

Opinion

Why do fish school?

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Abstract Synchronized movements (schooling) emit complex and overlapping sound and pressure curves that might confuse the inner ear and lateral line organ (LLO) of a predator. Moreover, prey-fish moving close to each other may blur the electro-sensory perception of predators. The aim of this review is to explore mechanisms associated with synchronous swimming that may have contributed to increased adaptation and as a consequence may have influenced the evolution of schooling. The evolutionary development of the inner ear and the LLO increased the capacity to detect potential prey, possibly leading to an increased potential for cannibalism in the shoal, but also helped small fish to avoid joining larger fish, resulting in size homogeneity and, accordingly, an increased capacity for moving in synchrony. Water-movements and incidental sound produced as by-product of locomotion (ISOL) may provide fish with potentially useful information during swimming, such as neighbour body-size, speed, and location. When many fish move close to one another ISOL will be energetic and complex. Quiet intervals will be few. Fish moving in synchrony will have the capacity to discontinue movements simultaneously, providing relatively quiet intervals to allow the reception of potentially critical environmental signals. Besides, synchronized movements may facilitate auditory grouping of ISOL. Turning preference bias, well-functioning sense organs, good health, and skillful motor performance might be important to achieving an appropriate distance to school neighbors and aid the individual fish in reducing time spent in the comparatively less safe school periphery. Turning preferences in ancestral fish shoals might have helped fish to maintain groups and stay in formation, reinforcing aforementioned predator confusion mechanisms, which possibly played a role in the lateralization of the vertebrate brain [*Current Zoology* 58 (1): 116–128, 2012].

Keywords Group synchrony; Hearing in fish; Lateral line; Electro-sensory system; Sensory reafference; Lateralization

1 Introduction

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 (Pitcher, 2001). No clear views currently exist on the evolution of schooling behaviour (Pavlov and Kasumyan, 2000). Mating, foraging, and reduction of energy expenditure have been discussed as possible advantages achieved by schooling (Domenici et al., 2007; Partridge and Pitcher, 1979; Pavlov and Kasumyan, 2000; Svendsen et al., 2003). However, fish tend to school in risky situations (Pavlov and Kasumyan, 2000), and many established ideas include predator defense, such as safety in numbers (Krause et al., 2000a; Pavlov and Kasumyan, 2000), reduction of encounters with predators (Turesson and Bronmark, 2007), and increased predator surveillance

(Pavlov and Kasumyan, 2000; Pitcher, 1998). Schooling has also been proposed to give confusing visual signals to predators (Pavlov and Kasumyan, 2000), including visual mimicry of a large fish (Breder, 1959; Springer, 1957). Fish shoaling with individuals different from themselves are more easily spotted and large shoals are considered to be safer (Krause and Ruxton, 2002).

In an earlier review (Larsson, 2009), I discussed evidence that schooling might confuse the lateral line organ (LLO) and electrosensory system (ESS) of predators. Fin movements of a single fish will act as a point-shaped wave source, emitting a gradient by which predators might localize it (Fig. 1a). Since fields of many fish will overlap (Fig. 1b), schooling should obscure this gradient, perhaps mimicking pressure waves of a larger animal, and more likely confuse the lateral line perception that is essential in the final stages of a predator attack (New et al., 2001).

Received Jan. 10, 2011; accepted Mar. 26, 2011.

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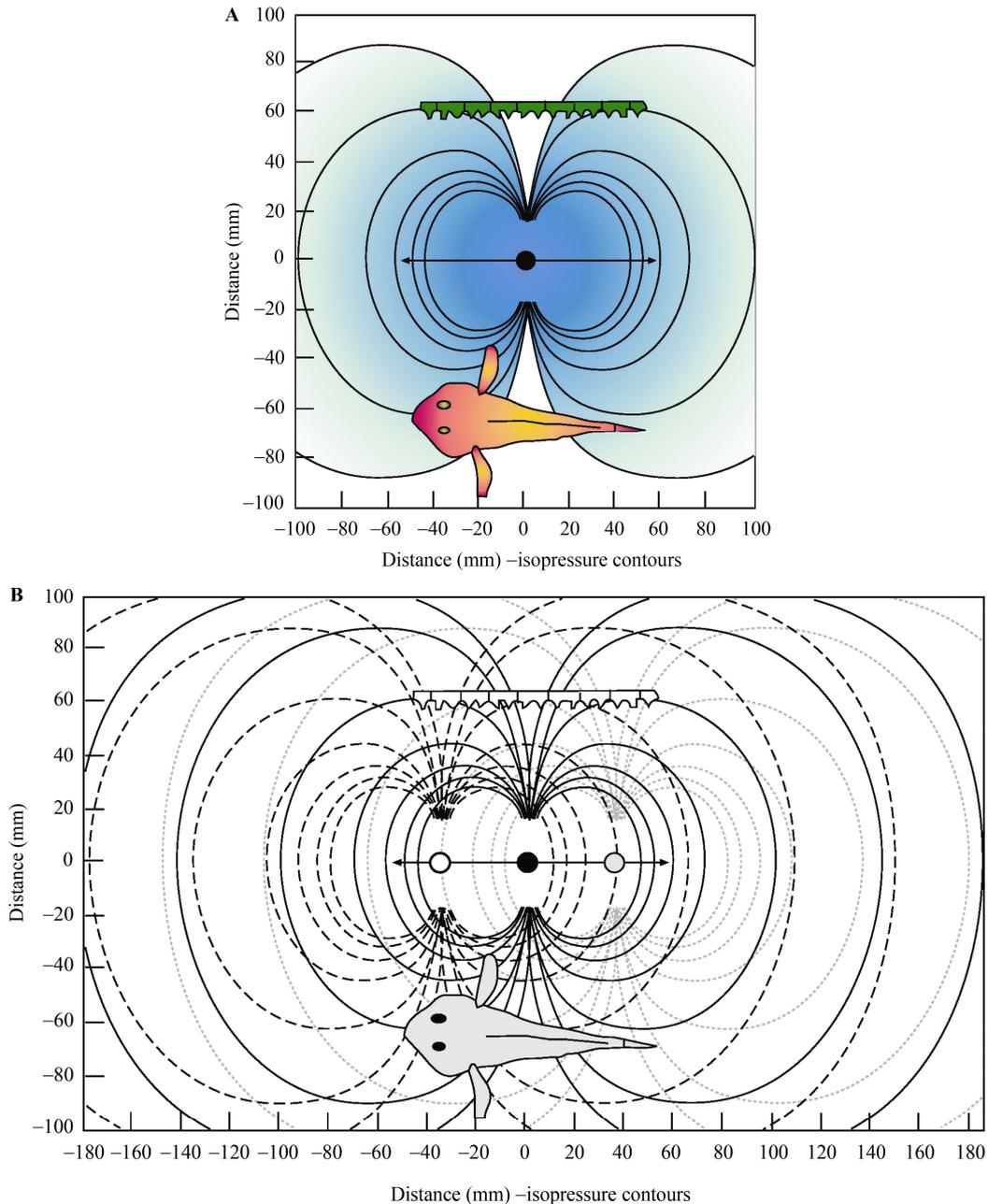


Fig. 1 Hydrodynamic signals (ISOL) produced by fish during locomotion

A. Solitary fish produces relatively uncomplicated hydrodynamic signals. The black dot in the centre is a dipole emitting sound and water-movements. Such hydrodynamic noise may be similar to ISOL produced by a moving prey-fish. ISOL from a solitary fish will be uncomplicated and help a predator fish (lower part in the figure) to detect the prey with its lateral line or inner ear. 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) [Braun and Coombs (2000) suggested the threshold distance of the Lake Michigan mottled sculpin, *Cottus Bairdi*, to be similar for the lateral line and inner ear, *ca.* 1–1.5 body length]. Isopressure contours were modeled after dipole flow equations (Kalmijn, 1988). The figure is reproduced from (Braun and Coombs, 2000) with kind permission from *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, Royal Society Publishing. **B.** Hydrodynamic signals (ISOL) produced by nearby fishes will overlap. When moving fish or in this case dipoles (white, black and grey dots) are closely spaced, the hydrodynamic signals they produce will overlap. Increasing the number and reducing the distance between hydrodynamic sources will create more overlapping signals. The figure is reproduced from (Larsson, 2009) with kind permission from *Fish and Fisheries*, Wiley-Blackwell.

Electro-receptive animals may localize a field source by using spatial non-uniformities (Freitas et al., 2006; Sawtell et al., 2005) (Fig. 2a). In order to produce separate signals, individual prey must be about five body widths apart. 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 ESS of predators (Fig. 2b).

Here I hypothesize that the development of schooling behavior was associated with an increased quality of perception, predatory lifestyle and size sorting mechanisms to avoid cannibalism. Incidental sounds and water movements produced as a byproduct of locomotion (ISOL), sensory reafference, ISOL as signal mechanisms, biological oscillators, the shape of the shoal, and turning biases at the population level are also discussed.

2 The Octavolateralis System in Fish

The lateral line organ (LLO) and the inner ear have several overlapping functions. Since the ultrastructure, development, and phylogeny of their receptors (hair cells) are similar, these organs are commonly grouped together as the octavolateralis system (OLS) (Braun and Coombs, 2000; Popper and Fay, 1993), and many principles concerning perception and masking will apply to both (Larsson, 2009).

The LLO is a superficial sensory system in fish and other aquatic vertebrates consisting of receptors (neuromasts) which are sensitive to 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 are progressively shorter with increased distance from the kinocilium (Baker et al., 2008). The LLO is sensitive to nearby water movements, low frequency vibrations, liquid currents, and movements of a travelling sound source (Cernuda-Cernuda and Garcia-Fernandez, 1996).

3 From Filter Feeding to Active Predation

In filter feeding ancestors, before vision and the OLS had developed, the risk of predation would have been limited and mainly due to invertebrate predators (Budd, 2001; Parker, 2004), hence, at that time, safety in numbers was probably not a major incentive for gathering together in shoals or schools. However, grouping could have been beneficial for other reasons, such as foraging and mating (Komdeur et al., 2008). In early ancestors, lacking vision or the OLS, chemoreception could have been sufficient to recognize conspecifics (Hara, 1993).

Northcutt and Gans (1983) proposed that many of the unique characteristics of vertebrates derive from the neural crest, cranial placodes, and a muscularized hypomere, and that these evolved in the vertebrate

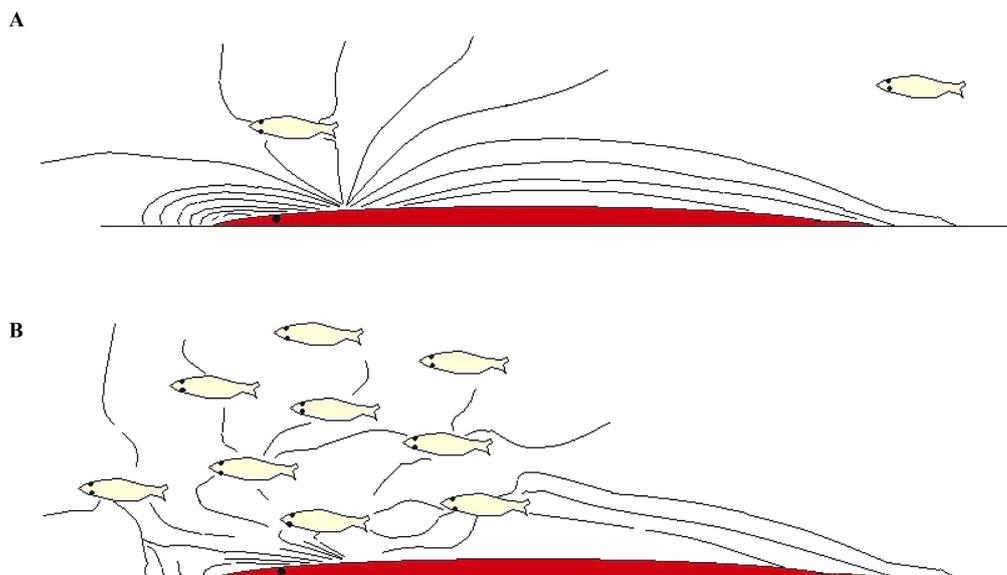


Fig. 2 A predatory fish (red) uses the electroreceptive system to detect and distinguish electrical fields of prey during an attack

A. A solitary fish may be easy to detect and localize. **B.** Individual fish in a school may be difficult to sense, since the “electrical landscape” will be more complicated. Individual prey (yellow) must be about five body widths apart to produce separate signals, otherwise they will form a blurred image (Babineau et al., 2007).

ancestor in association with a shift from filter feeding to active predation. Thus the extraordinary diversity of neural crest and placode derivatives could be seen as adaptations to a predatory lifestyle (Baker et al., 2008; Northcutt and Gans, 1983). It is likely that the inner ear and the LLO evolved from a primitive system of epidermal ciliated sensory receptor cells, most likely mechanoreceptors (Baker et al., 2008; Streit, 2001). This was probably long before vertebrate ancestors developed vision (Parker, 2004). Whatever the evolutionary background, the development of the OLS, and vision, would have permitted detection of

potential prey. This could have led to an increased potential for cannibalism within the shoal (Fig. 3, 4). On the other hand, increased quality of perception would also give small individuals a chance to escape or to never join a shoal with larger fish. It has been shown that small fish avoid joining a group with larger fish, although big fish do not avoid joining small conspecifics (Lachlan et al., 1998). This sorting mechanism based on increased quality of perception could have resulted in homogeneity of size of fish in shoals, which would increase the capacity for moving in synchrony (Fig. 5).

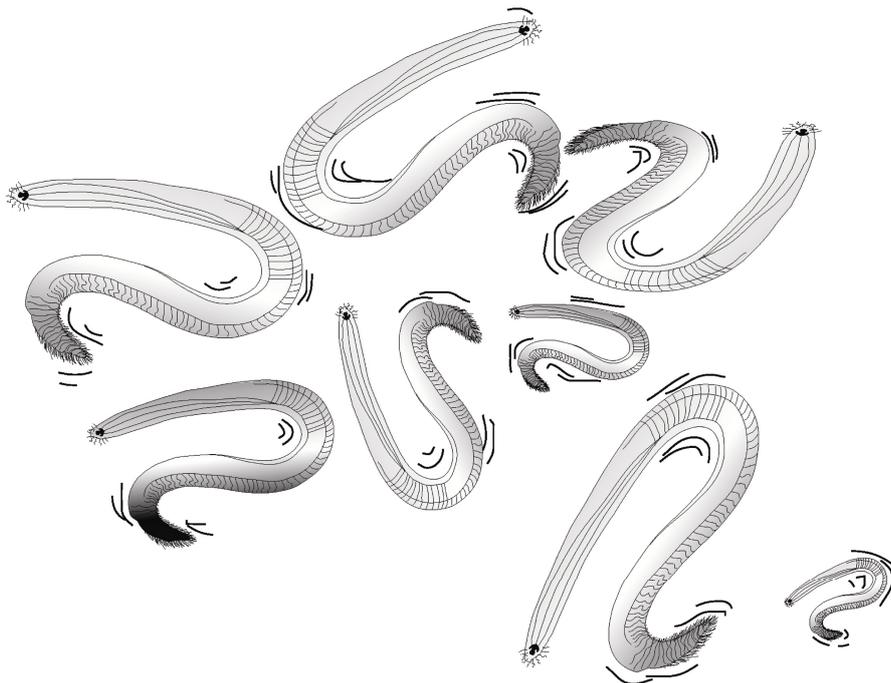


Fig. 3 Arbitrary (hagfish-like) filter feeding vertebrates with no or little developed OLS and vision

The risk of being eaten by a bigger fish in such a group of early filter feeders was probably small.

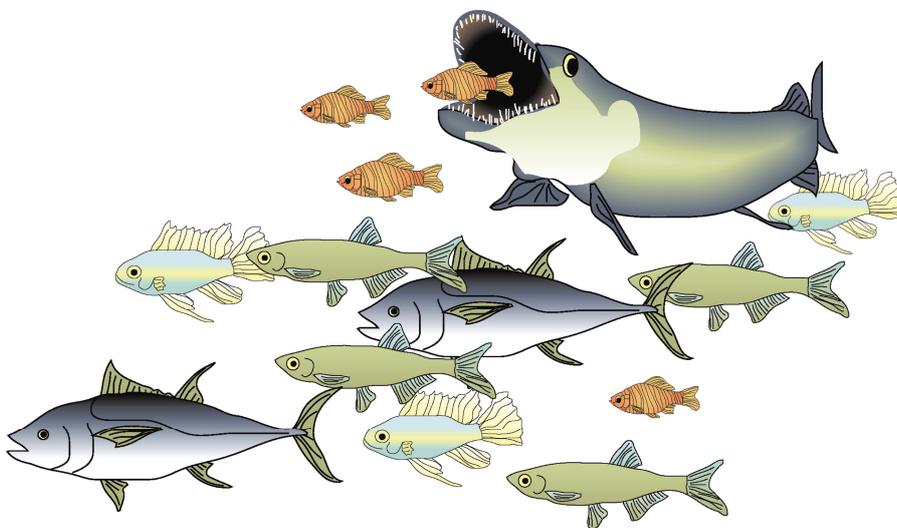


Fig. 4 The risk of being eaten may contribute to similarity in size

The development of the OLS probably was important in the initiation of a predatory life style (Baker et al., 2008; Northcutt and Gans, 1983). That may have increased the risk of being eaten by a larger fish in the shoal. The OLS would also have helped small fish to detect and avoid bigger fish.

4 Sensory Reafference in A School

Water movements and sound generated by a fish's locomotion (SOL) or vocalization might interfere with its perception of pressure waves and other stimuli originating in the surrounding environment. The neuronal control mechanisms to reduce this interference is referred to as *sensory reafference* (von Holst and Mittelstaedt, 1950) and has been systematically investigated in individual fish (Roberts and Russell, 1970; Russell, 1968; Tricas and Highstein, 1991). Since the LLO senses water displacement (Dijkgraaf, 1962), it seems likely that the fishes own movements could hinder its ability to detect signals from e.g. prey or predators. In terms of swim behavior, fish can be placed on a gradient, in one end ambush predators (stationary all the time), on the other end fish that are in constant motion, and in between fish that show "saltatory" search, i.e. fish will pause and scan for prey before moving a short distance and pausing again etc (Bassett et al., 2007). This has been suggested as a strategy to eliminate self generated noise, i.e., ISOL, in lateral line predators (Bassett et al., 2007; Coombs and Conley, 1997; Hoekstra and Janssen, 1985). It seems likely that schooling fish ceasing movements simultaneously and remaining immobile for a while may achieve similar perceptual advantages (i.e., reduced ISOL).

When many fish move close to one another, water movements will contain much more energy than that produced by a single fish, and pressure waves might be complex. Quiet intervals will be few. I recently suggested that synchronized movements in a group reduce noise that has the potential to mask auditory signals (Larsson, 2009). Fish moving in synchrony will have the capacity to discontinue movements simultaneously. Concurrent pausing may provide relatively quiet intervals to allow the reception of potentially critical environmental signals. Fish under predator threat that form non-moving "look around shoals" (Radakov, 1973) may be an example. In addition, fish possess efferent neurons that inhibit lateral line perception of noise produced by the fish's own movements (Montgomery and Bodznick, 1994; Roberts and Russell, 1972). Such inhibitive mechanisms may also reduce interference by group-produced noise.

5 Synchronized Movements and Auditory Grouping

I also suggested that synchronized movements may influence hearing through facilitating auditory grouping

of own-produced noise (Larsson, 2009). Many fish swim intermittently using a two-phase periodic behavior of alternating accelerations (burst phase) with glides (coast phase) (Videler and Weihs, 1982). Longer coast times were observed for trailing fish (Fish et al., 1991). It seems unlikely, or at least uncommon that swimming movements of schooling fish are produced in phase. Moreover, coast and burst cycles are usually short. In Golden shiners *Notemigonus crysoleucas* the cycle is approx. 0.5 seconds (Fish et al., 1991), which will result in only brief pausing (some milliseconds) before movements continue. Even if swimming movements should be in phase now and then that would be unlikely to provide significant attenuation of noise. However, the ability to locate sound sources is an important function of the auditory system. Auditory scene analysis is defined as the capability of animals to separate and group concurrent sounds from numerous sources, thus reconstructing the auditory scene (Bregman, 1990). Brains of humans and other vertebrates strive to group sounds that have a common origin (Bregman, 1990). At any given time the environment typically contains several active sound sources, and various strategies are used to organize them into distinct auditory events (Ciocca, 2008). In humans, common onset, the harmonic relations between frequency components, continuity of pitch, timbre, and overall sound level are important cues for grouping of sounds (Bregman, 1990; Darwin, 2008). Fish of similar size, moving concurrently, or nearly so, will produce similar and nearly concurrent ISOL, which may facilitate auditory grouping. In other words, group-noise caused by locomotion in a highly synchronized group may be perceived as a single source, facilitating its discrimination from other sound-sources.

In summary, individuals with a capacity to move synchronously with neighbors may gain perceptual advantages that could lead to timely awareness of predators or prey.

6 Join, Leave, or Stay?

When shoals of fish meet, the major factors determining whether individuals will join are body length and species. The mechanisms behind such decisions are not known, but seem to take effect within a few seconds (Krause et al., 2000a), and an active shoal choice has been shown (Krause et al., 2000b). Fish of similar shape and size will emit similar pressure waves (and water movements), and vice versa for fish differing in size and body-shape. The ability to discriminate among sounds on the basis of frequency is present in teleost fishes, and

temporal patterns of sound contribute important acoustic information (Popper and Fay, 1993). Moreover, it was suggested that water movements produced by a swimming goldfish *Carassius auratus* (Hanke et al., 2000) and three other fish species with differing swimming style (Hanke and Bleckmann, 2004) show a clear vortex structure that lasts in the order of minutes (or at least 30 s). The water disturbance was hypothetically sufficient to be sensed by a piscivorous predator at a distance where vision or hearing frequently fail. Moreover, Hanke and Bleckman (2004) suggested it is likely that a predator can extract information beyond the plain presence of a wake and learn to interpret such flow structures to a certain degree. If so, it seems likely that OLS perception may provide information about con-specifics especially when they are swimming close. Thus, I suggest that ISOL and water disturbance from fish encountered may provide information that is useful in making join, leave, or stay decisions.

7 Do Schooling Fish Use ISOL for Communicative Signals?

Vision has been considered to be of paramount importance and the sensory basis of schooling (Pavlov and Kasumyan, 2000; Pitcher, 1998), but evidence is strong that the LLO is also involved (Pitcher, 1998). The development of schooling in teleost larvae is closely connected to the development of the LLO (Blaxter, 1987). Water movements and sounds produced by locomotion may provide useful signals in group locomotion. Gray and Denton (1991) suggested that the merits of communication through vision, as opposed to sound, diminish as the speed of movement increases. They showed that when herring *Clupea harengus* and whiting *Merlangius merlangus* make rapid swimming movements, such movements are preceded by sound signals. Gray and Denton, (1991) also suggested that there are many means by which a fish might assess the distance to another fish from the sound that it makes, including changes in amplitude with distance and the phases of pressure and pressure gradients in the near-field.

Pitcher et al. (1976) showed that the LLO has an important role in fish schooling. Fish with a temporarily disabled LLO school in a different manner, making less accurate distance adjustments (Partridge and Pitcher, 1980). Firehead tetras, *Hemigrammus bleheri*, totally deprived of the lateral line system were unable to maintain a shoal (Faucher et al., 2010). Thus it seems likely that the OLS may be used to transfer information about position in space, such as direction, distance, and (rela-

tive) speed of neighbours in a school.

7.1 Appropriate distance

Maintaining an appropriate distance from school-mates while avoiding collision, i.e., to be a skillful follower, might increase chances of survival.

Teleost fish have acute hearing and usually determine the nature of action to take on the basis of very brief signals (Gray and Denton, 1991). The almost instantaneous adjustments to swimming direction and speed that characterize schooling are made possible by detection, via the OLS, of local water pressure changes resulting from the movements of adjacent fish (Gray and Denton, 1991). The sounds produced by fish bodies of similar size and phenotype, moving at the same speed, will be similar in frequency and amplitude, while fish differing in size will produce dissimilar and less predictable sounds.

Information embedded in ISOL will travel in all directions; hence it might be used in mutual adaptation among neighbours (Fig. 6). Knowledge of the precise location of nearby members is crucial to schooling fish. The distance to a neighbour may be assessed from a stereotypic sound with a stable sound level (ISOL, breathing, or vocal call) produced by the neighbour, since the relative amplitude will be influenced by distance. Moreover, when a complex sound travels through water its timbre changes, as higher frequencies are damped more than lower frequencies. Coleman (1962) showed that humans can use change in timbre effectively to estimate distance when a familiar sound is heard.

7.2 The school as a group of biological oscillators

Little is known of how the rapid transmission of information is accomplished in a fish school. Fish locomotion often displays a rhythmic alternating character, e.g. coast and burst swimming. Thus a school of fish might be depicted as a group of oscillators. A large system of biological oscillators, such as singing crickets, may spontaneously lock to a common frequency despite differences in the natural frequencies of individual oscillators (Strogatz, 2003). In biological oscillators, the ability to send and receive signals is crucial. Swimming fish will fulfil this criterion.

The Kuramoto model is a mathematical model used to describe synchronization. The model makes several assumptions: That there is weak coupling between the oscillators, oscillators are identical or nearly identical, and, when coupling is sufficiently strong, a fully synchronized solution is possible. In that situation, all the oscillators share a common frequency, although their phases are different (Strogatz, 2003).

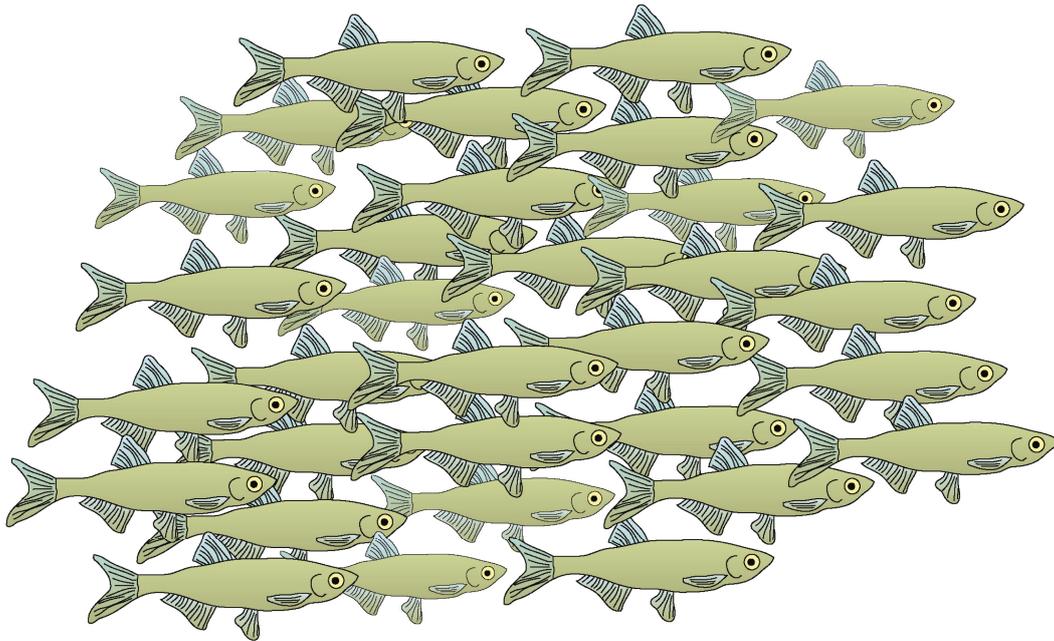


Fig. 5 Due to the risk of cannibalism, fish may have developed an instinct to join fish of almost the same size

Fish of similar size and body-shape will emit similar hydrodynamic signals (i.e. ISOL). ISOL may be useful in JLS decisions, which may contribute to shoal homogeneity.

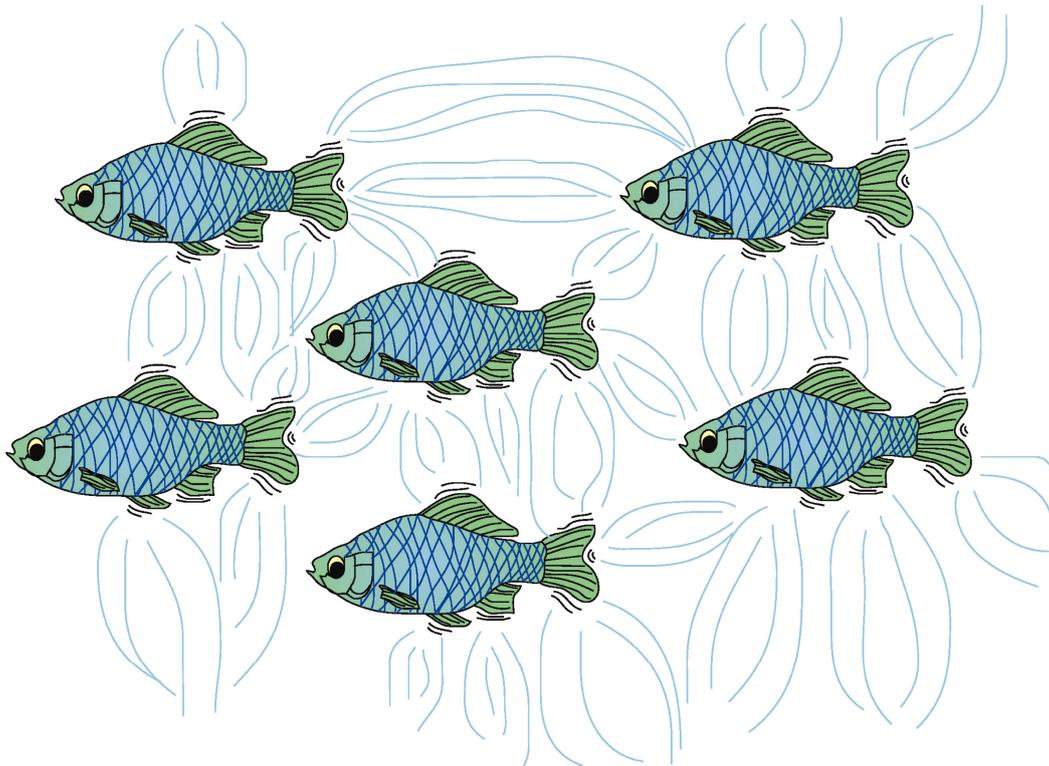


Fig. 6 The lines around fishes symbolize ISOL (sound and other hydrodynamic signals) produced by swimming fish

The lines between fishes represent ISOL. The form and shape is arbitrary. However, fish of similar size will emit similar ISOL. The amplitude is influenced by distance and moreover the timbre change, due to more dampening of high frequency sounds relative low frequency sounds. ISOL might in theory help fish to estimate the distance to their nearest neighbor. This may be used in mutual adaptation. Coast and burst swimming as well as pectoral fin movements often have an oscillating character. Thus swimming fish may produce oscillatory hydrodynamic signals.

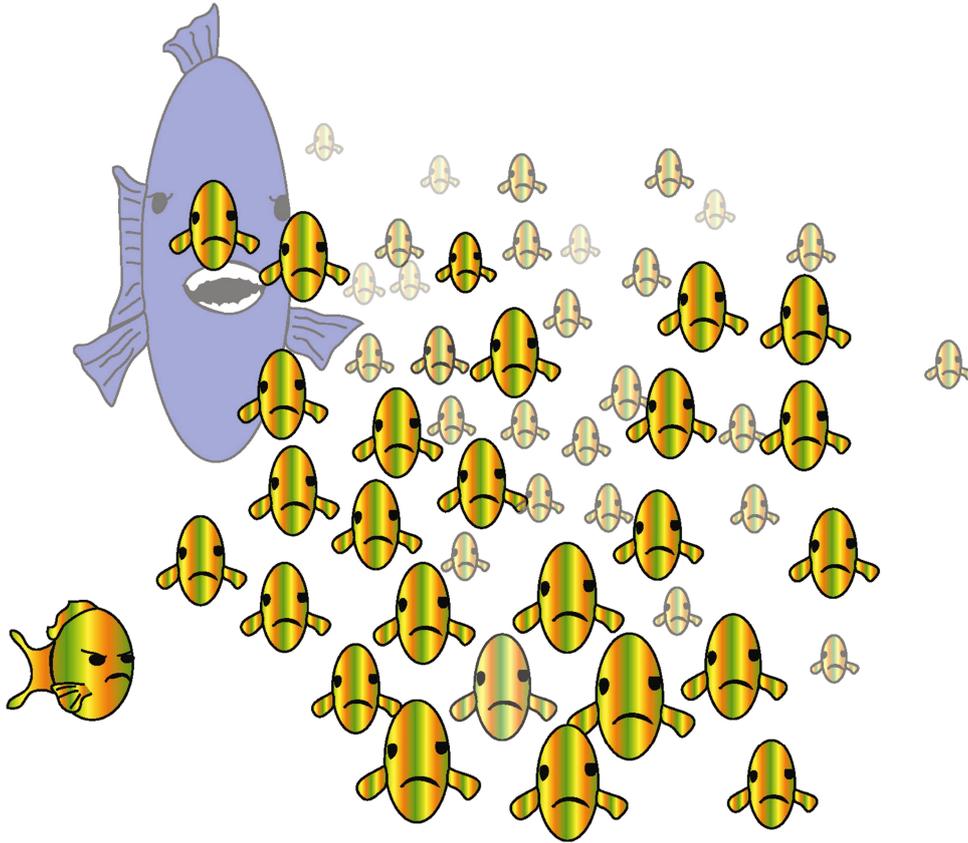


Fig. 7 Parasite infected fish are likely to be found in the school periphery

The grey fish is a predator attacking the school. Individuals with different size and body-form, and parasite infected fish are more likely to be found in the school periphery and regularly will be eaten first.

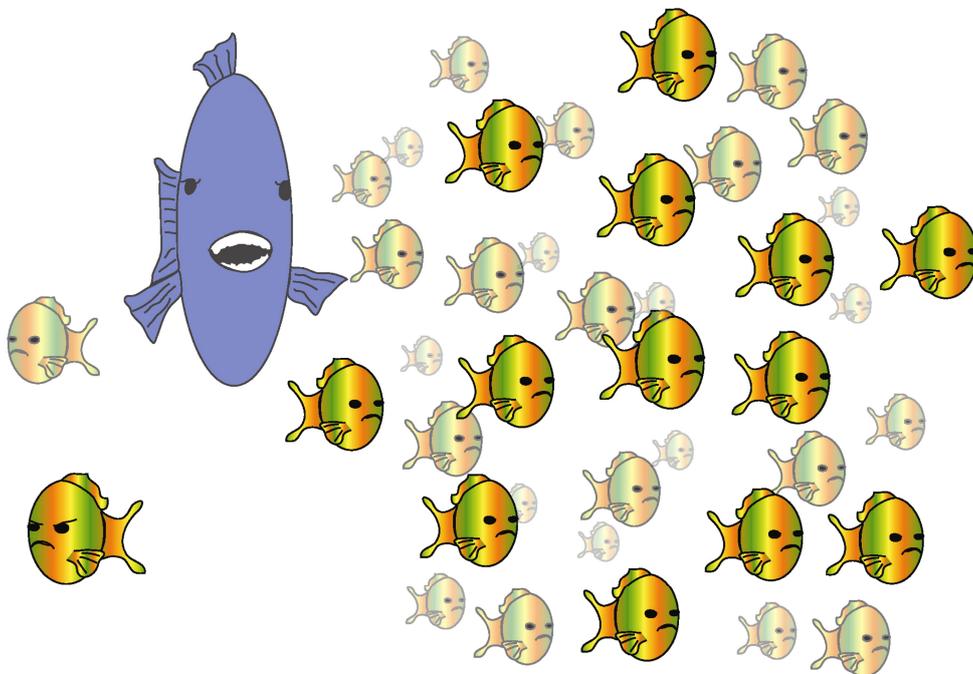


Fig. 8 Gregarious fish species show lateralization for turning biases at the population level

The grey fish is a predator attacking the school. Individuals with different turning bias or another body size or form than the majority may be more likely to be separated. When a fish is separated from the school it is easier to capture for predators, possibly due to less complicated ISOL emitted from a solitary fish, and moreover, confusion of the electro-sensory system of predators is likely to diminish when a fish is separated from the school.

Sounds produced by nearby fish will have greater amplitude; thus decisions of an individual fish ought to be primarily influenced by movements of close neighbors. However, sound waves can be transmitted through the bodies of surrounding fish, providing information about the movements of more distant fish in the school and facilitating the rapid transmission of information to reach a consensus, e.g. to move away from a predator. Thus sound cues might be a complement to visual information to aid in staying in formation while avoiding collisions. ISOL signals could aid schooling fish in achieving synchrony of frequency in coast and burst movements (Fig. 6).

8 The Shape of the School

The position in the shoal might influence the survival of its members. It has been shown that the leading fish of a shoal is attacked significantly more frequently than fish in other shoal positions (Krause et al., 1998), but, on the other hand, this position might provide a better food supply. Starving fish will be more likely to take a front position but also tend to leave this position when their nutritional state is improved (Krause, 1994). Central positions in the schools might be more protected (Pitcher, 2001). In addition, confusion of the OLS and electrosensory system of a predator might be less effective in the periphery. Hence, a fish that more often occupies a central position might gain an increased chance of survival. In an observation of thirty successful attacks on shoals by predators, the captured individuals swam in the center of the shoal in only three cases (Krause et al., 1998).

Schooling behavior alters significantly in the presence of a predator. Under an immediate hazard, schools become denser and take on a spherical shape, called a “defensive” or “look around” school. Fish also display agitation and increase movement speed (Breder, 1959; Pavlov and Kasumyan, 2000). Non-moving schools will have a tendency to be spherical, look-around schools (Radakov, 1973). These might become very compact and densely populated under predator-threat. It has been reported that, when frightened by a piscivorous bird, a school of approximately 500 sand eels, *Ammodytidae* of a size around 14 cm, could form a sphere of 50 cm diameter (Grover and Olla, 1983). An increased facility for watching for predators has been proposed (Cushing and Harden-Jones, 1968; Pavlov and Kasumyan, 2000). (As aforementioned, ceasing of movements may reduce masking of the inner ear and the LLO, which may increase the vigilance further). Pavlov and Kasumyan

(2000) suggested that the average density within a large school is higher in the central area than in the periphery, and might differ by a factor of ten or more. Well-functioning sense organs and skillful motor performance may be important to avoid occupying the periphery. To hypothesize, fish with reduced ability to anticipate moves of the school or with reduced sensory or motor function would be more likely to be found in the periphery or to lose contact with the school. Position-related differences in parasitism rates among group members are well documented, with per capita rate of parasitism being lower in the center of groups than at the periphery (Krause, 1994). Further, fish infected with parasites take up unusual positions and exhibit significantly greater nearest neighbor distances than uninfected shoal members (Barber and Huntingford, 1996) (Fig. 7). Following a simulated avian attack, infected fish don't reduce nearest neighbor distance as much as uninfected fish (Barber et al., 1995). Solitary individuals found outside shoals are more likely to be parasitized (Barber et al., 1995). In theory, parasite infection may affect schooling in several ways. The LLO function may be impaired by infection due to erosion or swelling of the lateral line (Roberts, 2001) or due to abdominal swelling (Barber and Folstad, 2000). The parasitic nematode *Anguillicola crassus* (Kuwahara et al., 1974) may infect the swimbladder of the European eel *Anguilla anguilla* (L.) resulting in a thickening of the swimbladder wall, bladder size reduction and changes in the bladder's gas composition (Haenen et al., 1989; Wurtz et al., 1996). Such swim-bladder dysfunction appears to be associated with reduced swimming performance (Sjöberg et al., 2009). Swim bladder size may also influence hearing abilities (Lechner and Ladich, 2008).

An individual fish's tolerance to hypoxia may also influence the capacity to maintain a more central position in the school. Oxygen level of water within a school can diminish along its axis of movement as a consequence of oxygen consumption by fish at the front, causing hypoxic conditions in fish in the central and rear positions (Domenici et al., 2007). A consequence might be that unhealthy fish with higher oxygen demands and/or a reduced capacity to take up oxygen will be more likely to occupy the periphery of the shoal.

In summary, healthy and skillful navigators will avoid the school periphery during a somewhat higher proportion of schooling time. In the long run, intra-specific competition for favorable positions in the school may benefit the species by contributing to evolu-

tionary adaptation and further refinement of sensory systems involved in the mediation of schooling, eventually resulting in more sophisticated and synchronized schooling behavior and better defense mechanisms against predators.

9 Schooling and Lateralization

Some predatory fish such as barracuda *Sphyraena*, and swordfish *Xiphias gladius* are in general successful when attacking a school. They typically do not pursue a specific individual, but try to evoke maximum chaos in the school, some use their armored rostrum, destroying the school's internal structure and unity (Pavlov and Kasumyan, 2000). Thereafter they begin attacks on particular individuals. Those leaving the school, even for a very short time, are the first to be eaten (Pavlov and Kasumyan, 2000). A relatively low degree of complexity in pressure curves and sounds produced by solitary fish (Fig. 1) may be part of that.

Gregarious fish species have been found to show lateralization for turning biases at the population level, while most species that did not shoal have been found to be lateralized at the individual level (Bisazza et al., 2000; Vallortigara, 2006) (Fig. 8). Lateralization of the brain, i.e. where each hemisphere carries out unique functions, is omnipresent among vertebrates (Andrew and Rogers, 2002; Vallortigara, 2006). Individual-level asymmetries in the brain may result in advantages, such as specialization of functions in each hemisphere and increased efficiency. For example in the teleost, the goldbelly topminnow, *Girardinus falcatus* fish selected for a high grade of lateralization were twice as fast as non-lateralized (NL) fish to catch prey during concurrent predator threat (Dadda and Bisazza, 2006). However, lateralization, such as preferences in the use of a limb, visual hemifield, or direction when turning, often also occur at the population level, with most individuals showing similar direction of bias. For instance there is evidence that most toads, chickens, and fish react more rapidly when a predator approaches from the left (Vallortigara, 2006). Such population-level lateralization may permit predators to take advantage of regularities and predictability of prey behavior. If a group of individuals shows a turning bias when they are under a predator threat, it may be disadvantageous, since this makes individual behaviors more predictable for predators (Vallortigara, 2006). In addition, Dadda et al. (2009) suggested that individuals with a marked cerebral lateralization may pay a higher cost in terms of reduced efficiency in tasks relying on hemispheric communication

and cooperation. When trained to use the middle door in a row of nine NL topminnows correctly chose the central door in most cases, and NL fish also chose the appropriate (high quality) shoal more often than strongly lateralized fish, whose performance was affected by eye preference for social stimuli. Dadda et al. (2009) suggested that costs and benefits from lateralization of the brain are likely to vary with ecological conditions such as predation risk, social density, food abundance and structure of habitat. In the experiment of Dadda et al. (2009) the information in regards of the shoal to join was purely visual. In natural life it seems possible that other information e.g. from the OLS may influence shoal choice. Vallortigara (2006) suggested that selective pressure to sustain directional asymmetry despite the potential disadvantage must be high. Turning biases will probably reduce the risk of a shoal splitting or separating (Vallortigara, 2006). Vallortigara (2006) proposed that individuals with the same turning preference as the majority would benefit, since following the shoal would increase the chance that another individual would be the predator target. Confusion of predator's OLS and ESS is an alternative, or complimentary, possibility.

10 Conclusions

The evolutionary development of the OLS also resulted in a capable prey detection system exploiting ISOL-signals, i.e. water movements and sounds produced as a by-product of locomotion. This may have influenced the evolution of synchronized movements in groups. The development of OLS resulted in increased potential for cannibalism in the shoal, and at the same time, perceptual skills that helped small fish avoid joining larger fish, most likely resulting in increased size homogeneity, which was fundamental to the ability of groups to move in synchrony. Synchronization of group movements increases the ability of individuals to swim in proximity to their neighbors. When swimming in close formation, electric signals and ISOL-signals produced by nearby prey-fish will overlap. A likely result is confusion of the OLS and ESS of predators. Concurrent pausing in swimming may reduce masking noise caused by the groups' movements and in addition, synchronization of movements may improve auditory grouping of ISOL.

Moreover, the OLS seems to be important for fish groups' ability to synchronize movements (e.g. Faucher et al., 2010; Partridge and Pitcher, 1980; Pitcher et al., 1976). Precise mechanisms are not known, but it is

likely that the OLS may be used to transfer information about direction, distance, and speed of neighbours in a school. This may help fish to swim close to one another and in so doing cause predator confusion.

Turning preferences, acute sense organs, skillful motor performance, good health and tolerance to hypoxia might influence the ability to swim close to neighbors. That, possibly in combination with competition for favorable positions in the school, may contribute to evolutionary adaptation and further refinement of sensory systems involved in the mediation of schooling resulting in more sophisticated and synchronized schooling behavior.

Theoretical models are persuasive, however the hypothesis that schooling may result in confusion of predator's OLS and ESS has hitherto not been investigated empirically. I suggest that further study may be fruitful and provide new insights in schooling fish behavior, ISOL as signal mechanisms, ecology, and interactions between prey and predators.

Acknowledgements I thank Ms Kathleen Hills and Dr Alan Pike at The Lucidus Consultancy for engaged and skillful help with the English language and editorial comments, and three anonymous reviewers and Guest Editor Dr Scott Pavey for valuable suggestions and ideas about the content. I am grateful to Dr. Christopher B. Braun, Department of Psychology, Hunter College, New York, and Dr. Sheryl Coombs, Bowling Green State University, Department of Biological Sciences, JP Scott Center for Neuroscience, Mind and Behavior for kind permission to reproduce and develop their figure. I thank the Swedish Research Council Formas, for a travel grant to the EEEF 2010 Meeting in Vancouver, and Margareta Landin at the Medical Library, Örebro University Hospital, Örebro, Sweden, for help with reference editing. Centre for Health Care Sciences, Örebro University Hospital, Örebro, Sweden, sponsored the translation to English language.

References

- Andrew RJ, Rogers LJ, 2002. The nature of lateralization in tetrapods. In: Andrew RJ, Rogers LJ ed. *Comparative Vertebrate Lateralization*. Cambridge, UK: Cambridge University Press.
- Babineau D, Lewis JE, Longtin A, 2007. Spatial acuity and prey detection in weakly electric fish. *PLoS Comput. Biol.* 3: 402–411.
- Baker CVH, O'Neill P, McCole RB, 2008. Lateral line, otic and epibranchial placodes: Developmental and evolutionary links? *J. Exp. Zool. B Mol. Dev. Evol.* 310B: 370–383.
- Barber I, Folstad I, 2000. Schooling, dusk flight and dance: Social organisations as amplifiers of individual quality? *Oikos* 89: 191–194.
- Barber I, Huntingford FA, 1996. Parasite infection alters schooling behaviour: Deviant positioning of helminth-infected minnows in conspecific groups. *Proc. R. Soc. Lond. B. Biol. Sci.* 263: 1095–1102.
- Barber I, Huntingford FA, Crompton DWT, 1995. The effect of hunger and cestode parasitism on the shoaling decisions of small fresh-water fish. *J. Fish Biol.* 47: 524–536.
- Bassett DK, Carton AG, Montgomery JC, 2007. Saltatory search in a lateral line predator. *J. Fish Biol.* 70: 1148–1160.
- Bisazza A, Cantalupo C, Capocchiano M, Vallortigara G, 2000. Population lateralisation and social behaviour: A study with 16 species of fish. *Laterality* 5: 269–284.
- Blaxter JHS, 1987. Structure and development of the lateral line. *Biol. Rev. Camb. Philos. Soc.* 62: 471–514.
- Braun CB, Coombs S, 2000. The overlapping roles of the inner ear and lateral line: The active space of dipole source detection. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 355: 1115–1119.
- Breder CM, 1959. Studies on social groupings in fishes. *Bulletin of the American Museum of Natural History* 117: 393–482.
- Bregman AS, 1990. *Auditory Scene Analysis: The Perceptual Organization of Sound*. Cambridge, Massachusetts: MIT Press.
- Budd GE, 2001. Ecology of nontrilobite arthropods and lobopods in the Cambrian. In: Zhuravlev A, Riding R ed. *The Ecology of the Cambrian Radiation*. New York: Columbia University Press, 404–427.
- Cernuda-Cernuda R, Garcia-Fernandez JM, 1996. Structural diversity of the ordinary and specialized lateral line organs. *Microsc. Res. Tech.* 34: 302–312.
- Ciocca V, 2008. The auditory organization of complex sounds. *Front. Biosci.* 13: 148–169.
- Coleman PD, 1962. Failure to localize the source distance of an unfamiliar sound. *J. Acoust. Soc. Am.* 34: 345–346.
- Coombs S, Conley RA, 1997. Dipole source localization by mottled sculpin. I. Approach strategies. *J. Comp. Physiol. A - Sens. Neural Behav. Physiol.* 180: 387–399.
- Cushing DH, Harden-Jones FR, 1968. Why do fish school? *Nature* 218: 918–920.
- Dadda M, Bisazza A, 2006. Does brain asymmetry allow efficient performance of simultaneous tasks? *Anim. Behav.* 72: 523–529.
- Dadda M, Zandona E, Agrillo C, Bisazza A, 2009. The costs of hemispheric specialization in a fish. *Proc. R. Soc. Lond. B. Biol. Sci.* 276: 4399–4407.
- Darwin CJ, 2008. Listening to speech in the presence of other sounds. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 363: 1011–1021.
- Dijkgraaf S, 1962. The functioning and significance of the lateral-line organs. *Biol. Rev. Camb. Philos. Soc.* 38: 51–105.
- Domenici P, Lefrancois C, Shingles A, 2007. Hypoxia and the antipredator behaviours of fishes. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 362: 2105–2121.
- Faucher K, Parmentier E, Becco C, Vandewalle N, Vandewalle P,

2010. Fish lateral system is required for accurate control of shoaling behaviour. *Anim. Behav.* 79: 679–687.
- Fish FE, Fegely JF, Xanthopoulos CJ, 1991. Burst-and-coast swimming in schooling fish *Notemigonus crysoleucas* with implications for energy economy. *Comp. Biochem. Physiol. A.* 100: 633–637.
- Freitas R, Zhang GJ, Albert JS, Evans DH, Cohn MJ, 2006. Developmental origin of shark electrosensory organs. *Evolution & Development* 8: 74–80.
- Gray JAB, Denton EJ, 1991. Fast pressure pulses and communication between fish. *J. Marine Biol. Assoc. UK* 71: 83–106.
- Grover JT, Olla B, 1983. The role of the rhinoceros auklet *Cerorhinca monocerata* in mixed-species feeding assemblages of seabirds in the Strait of Juan de Fuca, Washington. *The Auk* 100: 979–982.
- Haenen OLM, Grisez L, Decharleroy D, Belpaire C, Ollevier F, 1989. Experimentally induced infections of the European eel *Anguilla anguilla* L., with *Anguillicola crassus* (Nematoda, *Dracunculoidea*) and subsequent migration of the larvae. *Dis. Aquat. Organ.* 7: 97–101.
- Hanke W, Bleckmann H, 2004. The hydrodynamic trails of *Lepomis gibbosus* (Centrarchidae), *Colomesus psittacus* (Tetraodontidae) and *Thysochromis ansorgii* (Cichlidae) investigated with scanning particle image velocimetry. *J. Exp. Biol.* 207: 1585–1596.
- Hanke W, Brucker C, Bleckmann H, 2000. The ageing of the low-frequency water disturbances caused by swimming goldfish and its possible relevance to prey detection. *J. Exp. Biol.* 203: 1193–1200.
- Hara TJ, 1993. Role of olfaction in fish behavior. In: Pitcher TJ ed. *Behaviour of Teleost Fishes*. 2nd edn. London: Chapman & Hall, 171–199.
- Hoekstra D, Janssen J, 1985. Non visual feeding behavior of the mottled sculpin *Cottus bairdi* in Lake Michigan. *Envir. Biol. Fish.* 12: 111–117.
- Kalmijn AJ, 1988. Hydrodynamic and acoustic field detection. In: Atema J, Fay RR, Popper AN, Tavolga WN ed. *Sensory Biology of Aquatic Animals*. S New York: Springer-Verlag, 83–130.
- Komdeur J, Eikenar C, Brouwer L, Richardson DS, 2008. *The Evolution and Ecology of Cooperative Breeding in Vertebrates*. Chichester: John Wiley & Sons.
- Krause J, 1994. Differential fitness returns in relation to spatial position in groups. *Biol. Rev. Camb. Philos. Soc.* 69: 187–206.
- Krause J, Butlin RK, Peuhkuri N, Pritchard VL, 2000a. The social organization of fish shoals: A test of the predictive power of laboratory experiments for the field. *Biol. Rev. Camb. Philos. Soc.* 75: 477–501.
- Krause J, Hoare DJ, Croft D, Lawrence J, Ward A et al., 2000b. Fish shoal composition: Mechanisms and constraints. *Proc. R. Soc. Lond. B. Biol. Sci.* 267: 2011–2017.
- Krause J, Ruxton GD, 2002. *Living in groups*. Oxford, UK: Oxford University Press.
- Krause J, Ruxton GD, Rubenstein D, 1998. Is there always an influence of shoal size on predator hunting success? *J. Fish Biol.* 52: 494–501.
- Kuwahara A, Niimi A, Itagaki H, 1974. Studies of a nematode parasite in the air bladder of the eel: Description of *Anguillicola crassa* n. sp. I. *Philometridae, Anguillicolidae*. *Jpn. J. Parasitol.* 23: 275–279.
- Lachlan RF, Crooks L, Laland KN, 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Anim. Behav.* 56: 181–190.
- Larsson M, 2009. Possible functions of the octavolateralis system in fish schooling. *Fish and Fish.* 10: 344–355.
- Lechner W, Ladich F, 2008. Size matters: Diversity in swimbladders and Weberian ossicles affects hearing in catfishes. *J. Exp. Biol.* 211: 1681–1689.
- Montgomery JC, Bodznick D, 1994. An adaptive filter that cancels self-induced noise in the electrosensory and lateral line mechanosensory systems of fish. *Neurosci. Lett.* 174: 145–148.
- New JG, Fewkes LA, Khan AN, 2001. Strike feeding behavior in the muskellunge *Esox masquinongy*: Contributions of the lateral line and visual sensory systems. *J. Exp. Biol.* 204: 1207–1221.
- Northcutt RG, Gans C, 1983. The genesis of neural crest and epidermal placodes: A reinterpretation of vertebrate origins. *Q. Rev. Biol.* 58: 1–28.
- Parker A, 2004. *In the Blink of an Eye: How Vision Sparked the Big Bang of Evolution*. Cambridge MA: Perseus Basic Books.
- Partridge BL, Pitcher TJ, 1979. Evidence against a hydrodynamic function for fish schools. *Nature* 279: 418–419.
- Partridge BL, Pitcher TJ, 1980. The sensory basis of fish schools: Relative roles of lateral line and vision. *J. Comp. Physiol.* 135: 315–325.
- Pavlov DS, Kasumyan AO, 2000. Patterns and mechanisms of schooling behavior in fish: A review. *J. Ichthyology* 40: S163–S231.
- Pitcher TJ, 1998. Shoaling and Shoaling Behaviour in Fishes. In: Greenberg G, Hararway MM ed. *Comparative Psychology: A Handbook*. New York: Garland, 748–760.
- Pitcher TJ, 2001. Fish schooling: Implications for pattern in the oceans and impacts on human fisheries. In: Steele JH, Turekian KK, Thorpe SA ed. *Encyclopedia of Ocean Sciences*. London, UK: Academic Press, 975–987.
- Pitcher TJ, Partridge BL, Wardle CS, 1976. Blind fish can school. *Science* 194: 963–965.
- Popper AN, Fay RR, 1993. Sound detection and processing by fish: Critical review and major research questions. *Brain Behav. Evol.* 41: 14–38.
- Radakov DV, 1973. *Schooling in the ecology of fish*. New York: John Wiley.
- Roberts BL, Russell IJ, 1970. Efferent activity in the lateral line nerve of dogfish. *J. Physiol.* 208: 37.

- Roberts BL, Russell IJ, 1972. Activity of lateral-line efferent neurones in stationary and swimming dogfish. *J. Exp. Biol.* 57: 435–448.
- Roberts RJ, 2001. The pathophysiology and systematic pathology of teleosts. In: Roberts RJ ed. *Fish Pathology*. 3rd edn. Oxford, UK: Elsevier Limited, 55–132.
- Russell IJ, 1968. Influence of efferent fibres on a receptor. *Nature* 219: 177–178.
- Sawtell NB, Williams A, Bell CC, 2005. From sparks to spikes: Information processing in the electrosensory systems of fish. *Curr. Opin. Neurobiol.* 15: 437–443.
- Sjöberg NB, Petersson E, Wickström H, Hansson S, 2009. Effects of the swimbladder parasite *Anguillicola crassus* on the migration of European silver eels *Anguilla anguilla* in the Baltic Sea. *J. Fish Biol.* 74: 2158–2170.
- Springer S, 1957. Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. *Ecology* 38: 166–171.
- Streit A, 2001. Origin of the vertebrate inner ear: Evolution and induction of the otic placode. London, England: Cambridge Univ Press, 99–103.
- Strogatz SH, 2003. *Synch: The Emerging Science of Spontaneous Order*. New York: Hyperion.
- Svendsen JC, Skov J, Bildsoe M, Steffensen JF, 2003. Intra-school positional preference and reduced tail beat frequency in trailing positions in schooling roach under experimental conditions. *J. Fish Biol.* 62: 834–846.
- Tricas TC, Highstein SM, 1991. Action of the octavolateralis efferent system upon the lateral line of free-swimming toadfish *Opsanus tau*. *J. Comp. Physiol. A - Sens. Neural Behav. Physiol.* 169: 25–37.
- Tureson H, Bronmark C, 2007. Predator-prey encounter rates in freshwater piscivores: Effects of prey density and water transparency. *Oecologia* 153: 281–290.
- Vallortigara G, 2006. The evolutionary psychology of left and right: Costs and benefits of lateralization. *Dev. Psychobiol.* 48: 418–427.
- Videler JJ, Weihs D, 1982. Energetic advantages of burst-and-coast swimming of fish at high speeds. *J. Exp. Biol.* 97: 169–178.
- von Holst E, Mittelstaedt H, 1950. Das Reafferenzprinzip. (Wechselwirkungen zwischen Zentralnervensystem und Peripheri.). *Naturwissenschaften* 37: 464–476.
- Wurtz J, Taraschewski H, Pelster B, 1996. Changes in gas composition in the swimbladder of the European eel *Anguilla anguilla* infected with *Anguillicola crassus* (Nematoda). *Parasitology* 112: 233–238.