and the individual occupying the lead position was subject to peak risks (Bumann *et al.* 1997; Krause *et al.* 1998b). In Krause *et al.*'s (1998b) experiments, the lead fish was attacked in more than 80% of the trials. Interestingly, there was no indication that the predation risk for a leading fish decreased as shoal size increased, which might suggest that leaders do not benefit from antipredator benefits of shoaling in the same way as other shoal members. This clearly needs further investigation.

Experimental studies in which the positioning behaviour of individual fish in shoals was manipulated using alarm substance showed that individual minnows, *P. phoxinus*, adopted positions in which they were surrounded by near neighbours rather than exposed on the periphery of the group (Krause 1993). Given that front positions at least in some environments are more risky, the question then arises why individuals would occupy such positions. It appears from a number of studies that front positions provide higher net food intake and also afford access to higher quality diets (O'Connell 1972, northern anchovy, *Engraulis mordax*; Major 1978, giant trevally, *Caranx ignobilis*; Krause *et al.* 1992 and Krause 1993, roach, *R. rutilus*; DeBlois and Rose 1996, Atlantic cod, *Gadus morhua*). Experimental manipulations of small freshwater shoals showed that food-deprived fish were found predominantly in front positions (where they had high feeding rates) but only on the first day of release, after which they resumed the same positioning behaviour as control fish (Krause *et al.* 1992; Krause 1993). DeBlois and Rose's (1996) study provides a rare example of a detailed data set for a large (more than 10 km long) pelagic shoal that comprised several million individuals. Cod in front positions were found to have fuller stomachs with a higher proportion of high quality prey items than individuals elsewhere in the school. They also reported that front fish tended to be larger and older than other shoal members (see section on Mechanisms of leadership behaviour, above). DeBlois and Rose (1996) reported that not all large fish were in the front part of the shoal, so that positioning within size

classes may well be a result of differences in nutritional state. Krause (1993) only manipulated the nutritional state in fish and did not investigate the potential role of size differences for positioning in free-ranging roach shoals. There is clearly a need to study how these two factors might interact to determine positioning behaviour in fish shoals (DeBlois and Rose 1996).

So far we have only discussed the positioning of fish in shoals that are already in motion. However, once a shoal has become stationary because of feeding in a particular area, directional movement will subsequently need to be re-established, a process that has received some attention by modellers (Huth and Wissel 1992; Reuter and Breckling 1994) but little by empirical researchers (Krause *et al.* 1998a). A recent study did not find any effects of body length and nutritional state on the probability of initiation of new swimming directions (Krause *et al.* 1998a). However, once in motion, larger individuals and food-deprived ones quickly adopted front positions. Krause *et al.* (1998b) tested only pairs of fish and larger groups need to be studied in order to investigate the potential link between group size and group dynamics.

The results from these studies suggest that there are benefits for front positions in terms of high feeding rates and priority access to food at the cost of higher predation risks. Based on this, we might expect the positioning behaviour of fish within shoals to be highly dynamic depending on their nutritional needs (see Krause 1993), such that all fish can become leaders and leadership is rotated among shoal members. However, it is also possible that individual variations in boldness (see Coleman and Wilson 1998) have implications for medium- or long-term differences in positioning behaviour between individuals – bolder individuals taking up front positions more often and for longer than other fish. It has also been suggested that different individuals play different roles within a shoal and that the decision of which becomes the leader is context-dependent (Levin 1996). Neither idea has been rigorously tested to date.

A number of group-living fish species do not feed at certain times of the year (Nøttestad *et al.* 1996). For these fish we can only speculate what the benefits are of taking up front positions when, by its absence, food intake cannot be deterministic. Experimental work on positioning behaviour of fish in non-feeding shoals might shed some light on the underlying costs and benefits in such cases.

## Summary and conclusions

**1** Leadership is not an inherent quality of animals groups that show directional locomotion. However, there are other factors that may be responsible for the occurrence of leadership in fish shoals, such as individual differences in the nutritional state between group members.

**2** It appears that front fish have a strong influence on directional shoal movements and that individuals that occupy such positions are often characterised by larger body lengths and lower nutritional state. Potential interactions between the two factors and their importance for positioning within shoals need further attention.

**3** Initiation of directional movement in stationary shoals and position preferences in mobile shoals need to be addressed separately because they are potentially subject to different constraints. Individuals that initiate a swimming direction may not necessarily be capable of the sustained high swimming performance required to keep the position or, for that matter, have the motivation to do so.

**4** More empirical and theoretical work is necessary to look at the factors controlling positioning behaviour within shoals, as well as overall shoal shape and structure. Tracking of marked individuals whose positioning behaviour is monitored over extended time periods of hours or days would be useful. There is an indication that shoal positions are rotated by individuals according to their nutritional needs, with hungry fish occupying front positions only for as long as necessary to regain their nutritional balance. This suggests that shoal members effectively take turns at being leaders.

**5** There is a need for three-dimensional recordings of shoaling behaviour using high-speed video systems that allow a detailed analysis of information transfer in shoals of different size.

**6** The relationship between leadership and shoal size might prove an interesting field for future research. Most studies to date have been restricted to shoals of small and medium size, and more information on larger shoals would therefore be useful.

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