



Ghoti

Ghoti papers

Ghoti aims to serve as a forum for stimulating and pertinent ideas. Ghoti publishes succinct commentary and opinion that addresses important areas in fish and fisheries science. Ghoti contributions will be innovative and have a perspective that may lead to fresh and productive insight of concepts, issues and research agendas. All Ghoti contributions will be selected by the editors and peer reviewed.



Etymology of Ghoti

George Bernard Shaw (1856-1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

Possible functions of the octavolateralis system in fish schooling

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Abstract

The development of the octavolateralis system in fish ancestors created the phenomenon of sensory reafference associated with the fish's own locomotion. Particularly in fish species living and moving in groups, there is a potential to produce complex pressure waves and other water movements interfering with the octavolateralis perception of critical environmental signals. The hypothesis presented is that the development of the octavolateralis system may have initiated, or been a factor in, the evolutionary development of synchronized group locomotion, eventually leading to schooling behaviour. Theoretical models suggest that schooling may be related to a reduction in masking of environmental signals, as well as to survival mechanisms, e.g. confusion of the lateral line and electro-sensory systems of predators by overlapping pressure waves and overlapping electrical fields. The combined effects of reduced masking and predator confusion may help explain why schooling became an evolutionary success. Including pressure waves and other water movements in the model of join, stay or leave decisions might shed some light on fish shoal assortment. A model encompassing the complex effects of synchronized group locomotion on octavolateralis and electro-sensory perception of both prey and predator fish might increase the understanding of schooling behaviour.

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Received 17 Aug
2008
Accepted 19 Feb
2009

Keywords Auditory masking, electro-sensory system, group synchrony, hearing in fish, lateral line, sensory reafference

Introduction

'The iridescent, glinting bodies of fish swimming together in a school, darting and wheeling in formation almost as a single body, have attracted the attention of naturalists and poets from ancient times' (Pitcher 1998). But why do fish school?

The majority of known fish species form cohesive social groups at some stage of their life history. The term 'shoal' is most often defined as a loosely organized group of fish, while 'school' refers to coordinated swimming groups. Fish have the ability to make decisions about behaviours based on the immediate situation, enabling them to make a flexible 'on-line' response to an environment that can change rapidly, for example when a food source is found or when a potential predator appears (Pitcher 1983, 1998). Fish tend to school in risky situations (Pavlov and Kasumyan 2000). Traditional ideas of the evolutionary advantages of schooling encompass, at a minimum: safety in numbers, visual confusion of predators (Krause *et al.* 2000a; Pavlov and Kasumyan 2000), reduction of encounters with predators (Turesson and Bronmark 2007), watching for predators (Pitcher 1998; Pavlov and Kasumyan 2000), mating and foraging, and reduction of energy expenditure (Partridge and Pitcher 1979; Pavlov and Kasumyan 2000; Domenici *et al.* 2007). Svendsen *et al.* (2003) suggested that roach in trailing positions experienced energy conservation. Fish in a school tend to maintain a certain neighbour distance in given conditions (Pitcher 1998). Schooling minnows, saithe, cod and herring occupy a water volume of approximately one body length cubed, with neighbours *c.* 0.7 of a body length away. This alters with swimming speed and degree of fish agitation (Pitcher 1998, 2001). Fish of similar size tend to shoal and school together. For example, studies of mackerel and herring have shown that they choose school neighbours of a size within 15% of their own (Pitcher *et al.* 1985).

Many factors influence decisions, movements, and, thereby, possibly, synchronization in a school. Among these are avoiding obstacles, minimizing energy expenditure (Couzin and Krause 2003), and avoiding (or acquiring) a lead position that is more

exposed to predator attacks and possibly demands higher energy expenditure, but may increase food intake (Krause 1994; Svendsen *et al.* 2003).

The phrase 'synchronized movements' implies a precision that does not exist in the natural world. Although the movements of a school are often apparently well coordinated on the large scale, with simultaneous turning, stopping, and starting, close observation shows that individual fin and body movements will not be perfectly coordinated with those of neighbours. Responses of fish swimming at the rear of the school usually lag slightly behind (Pavlov and Kasumyan 2000). Dissimilarities in swimming performance between leading fish and trailing fish in schools have been quantified (Fish *et al.* 1991). There are little data describing fish-to-fish synchronized swimming movements (or lack of), and also a lack of information on how vertebrate groups maintain their internal structure (Couzin and Krause 2003). The extent to which schooling fish move in synchrony with immediate neighbours is an important and relevant question, but an even more basic question will be focused on here: Does some (even a modest) degree of synchronization in fish group locomotion provide advantages in comparison to less synchronized behaviour? This review will explore how the acoustic and hydrodynamic situation within a moving group might be influenced by highly coordinated movements of its members and possible consequences for the interaction between prey and predators; in particular how schooling might affect octavolateral perception within a school, and whether non-visual predator-confusing effects might be achieved through synchronized movements. Join, leave, or stay (JLS) decisions will also be discussed, and finally schooling (or schooling-like) behaviour in vertebrates other than fish.

Involvement of the octavolateralis system in schooling

Vision is considered to be of paramount importance and the sensory basis of schooling (Pitcher 1998; Pavlov and Kasumyan 2000). However, evidence is strong that the lateral line is also involved (Pitcher 1998). Partridge and Pitcher (1980) demonstrated

that blinders had little effect on the position experimental fish assumed relative to their neighbours in the school, while fish with a temporarily disabled lateral line school differently, making less accurate distance adjustments (Partridge and Pitcher 1980). Furthermore, the development of schooling in teleost larvae is closely connected to the development of the lateral line organ (LLO) (Blaxter *et al.* 1981). Knowledge of the precise location of nearby members must be crucial to schooling fish. The almost instantaneous adjustments to swimming direction and speed that characterize schooling are made possible by detection, via the octavolateralis system, of local water pressure changes resulting from the movements of adjacent fish (Gray and Denton 1991).

According to Gray and Denton (1991), pressure waves produced in water during very slow movements are small and vision has an evident advantage, but the relative merits of communication through light rather than sound will diminish as the speed of movements increases. They also suggested that the first indications of quick movements will be communicated through sound.

The LLO is a superficial sensory system in fish and other aquatic vertebrates consisting of receptors (neuromasts) which detect water displacement. In adult fish, two forms of neuromasts are usually present: those within the lateral line canal, and the superficial, or free, neuromasts in the epithelium of the head, trunk and caudal fin. The neuromasts contain axonless mechanosensory hair cells similar to those found in the inner ear, each with a kinocilium and a polarized bundle of linked microvilli that decrease in height with increasing distance from the kinocilium (Baker *et al.* 2007). The LLO is sensitive to nearby water movement, to low frequency vibrations, and liquid currents, including movements of a travelling sound source. The term 'lateral line' is derived from the bilateral line that can be seen on the trunk of many fish, although neuromasts may be located elsewhere, for example on the head (Cernuda-Cernuda and Garcia-Fernandez 1996). The ultrastructure, development, and phylogeny of these hair cells are similar to those of the inner ear; therefore these organs are commonly grouped together as the octavolateralis system (OLS) (Popper and Fay 1993).

The lateral line and the inner ear will have many overlapping functions (Popper and Fay 1993; Braun and Coombs 2000). Thus many principles concerning perception and masking will

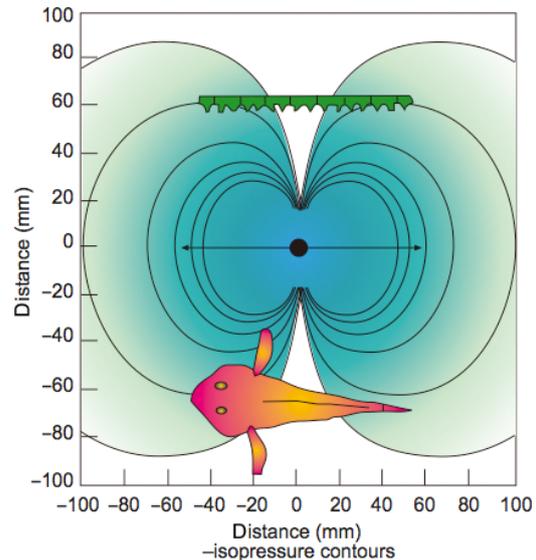


Figure 1 Vibrations, swimming animals, vocalizations and other mechanical disturbances will generate a steep pressure gradient close to the source, giving rise to a net flow of water. This water flow will eclipse particle compressions and rarefactions, so that, near the source, water movements will be more powerful than the propagated pressure wave (e.g. the distance from the sound source to the fish or the schematic lateral line in the figure). These pressure changes surrounding a hydrodynamic source are perceived by the lateral line system as well as by the inner ear. The lateral line, with many densely grouped sampling points, requires a steep spatial gradient for stimulation, but, as a consequence, it will be able to resolve that gradient in spatial detail. The auditory system may respond to a similar pressure gradient by integrating the differences in pressure along contralateral sides of its body, but the inertial sensors of the inner ear will be unable to resolve spatial details of the stimulus field (Braun and Coombs 2000). The figure is from Braun and Coombs (2000) with permission. Isopressure contours were modelled after dipole flow equations (Kalmijn 1988).

be analogous. Therefore, water movement/sound that stimulates the lateral line is in general not differentiated here from that perceived by the inner ear (Fig. 1).

Electro-sense and schooling

Evolutionary modifications of the lateral line led to development of the electro-sensory system (Bullock 2007), which may also play a role in schooling. In some weakly electric fish (e.g. *Marcusenius cyprinoides*, Mormyridae), electric signals and the electro-

sensory system appear to function as part of a schooling mechanism adapted to aid group cohesion in turbid water and during migration at night (Moller 1976).

Sensory reafference

Most objects in the underwater environment contribute to water movements and the scattering of sounds: the water surface, the substratum, animals and plants, and anything that moves. 'An awareness of the presence and location of objects – the general structure of the environment – certainly is necessary for moment-to-moment and longer-term behaviour that is appropriate for feeding, social interaction, avoiding predation, reproduction, and all the behaviours that tend to propagate the animal's genes' (Popper and Fay 1993). The sounds and water movements an animal produces through vocalization or motion will, to some extent, stimulate its own auditory system. This is referred to as sensory reafference (von Holst and Mittelstaedt 1950). Water movements generated by a fish's locomotion might interfere with its perception of pressure waves and other stimuli originating in the surrounding environment. This has been extensively explored in individual fish (Russell 1968; Roberts and Russell 1972; Tricas and Highstein 1991; Montgomery and Bodznick 1994; Palmer *et al.* 2005; Liao 2006), but not at all in groups.

Acoustic and hydrodynamic characteristics of a moving group

'Given the relatively underdeveloped state of schooling behaviour models...it is unavoidable that studies of the evolutionary hows and whys of schooling remain somewhat speculative and oversimplified' (Parrish *et al.* 2002). An example of this might be the lack of information about the acoustic and hydrodynamic situation in a moving shoal.

As said, sensory reafference caused by locomotion of individual fish has been thoroughly investigated, but how might OLS perception be affected in a large group of densely packed individuals? Although such a group would undoubtedly produce perceptible pressure waves and other water movements during locomotion, its possible impact on fish perception and behaviour seems not to have been investigated.

Synchronization and perception within the school

When many fish move in close proximity to one another, the resulting water movements will contain much more energy than that produced by a single fish; furthermore, pressure waves might be complex and quiet intervals few, thus increasing the potential for masking of other signals.

There are several possible mechanisms through which synchronized group movements might influence perception via the inner ear and lateral line in the natural environment. A basic principle is that fish moving in synchrony will have the capacity to discontinue movements simultaneously, providing quiet intervals to allow the reception of potentially critical environmental signals.

Schooling fish are generally of similar size and species (Pitcher *et al.* 1985; Pavlov and Kasumyan 2000), and the hydrodynamic noise they produce in swimming will be similar in amplitude and frequency, which may facilitate the discrimination of self- and neighbour-produced water movements from environmental signals.

The ability to locate sound sources is probably one of the most important functions of the auditory system in all animals (Popper and Fay 1993). In humans, synchrony fully fuses short duration noise-bursts across frequency and across space, while un-synchrony of 20–40 ms produces no fusion. There is empirical evidence that the evolutionary advantage of such auditory grouping is sound-source determination (Turgeon and Bregman 2001). The detection of a given signal is likely to be influenced by the presence of simultaneous interfering signals. Therefore, adaptations for sound detection sensitivity probably include strategies for grouping the sound components from discrete sources and segregating those that belong to different sources (Popper and Fay 1993). Hearing specialist fish have been shown to exhibit excellent temporal resolution abilities, enabling them to accurately process temporal patterns of sounds (Wysocki and Ladich 2005). When fish succeed in moving concurrently (or nearly so) auditory grouping is possible. Water movement noise produced by the group, even though coming from various directions, may be perceived as a single source, facilitating its discrimination from other sound-sources.

The existence of efferent neurons that inhibit the lateral line perception of noise produced by the fish's

own movements has been shown in individual fish (Roberts and Russell 1972; Montgomery and Bodznick 1994). 'Vigorous movements of the fish, involving the white musculature, were preceded and accompanied by activity of the efferent fibres, which persisted as long as the white muscle fibres were contracting...thus the role of the efferent system is obviously related to the behaviour of the LLO during movement, because it's only at these times that the efferent neurones are active' (Roberts and Russell 1972). To the extent that neighbouring fish in a school move concurrently, the masking caused by group-produced noise may be reduced by the same inhibitive mechanisms. In the African clawed frog (*Xenopus laevis*, Pipidae), the lateral line inhibition is followed by a short period during which a response is 1.25–3.0 times higher than for baseline measures (Russell 1971). Thus schooling fish may benefit, not only from silence, but also from an enhanced perception of surrounding sounds when group movements temporarily cease.

Fish in schools generally move at a similar speed and in a common direction, hence motion relative to neighbours will be reduced compared to that in a less coordinated group (B. Regnström, personal communication). Thus schooling could reduce masking, by noise from nearby fish, of canal neuromasts, which detect water acceleration (Kroese and Schellart 1992). However, the masking reduction may be limited due to complicated flow patterns in the wake of fish (Hanke and Bleckmann 2004).

The distance to source over which the LLO responds is 1–2 body lengths (Popper and Fay 1993). Dipole sources used in experiments to simulate another fish can be detected if the distance lies within the length of the lateral line canal (Curcic-Blake and van Netten 2006). Distance to the nearest school-neighbour is commonly 0.7 body length (Pitcher 2001), which approximates the length of the lateral line. Hence, schooling individuals usually move close enough to trigger perception by the lateral line. The distance over which the inner ear responds has been shown to be greater (Curcic-Blake and van Netten 2006).

Manoeuvres of the school as a whole will exhibit varying degrees of synchronization. As said, responses of fish swimming at the rear of the school usually lag slightly behind (Pavlov and Kasumyan 2000). The most potentially disturbing masking noise will be that produced by fish close to the reference (perceiving) fish, thus a reduction of

synchronization with fish at some distance should not significantly reduce the anti-masking benefits of schooling.

Predator confusing effects of schooling

Schooling has been proposed by many to give confusing visual signals to predators (Pavlov and Kasumyan 2000), including visual mimicry of a large fish (Springer 1957; Breder 1959). However, is it possible that schooling might confuse other senses of predators, including OLS perception?

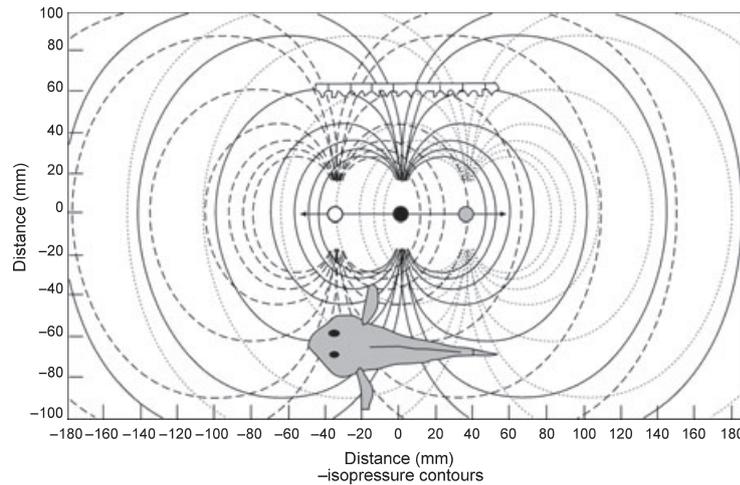
At least in the final stages of a predator attack, lateral line perception has been shown to be important. 'When muskellunge (*Esox masquinongy*, Esocidae) attacks, vision is of primary importance in the initial location of, and orientation to, the prey, while the lateral line may be of principal importance in the capture of the prey in the final stages of the attack' (New *et al.* 2001).

Fin movements of a single fish will act as a point-shaped wave source, emitting a gradient by which predators might localize it (Fig. 1). Schooling should obscure this gradient, as fields from many fish will overlap, possibly confusing the lateral line perception of predators (Fig. 2). Nevertheless, a large group of fish might produce more readily detectable signals, possibly attracting predators. However, schooling fish are arranged in a symmetrical fashion. This kind of wave-source might emit a flat wave-front, mimicking the pressure waves of a large animal (B. Regnström, personal communication). If so, it might balance the risk of readily detectable signals.

The pressure waves generated by schooling fish can also be perceived by the inner ear. The source distance over which the inner ear responds is greater than that for the lateral line (Popper and Fay 1993; Curcic-Blake and van Netten 2006). Thus, synchronized movements might induce predator confusion at distances greater than the reach of the lateral line.

It has been suggested that an important function of the lateral line is to mediate wake-tracking in predatory fish (Hanke and Bleckmann 2004; Pohlmann *et al.* 2004). Wake height and the lateral distance between vortices correspond to the size of the fish. The wake also provides information about swimming style and direction (Dehnhardt *et al.* 2001). Wake tracking abilities have been demonstrated in a nocturnal predator tracking single prey (Hanke and Bleckmann 2004; Pohlmann *et al.*

Figure 2 If hydrodynamic sources (for example moving fishes) are closely situated, the hydrodynamic signals they produce will overlap. Increasing the number and reducing the distance between hydrodynamic sources will create more overlapping signals. This may result in difficulties in perceiving the single source.



2004). Fish rarely or never school in darkness, however, in principle, such wake tracking should be possible in light. If so, it presents another possible means by which schooling may confuse predators, one that may have been effective before vision developed in most predators.

The natural stimuli for electro-reception and for the lateral line have common attributes. Information is conveyed by stimulus intensity, orientation, and polarization (direction) (Bodznick 1989), and within a couple of body lengths of local dipole electric fields, electro-receptive animals may localize the field source using spatial non-uniformities (curvature of field lines or direction of the intensity gradient) (Sawtell *et al.* 2005; Freitas *et al.* 2006). Certain predatory fish, e.g. sharks, use the electro-sensory system to detect and distinguish electrical fields of prey during an attack. Individual prey must be about five body widths apart to produce separate signals. If objects are too close together to be distinguished, they will form a blurred image (Babineau *et al.* 2007). Hence, schooling may have the potential to confuse the electro-sensory system of predators.

It is also possible that schooling affects the biosonar performance of whales. At least whales seem to select targets at the periphery of dense echo clouds (Madsen *et al.* 2005).

Join, leave or stay?

When shoals of fish meet, the major factors determining whether individuals will join are body length and species. The exact mechanisms behind such JLS decisions are not known, but seem to take effect within a few seconds (Krause *et al.* 2000b).

Research concerning assortment of fish shoals generally describe patterns rather than processes and, to the extent that sensory mechanisms have been explored, research has mainly concerned vision. Fish have been shown to use visual cues to join larger groups (Keenleyside 1955; Hager and Helfman 1991). Engeszer *et al.* (2004) found that zebrafish (*Danio rerio*, Cyprinidae) exhibit strong colour shoaling preferences. In experiments using normally coloured zebrafish and the mutant, *nacre* (with reduced pigmentation on the body), they found that colour preference was learned; wild-type zebrafish reared with *nacre* siblings prefer to shoal with *nacre* zebrafish.

However, there is evidence also for a role of the lateral line in JLS decisions. In an experiment by Pitcher *et al.* (1976), saithe (*Pollachius virens*, Gadidae) fitted with temporary blinders were eventually able to join and school with normal fish, while saithe with disabled lateral lines in addition to blinders were not. Simultaneous contributions of vision and the lateral line are considered to be important during fish locomotion (Partridge and Pitcher 1980; Montgomery *et al.* 2002; Liao 2006). In animals, input from several sensory modalities is integrated in the central nervous system to supply information related to behavioural aims. This may take the form of a quasi-hierarchical arrangement of responses to cues during the changing phases of a behavioural sequence. As mentioned, when the muskellunge attacks, vision is of primary importance in the initial location of, and orientation to, prey, while the lateral line may be of principal importance in the capture of the prey in the final stages of the attack, demonstrating a sliding

hierarchy of sensory system dominance during each portion of the strike (New *et al.* 2001). Could a similar hierarchy of sensory systems be involved in JLS decisions? If so, what possible roles could vision and the LLO play? Muskellunge in which the lateral line has been suppressed by CoCl_2 significantly decrease their angular deviation to prey, approaching in a more directly head-on fashion. This suggests that the visual system may be directed more towards stimuli located in front of the animal, whereas the LLS, which is distributed along the sides of the head and the body, is more laterally directed (New *et al.* 2001). Although this study investigated the role of vision and lateral line in predation, it may also give clues to sensory mechanisms in JLS decisions. In both situations, one fish is approaching another.

An exclusive role of vision in JLS decisions may also be called into question by the fact that Atlantic herring (*Clupea harengus*, Clupeidae) and the Atlantic mackerel (*Scomber scombrus*, Scombridae) have been shown to display equal preference for associating with similar-sized conspecifics in varying light conditions (night or day) (Pitcher *et al.* 1985). However, light required for filming in the experiment may have been sufficient for the fish to have received some visual input.

While little is known about the decision-making process, an active shoal choice has been shown (Krause *et al.* 2000a). Water movements may play a role in these decisions. The ability to discriminate among sounds on the basis of frequency is present in all vertebrates investigated, including fish, and temporal patterns of sound are thought to be the most important carriers of acoustic information for teleost fishes (Popper and Fay 1993). Goldfish (*Carassius auratus*, Cyprinidae) not only can discriminate between pure tone frequencies, but also appear to order them on a perceptual continuum similar to the human perception of pitch (Fay 2005). As fish of similar shape and size would emit similar pressure waves (and water movements), and vice versa for fish differing in size and body-shape, water movements from fish encountered could provide information which is potentially useful in making JLS decisions. This is reinforced by evidence that fish are able to use information carried in water movements during wake tracking (Hanke and Bleckmann 2004). The learned colour preference in zebrafish shown by Engeszer *et al.* (2004) does not contradict this, as fish may learn to associate neighbour colour with identifiable pressure waves

and water movements (siblings reared with the experimental fish would have been almost identical in size and body-shape). Investigation to determine how long such colour preference persists in a colour and size mixed shoal would be of interest.

Intra-school fission, rather than fusion, is important in generating body length-, as well as phenotypic-based assortment (Croft *et al.* 2003). Swimming speed has been suggested to be a passive mechanism determining fish shoal assortment (Krause *et al.* 2005). To speculate, intra-school fission could also be indirectly related to OLS perception, as fish differing appreciably in size may not succeed in achieving a suitable degree of synchronization of movement, increasing the likelihood of separation. Including pressure waves and water movements in a shoal assortment model could help to explain why fission rather than fusion is the major mechanism affecting shoal assortment.

Discussion

A group of fish moving in synchrony (compared to a less synchronized or an un-synchronized group) seem to gain advantages that have not been previously recognized.

Inside the school, synchronized movements may reduce masking and so boost the perception of critical environmental signals, e.g. of an approaching predator. In addition to affecting the perception of schooling fish, synchronicity may have an impact on how the fish (or group of fish) is perceived by those outside the school, contributing to defence against predators. Overlapping pressure waves might confuse predators (or frighten by mimicking a larger animal) through interference with octavolateralis perception. Overlapping electrical fields might blur electro-sensory systems. Thus, the speculated effects, outside as well as within the school, could be associated with significant evolutionary benefits.

Species other than fish may also have benefited from the development of synchronization. In bottlenose dolphins, 30.5% of schools showed synchronous breathing, i.e. surface-diving. Synchrony was negatively related to the presence of calves in a school (Hastie *et al.* 2003), to age- and sex-difference of a dyad, and to separation distance (Perelberg and Schuster 2008); but positively related to the presence of boat traffic and school size (Hastie *et al.* 2003). The background behind synchronous swimming in dolphins is far from

clear. However, the presence of calves and differences in age or sex implies heterogeneity in body size (Stolen *et al.* 2006), which may reduce synchronization. Increased proximity may result in more disturbing sounds from neighbours, while boats cause noise and may be considered a threat (Hastie *et al.* 2003), both factors that might trigger synchrony to enhance auditory perception.

Some birds fly with highly synchronized wing-beats, and, although energy may be saved (Weimerskirch *et al.* 2001), wing-beats and breathing also generate noise. Might birds also gain acoustical advantages through synchrony?

Although this review is speculative, the ambition is that the suggestions respect physical laws and are reinforced by observations from the cited research. Before the list of evolutionary advantages related to schooling can be expanded, empirical studies will of course be mandatory.

As a start, sound recordings could provide information concerning the masking properties of SOL produced by individuals or groups of animals and predict the extent to which self-produced SOL may mask critical sounds of the surroundings. This may also be a first step in testing the hypothesis that schooling may create a flat wave-front, mimicking a large animal. Further investigation might also include a continuation of experiments such as those of Gray and Denton (1991) looking at sound communication of fish during locomotion. Interesting but intricate would be sound and pressure recordings inside a group of fish (or dolphins). A crucial question is the extent to which neighbours in schools move in synchrony. An experimental technique for charting the individual positions of thousands of animals has recently been described (Cavagna *et al.* 2008). This can provide a vehicle for investigating large groups of animals with respect to such features as shape, movements, density, and structure, providing a new experimental benchmark for testing and improving theoretical models of self-organized motion in groups (Ballerini *et al.* 2008).

Including sounds and water movements produced during locomotion of animal in groups could expand such models. Data obtained may also demonstrate the level of synchrony between neighbouring fish.

The speculated predator confusing effects of schooling might be tested by systematically disabling the senses of predators, as in the experiments

of New *et al.* (2001), to learn how this influences the capture of schooling and non-schooling prey. Modelling the electric field of weakly electric predator fish, similar to studies of Babineau *et al.* (2007), may increase understanding of the electrosensory landscape surrounding prey-fish and schooling's effects on it.

Hopefully, this review may stimulate debate and empirical studies and have the end result of increasing the understanding of complex acoustical aspects of group locomotion.

An increased understanding might not be solely good, as man is the principal predator of many fish species, but if it leads to an increase in the understanding of biology and ecology, it will be truly beneficial.

Acknowledgements

Björn Regnström, Technology DR, Chalmers institute, Gothenburg, Sweden, for consultations about wave physics. The Lucidus Consultancy for engaged and skilful help with the English language and editorial comments. Christer Brönmark, Professor, Department of Ecology, Limnology Lund University, Sweden for reading an early version of the manuscript and encouraging support. The Editors, Professors Paul Hart and Tony Pitcher for good advice, encouraging support and patience. Christopher B. Braun and Sheryl Coombs for kind permission to reproduce and develop their figure. Four anonymous reviewers who gave important suggestions about structure and content. Maria Bergman, Department of Medical Photography, Örebro University Hospital, Örebro, Sweden, for help in the production of figures. Margareta Landin and colleagues at the medical library, Örebro University Hospital, Örebro, Sweden, for help with literature research.

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