

# The role of the lateral line in schooling



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## **Introduction**

A lot of fish spend parts of their life schooling with other fish. The reasons and mechanics behind schooling have been well studied, however parts of this behaviour still remains unknown. Not all fish school in the same way, for example schools of anchovies contain over a thousand fish and look very well organized whereas schools of several predatory fish mostly exist of small amounts of fish swimming around more randomly. To school successfully fish have to adapt their movements continuously to the other fish swimming around them. A lot of this is done by visual information, but we also see schools of fish at night and in deep murky waters. These waters are devoid of daylight, so fish cannot rely only on their eyesight here. Therefore they need a mechanism to sense other fish without actually seeing them. There is a good possibility this sensing mechanism might be the lateral line system.

The lateral line system makes it possible for aquatic vertebrates to detect very small mechanical disturbances in the water surrounding the animal. All fish and some amphibians have such organs to some extent, however in some species it is more evolved than in others. In many fish species the lateral line system is clearly visible as a line running from the snout of the fish all the way to the base of its tail. Multiple studies show that the lateral line potentially plays a role in almost everything fish do. It senses differences in water pressure and flow velocity around the fish, and can therefore be used to sense other animals and objects nearby. There are good arguments and studies which show that the mechanosensing properties of this lateral line system are indeed used during schooling.

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## SCHOOLING BEHAVIOR

### Definition and shape of schools

The definition of a school is harder to give than one might think, because the size and shape of groups of fish differ a lot. Also the reasons for groups of fish to stay together are not always the same. Three common used terms to address fish groupings are: Aggregations, shoals and schools. When multiple fish are gathered in one place, but do not show social contacts they are aggregating. Fish swimming together for social reasons are often called shoaling. Schooling is the behaviour where all fish of group swim in the same direction in a coordinated matter. These definitions are not always that different from each other, and in certain cases it is difficult to say whether fish are actually schooling or shoaling. Some fish school their entire life, some only for specific parts of their life, and some fish never school and live practically alone their entire life (Shaw 1978).

Fish schools do not stay in one static pattern, they change shape constantly. In most types of schools individuals change their position within the school constantly. Smaller and larger fish may swim at the in- or the outside of the school depending on several conditions (Hemelrijk 2005). Some fish like Blackchin shiners *Notropis heterodon* change the shape of their school depending on the risk of predation. Under safe conditions and a constant waterflow the fish swim in a flat hydrodynamically efficient structure. (Abrahams 1985) In this flat shape the fish do block each others visual field of sight. When predators are introduced however the school starts to change shape in the vertical direction. By spreading out in the vertical direction fish school can take advantage of the eyes of all the fish in the group, making it harder for predators to approach the school unnoticed. In Abrahams study the fish that are never confronted with predators always keep swimming in the more hydrodynamically efficient flat structure.(Abrahams 1985)

### Benefits of schooling

There are a number of reasons for fish to school. One of the reasons for small fish to school is protection. When small fish swim in schools they can decrease the odds of being eaten by a predator. Anchovies for example swim in huge schools of thousands of fish. With all those eyes, predators are often noticed and evaded before they impose a threat to the school. When a predator does approach one of these schools the "ball" of fish evades the predator by changing shape, splitting up, or even make a ball around the predator (Inada 2002). Because the fish never isolate themselves this way it is very hard for the confused predator to pick out one fish to eat. Even if a predator is able to catch a fish, it will only eat some of them and leave the rest of the school alive, so the chances for one particular fish to be picked out of the large school is very small. Some predatory aquatic animals have evolved countermeasures against schooling prey. Certain species of fish and dolphins are known to encircle schools of prey, forcing the school to become a compact ball of prey. Once the school is compact enough the predators start feeding on the fish. Groups of humpback whales are known to lay barriers of bubbles around schools to make the groups more compact and only able to go up or down. After that they attack the school from below leaving the prey no chance of escape. Acklin filmed whales feeding this way by attaching a camera on the back of a whale (Acklin 2003).

Not only aquatic animals hunt on fish. The main reason for the rapid decline of fish abundance in the seas are humans. We also benefit from the schooling behaviour of commercially caught fish like tuna and cod. By using nets that encircle entire schools we can catch huge amounts of fish. Some fisherman use small air planes and sonar equipment to search for schools.

Even though predators and humans take advantage of the schooling behaviour of fish, the advantages of schooling are probably large enough to outweigh these disadvantages.

Fish schools can cover a broad area, and can spot food sources earlier because of the many eyes. Fish swimming in schools therefore have a higher chance of finding food sources. Predatory fish

like bluefin tuna work together in schools to hunt more efficiently. Partridge studied the shape of Bluefin tuna *Thynnus thynnus* schools from aerial pictures and saw that they often school in a parabolic C-like pattern, like the opposite of the V-shaped flocking often seen in birds. This shape suggests that they are hunting together. Hunting in a parabola shape increases the chance of finding food, and once its found, the school can work together by attacking the prey from multiple sides. Possibly the parabola shape also gives hydro dynamical advantages to the tuna swimming next to each other (Partridge 1983). The benefits of schooling together with con-specifics can be exploited by other fish. Sometimes fish enter schools of foraging fish because it makes it a lot easier for them to forage (Ward 2004). When foraging in schools fish have to share the food resources, so the advantage of finding food sources quicker might not always be that high because of the disadvantage of having to share the food source with the rest of the school.

There is also a reproductive benefit for fish swimming in schools. Finding a mate is a lot easier when swimming in a large school, and some schools protect small fish by letting them swim in the middle (Hemelrijk 2005). Certain species of fish travel together in schools to the spawning sites where they reproduce. Schooling protects them during their journey and therefore may increase their reproductive fitness.

### Hydrodynamic advantages of schooling

One of the less known benefits of swimming in a school is that it also gives individual fish an energetic advantage. They get this advantage by swimming at the right place behind other fish. When swimming at a constant velocity fish shed a trail of vortices from the tip of their tails (Muller et al. 1997). These vortices can create a zone behind fish in which the water velocity is slightly lower compared to the surrounding water. According to this theory fish swimming behind others can swim a little bit slower than the fish swimming in front of them. This effect can be compared to the way cyclists ride behind each other to slightly reduce the effort they have to put in cycling..

Another hydrodynamic advantage of schooling is that fish which swim behind two other fish in a diamond pattern may encounter a kármán street (Liao 2007, fig.1). Swimming in a so called kármán gaiting behaviour may reduce the energy fish have to spend by a very large amount and even though the benefits of swimming in a school is smaller than expected by this theory, kármán gaiting may still have a small effect on effort reduction.(Liao 2007).

In a school of fish, the respiratory rate of the entire school can be 13% lower than the sum of the respiratory rate of the individuals when they are swimming alone (Abrahams 1985). This means that fish swimming behind other fish can afford spending less effort in swimming. The amount of effort that is saved this way is quite large, and therefore the reduction of swimming effort is possibly one of the main reasons for fish to swim in schools.

The shape of the school and the distribution of fish within it has a large effect on the hydrodynamic efficiency of the school. The most advantageous shape is the diamond shape (Weihs 1973) in which all fish swim in a two dimensional diamond pattern. In this shape every fish swims between the wakes of two other fish, giving every fish the maximum energetic advantage. Even though this shape is energetically the most advantageous, the shape of fish schools swimming in nature is often quite different depending on factors like predation and foraging behaviour. Moreover, even experimental studies show that under controlled conditions fish will not school in the theoretical

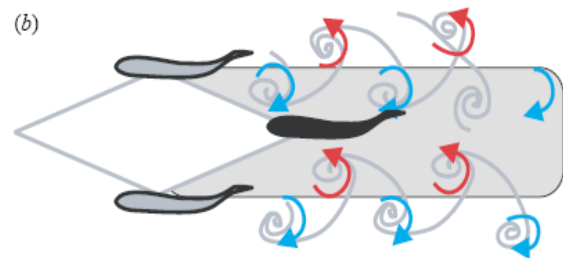


Fig.1) Fish swimming in the karman street produced by two other fish. Picture from Liao 2007 \*\*

diamond pattern. (partridge et al 1979; Partridge et al 1980)

### Rules behind schooling

Swimming in distinct patterns provides fish with social and energetic advantages. Individual fish swimming in schools have to continuously adjust their position to the fish swimming around them. Without coordinated movements the school would certainly become a chaos, and chaos is not what we see in most schools of fish. There have to be rules for how to swim in a school. These rules have been well studied, and although there are differences in group shape and composition (partridge 1980) most fish seem to use the same rules for schooling (Inada 2002, Hemelrijk 2005). Between different studies involving schooling behaviour the rules have been formulated differently.(e.g Fig.2) These variations can all be simplified in a model which uses only three simple social rules:

1. Avoid fish that are too close to you. (Repulsion zone)
2. Swim parallel to fish swimming at the right distance. (Alignment zone)
3. Swim towards fish that are too far away. (Attraction zone)

If all fish follow this set of rules they will theoretically always keep schooling. If a fish gets too close to his neighbour it will swim away from him. As soon as the distance between the fish has become large enough the fish will start to adjust its body angle and swimming speed to align himself with the neighbour. When the gap between a fish and its neighbour becomes too big the fish will swim towards him. Even when schools change shape because of a predator or for a different reason, this set of rules may be used by the individual fish to recombine into a school again.

The three simple rules are derived from models however, and even though the rules seem to give a good reflection of the mechanisms behind schooling, schooling might be much more complicated in reality.

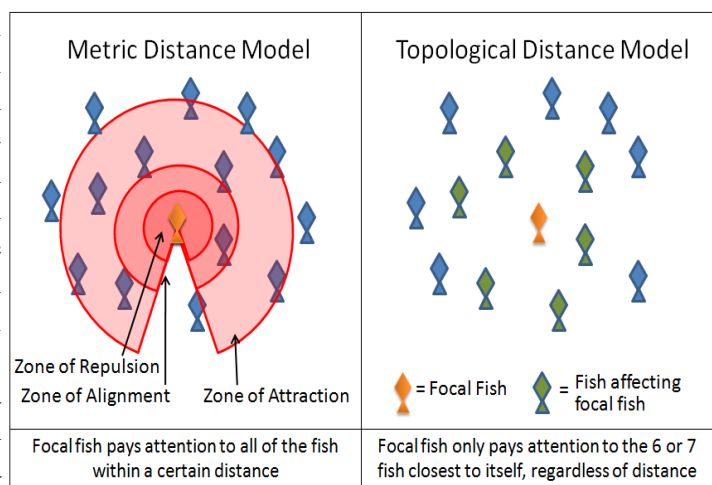


Fig.2) Two slightly different models for defining the rules of schooling in fish. a) fish use three different distance zones. b) Schooling fish only pay attention to an amount of fish which are closest to itself \*\*\*

## LATERAL LINE

### Morphology and development of the line

The lateral line is a mechanosensory organ present in fish and some other aquatic vertebrates. The lateral line is composed of mechanosensing units called neuromasts and runs along the body of the fish lengthwise, starting at its snout all the way to the base of its tail. Part of the neuromasts lie in canals just beneath the skin of fish (van Netten 2006). The neuromasts are the real sensory parts of the system. There are multiple variations on the basic morphology of the lateral line seen in nature. Even though there are differences in morphology, the basic primitive lateral line system has not undergone a lot of changes. The basics of the lateral line of amphibians share a lot of similarities with primitive fish like sturgeons. And even though the differences in lateral line morphology are bigger between higher groups of fish, the basic function stays the same. (Pichons 2004).

The development of the lateral line can already be seen in fish who are just one day old. African catfish *Clarias gariepinus* develop sensory organs very rapidly as they grow. When they are just



one day old, free neuromasts are formed around the snout and trunk of the fish (Mukai 2007) from then on the amount of free neuromasts increases as the young fish larvae grows. In 10 day old larvae part of the neuromasts become oval shaped and start to sink in the skin, these neuromasts will most likely form the canals of the lateral line as the fish will continue growing. The fast growth of the amount of neuromasts in a young fish suggest that the lateral line plays an important role in fish.(Mukai 2007)

### The neuromasts and mechanosensing

The neuromasts are the actual sensory parts of the lateral line system. There are two basic types of neuromasts found in aquatic animals (Fig.3). The first type composes the lateral line and is found in practically all fish species. The lateral line consists of this first type of neuromasts laying in a canal like structure just beneath the scales. These neuromasts are composed of hundreds to thousands of sensory hair cells surrounded by a jelly like cupula (Flock 1962). When the cupula is moved by water motion, the hair cells in it transform the motion in an electronic signal. This signal is then passed on to the brains by neurons. (van Netten 2006)

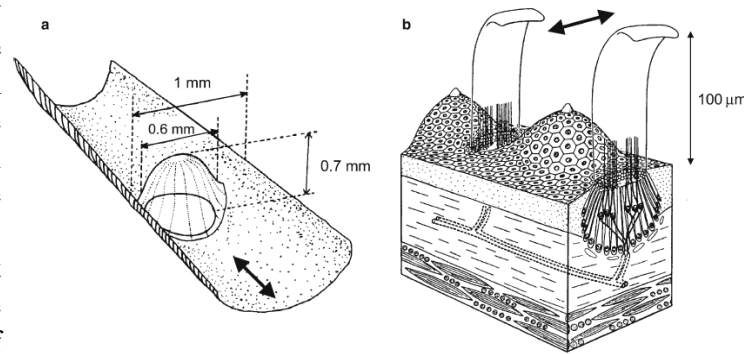


Fig.3 a) Schematic overview of a lateral line neuromast in a canal in the absence of skin. b) Schematic of a super-ficial neuromast on the surface of the skin of a clawed frog. Picture from van Netten 2006 \*

There is another type of neuromast mostly referred to as a superficial neuromast. These neuromasts can not only be found on fish, but also on a wide range of other aquatic animals. Superficial neuromasts are quite different from the neuromasts found in the lateral lines of fishes. Superficial neuromasts don't lay in a canal beneath the scales and are composed of just tens of hair cells. They are positioned on the surface of the skin, with the cupula directly positioned in the surrounding water. The neuromasts are the actual mechanosensors of the lateral line system. Both types of neuromasts are morphologically very different from each other, and this probably leads to a difference in mechanosensing as well. Even though not everything is known about the neuromasts, the two groups obviously both have different functions. Superficial neuromasts mainly detect water velocity, whereas neuromasts in the canals of the lateral line detect the acceleration of water (Coombs 1990; van Netten 2006).

The distribution of neuromasts over the body differs between species of fish, depending on their lifestyle. Active swimming fish often have more canal neuromasts within their skin than superficial neuromasts on their surface. This can be traced back to the difference in neuromast function. Fish constantly swimming probably require a lot of information about acceleration trends in the water. Whether this means that the lateral line is less important for less active fish is unknown.

How fish actually use the information on water velocity to locate objects in the surrounding water is quite amazing. By using the distance between the neuromasts inside the canals of the lateral line system, they can estimate from which direction the disturbance in the water is coming (van Netten 2006). When a living organism in front of a fish sheds a wake into the surrounding water, the wake will first be noticed by the lateral line canals on the front side of the fish, and a little later by the canals behind it. By sensing in which order the neuromasts are activated, and by taking the delay between the activation of the neuromasts into account, the fish can "measure" from which direction the signal came, and how far away the source of the signal is from the fish. The mechanisms behind this is comparable to human hearing. When we hear a sound we can tell from which direction it is

coming because of the shape of our ears, and the delay between the soundwaves reaching our left and right ear.. In the same way fish can tell from where water waves are coming by the shape of their lateral line system.(van Netten 2006)

### **Functions of the line**

Even though the lateral line has only one main function in fish, namely sensing disturbances in the water, the fish uses the information it gets from the lateral line system for multiple purposes. It is known that the lateral line organ detects mechanical disturbances in the surrounding water, like movements, vibrations and small changes in water pressure. This makes it a useful organ in a lot of different situations. The ability to sense disturbances in the water can aid in locating food sources. Species of catfish use mechanosensing to track down prey by sensing the wake they leave behind. They are able to follow a track seven body lengths behind their prey by only sensing the chemicals and the wake left behind by the prey (Pohlmann 2004). Species of Killifish use the lateral line to detect ripples on the water surface made by insects. Certain species of scorpionfish use the lateral line to search and follow their prey (Basset 2007). The system can also be used to detect and avoid predators.

Fish also use the information they get from the lateral line in normal swimming behaviour. Under certain conditions fish are able to swim in a steady flow without a functional lateral line, however in more turbulent water the kinematics of fish with a damaged lateral line differ noticeably from healthy fish (Liao 2006). In one of his studies Liao examines which sensing organs fish use when they exhibit so-called kármán gaiting behaviour. This behaviour involves sensing vortices in the water and using them to your advantage when swimming. Fish who had their lateral line disabled increased their wavelength and wave speed compared to fish in the control group. Fish with an intact lateral line sytem kármán gaiting in the dark did not significantly change their swimming behaviour compared to fish swimming in the light. This probably means that fish make use of their lateral line rather than vision to obtain information when they are kármán gaiting and when they are swimming normally (liao 2006; Chagnaud 2007).

In some fish parts of the lateral line evolved to suit more specialistic tasks. In sharks part of the line acts as an electro receptor which is used to locate living prey. In this case part of the neuromasts have turned into the Ampullae of Lorenzini. The ampullea are very abundant around the snout and other parts of the head of sharks. Sharks and some other fish use these ampullae to detect very small electrical signals from their surroundings. (Kajiura 2002). All living creatures emit some kind of electrical signal so it is an efficient way of finding prey. It is possible that sharks and other fish also use these ampullae to detect the magnetic fields of the earth, making it plausible that they use magneto-electro-sensing for navigation.

### **Lateral line as a replacement of vision**

Fish can not always depend on their visual senses. A lot of fish swim and school at night or very deep in the water column where there is no daylight. These fish can only sense their environment by tasting chemical clues and by sensing mechanical clues with their lateral line.

Some predatory fish also hunt at night. Hunting at night gives predatory fish multiple advantages. In a dark environment prey fish are less evasive, and the chance of getting eaten by even larger predators is a lot smaller. Because fish can not rely on visual information when they are hunting in the dark, some of these species have even evolved wider lateral line canals to compensate for the fact that they can not visually see their prey (Janssen 1998). To track prey in the dark piscivorous catfish use both their lateral line and their chemoreceptive organs to detect traces of a wake and chemical signals to locate fish. In the dark european catfish *Silurus glanis* of which the lateral line is disrupted have a lot of trouble with tracking and catching prey fish. They are still able to find and



eat dead prey, however they just can not react fast enough anymore to prey on living fish. With their taste sense they can still follow the wake of the prey, because fish excrete small amounts of chemicals. Their attacks however are considerably delayed when they can not use their lateral line. (Pohlmann 2004)

animals living in caves devoid of daylight are often completely blind. They have often evolved a very different morphology (troglomorphs) compared to their cousins living in the daylight. Aquatic animals living in cave streams are often totally devoid of pigment and are mostly white or pink in colour. Because there is no need for eyes in a completely dark environment the eyes of some species of fish have also completely disappeared over time. This deterioration of the visual systems can be quite fast (Protas 2007) Blind mexican and their eyed cousins are still interfertile, and can be crossbred. To navigate through the dark cave streams they need another kind of sensory system. The lateral line system of Mexican cave fish is much more evolved than the lateral line of its cousin the Mexican tetra. *Astyanax* . Blind cavefish perform wall following behaviour at higher velocities than fish with normal vision which is caused by their enhanced abilities to sense changes in water flows (Sharma 2008). It is believed that blind fish feel the reflection of their own wake bouncing off nearby objects. This way they receive information about their surroundings which prevents them from bumping into walls. This might also explain why the blind fish swim faster than the normal fish, because in order to sense the environment with its lateral line, the blind fish has to keep swimming fast enough to produce strong enough wakes around its body and against the walls.

## THE ROLE OF THE LATERAL LINE IN SCHOOLING

For a long time people thought that fish only use vision when they are swimming and schooling. Studies done by Chagnaud have shown that fish need their lateral line system to perform normal everyday swimming behaviour (Chagnaud 2007). This makes it possible that fish also use the lateral line to coordinate their position within schools. One way to study which sensing organs are used in schooling is to numb or inactivate the sensing organs one at the time. To get good results it is important that the sensing organs are carefully inactivated. Some studies on the lateral line done in the past only inactivated a part of the lateral line, leaving parts of the system located on the head intact. therefore the results of these studies can not always be fully trusted. (Faucher 2010).

One of these older studies has been done by Partridge in schooling saithe *Pollachius virens*. When the fish were blinded they were able to school but they did show different behaviour compared to control groups. Blinded fish are still able to keep their position within a school, but they increase the distance between them and their neighbours. Fish in which the lateral line is cut are also still able to school, however they have a tendency to swim directly next to their neighbours. Contrary to blinded fish, fish that can only rely on vision decrease the distance between them and their neighbours. (Partridge 1980). The outcome of this study is confirmed by Pitcher. He blinded five saithe *Pollachius virens* with eye covers and put them in a tank together with twenty normal schooling saithe. The blinded fish were able to join the school without any problems. Pitcher notes that the behaviour of the blinded fish was slightly different, but they were able to keep schooling for a long time. As a control group he also cut the lateral lines of five blinded fish which were unable to school afterwards (Pitcher 1976).

In a more recent research Faucher not only cut the lateral line at the trunk of the fish, but inactivated the entire lateral line by also taking out the neuromasts on the head with antibiotics. With the entire lateral line inactivated fish were unable to perform shoaling behaviour. As soon as the effect of the antibiotics wore off the damage to the neuromasts recovered and they were able to shoal again within a month after the treatment (Faucher 2010). His research shows that fish of the species *Hemigrammus bleheri* can not shoal without the lateral line, even if their visual senses are kept unharmed. According to Faucher this shows that the role of the lateral line is crucial in shoaling

behaviour. The role of the lateral line in schooling behaviour is indeed very large, and there are some studies that speculate that schooling behaviour could not have evolved without the lateral line system (e.g Larsson 2009).

## CONCLUSION

The lateral line is the most important sensory organ used in schooling. The amount of arguments that support this statement are overwhelming. It has been shown that fish need the lateral line to perform normal swimming behaviour, meaning that they use it all the time. When the lateral line is damaged fish are unable to perform basic schooling behaviour, even if the part of the line located in the head is still intact. We know that some fish are able to school in the dark which diminishes the role that vision could have in schooling. Blinding fish has no major effects on their schooling capabilities unless the lateral line is also cut. This does not mean that vision is unimportant, but the role it has in schooling is much smaller than thought before.

Insights in the formation and stabilisation of schools of fish may hold future benefits, and we should use that knowledge to protect ecosystems and make our fisheries less harmful to other wildlife. Even so, research on the mechanisms at work within the lateral line system can hold great benefits in advanced sensory and mechanical technologies.

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Figure sources:

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- \*\* Liao 2007, A review of fish swimming mechanics and behavior in altered flows
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