Predator-prey relations in fish

a battle of intellects

By Johanneke Oosten
Supervized by Charlotte Hemelrijk
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Index

Introduction

Until the 1970's research on predator-prey inter- actions in fish was rare. But in the last few decades, interest in the topic has grown explosively. By now there are thousands of articles on the topic. One as- pect that has received special attention is learning. Research makes it increasingly clear that fish are not the anti-social, memory-impaired blobs they were once thought to be, but that they are intelligent crea- tures that form social relationships with their shoal mates and perform sophisticated techniques to out- wit their predators and / or prey (Laland et al 2003; Bshary et al 2002).

Many fish species live in groups or *shoals*. Shoals provide their members with advantages, such as a choice of breeding partner, as well as disadvantages, such as food competition (Krause & Ruxton 2002). When shoaling fish detect a predator they aggre- gate, forming a more compact shoal (e.g. Templeton & Shriner 2005: guppies; Ferrari et al 2005: fathead minnows; Brown et al 2004: glowlight tetras; Magur- ran & Pitcher 1987: European minnows). Also, several studies find that fish living in predator-dense areas spend more time aggregated than their conspecif-

ics in less predator-dense areas. So it seems protec- tion from predation is a major advantage of shoaling (Seghers 1974: guppies; Magurran 1986: minnows).

In this review I will focus on how this protection by shoaling arises. I will show that shoaling does not always protect, but may expose their members to predation instead. In addition I will discuss vari- ous techniques employed by predators to deal with shoaling prey. Finally I will show how these predator- prey interactions are shaped by learning.

In the course of this review it will become clear that the theories commonly used to explain the anti-predator benefits of shoaling are difficult to prove with empirical data. In their attempts to do so, researchers use experimental set-ups, so tightly controlled, that their naturalness becomes doubtful. Also, the number of species used in research is lim- ited, casting doubt on the universality of our current knowledge.

The text is accompanied by examples from vari- ous studies. These either illustrate the issues dis- cussed or add an extra dimension to them.

Hoare et al (2004) found that banded killifish increase their shoal size when exposed to alarm cues and decrease it when exposed to food odours. When both were present intermediate shoals were formed.

How shoaling protects fish from, or exposes them to predation

In this chapter I will describe how shoaling fish may respond when they detect a predator. I will discuss how these responses may protect them from or expose them to predation. Then I will show how shoaling may aid fish in evading a predator's attack.

fathead minnow

threespine stickleback

banded killifish

northern redbelly dace

Image 1: a shoal of mackerel has detected approaching skipjack and has aggregated into a tight ball (from *BBC's The Blue Planet*)

Shoal aggregation

When a fish shoal detects a predator, its members often aggregate (e.g. Templeton & Shriner 2005: guppies; Ferrari et al 2005: fathead minnows) (*image 1*). Possibly aggregation provides protection from predation. I will discuss four theories that explain how this protection may arise: *the-many-eyes theory, the selfish herd theory; the dilution effect, the confusion effect*.

Theory 1: the many-eyes-theory

According to the *many-eyes-theory*, compared to an individual, a shoal will detect a predator sooner and keep better track of its movements, because a shoal with many fish has many eyes watching in many directions. This can save lives: predators' capture success increases when prey are unaware of their presence (Turesson & Brönmark 2004, Webb 1982: pike; Krause et al 1998a: rock bass). A fish that is aware of danger can anticipate the moment of a predator's strike. The exact tell-tale signs are unclear, but may involve an unnatural stillness in the predator's body (Magurran & Pitcher 1987: pike hunting minnows). An

Morgan & Godin (1985) found that information transmission in shoals of banded killifish was independent of shoal size, i.e. independent of the number of individuals in a shoal, and about twice as high as approaching predator speed.

additional benefit of having many eyes is that part of the shoal can keep watch while the rest forages, rests, etc.. In support of the many-eyes-theory various studies find that, compared to individuals, shoals detect approaching predators sooner (Godin et al 1988: guppies; Magurran et al 1985: minnows; Treherne & Foster 1980: marine insect, but see Godin & Morgan 1985: banded killifish).

Prey will only benefit by their shoal mates' vigilance if information is transmitted fast across the shoal (Krause & Ruxton 2002). This seems to be the case (Morgan & Godin 1985; Webb 1982). Webb (1982) showed that the delay between escape stimulus, such as a predator, and escape response was smaller for shoals than for individuals. This fast information transmission was dubbed the Trafalgar effect (Treherne & Foster 1981), in reference to the use of flag signals in Trafalgar's fleet (Krause & Ruxton 2002). Possibly the information is transferred faster if the shoal mates are closer together. This may be one reason for fish to aggregate on detection of a predator.

Foraging fish are less alert

Foraging reduces vigilance: Godin & Smith (1988) showed that foraging guppies were more vulnerable to predation than non-foraging conspecifics. Vertically foraging fish are even less responsive to their environment than horizontally foraging ones (Krause & Godin 1996: guppies). Krause & Godin (1996) suggest that vertically foraging fish may have:

- a smaller visual horizon.
- a greater probability of visual obstacles (such as vegetation)
- an increased difficulty of performing a quick escape.

When a predator is detected fish may change their foraging posture to better observe the predator (Godin 1986: banded killifish; Foam et al 2004: convict cichlids; Krause & Godin 1996: guppies). Often they stop foraging entirely (e.g. Abrahams 1995: brook sticklebacks; Godin & Smith 1988: guppies; Godin 1986: banded killifish). Vigilance reduction may also cause starved guppies and guppies enjoying high food-densities to suffer higher predation rates (Godin & Smith 1988: guppies; Godin 1986: banded killifish).

Krause & Ruxton (2002) wandered why fish do not take advantage of their shoal mates' vigilance, while lazing about themselves. They suggest that the vigilance of others is not as good as being vigilant yourself. Predators may prefer to attack unwary prey (Krause & Godin 1996). Also, transfer of information across the shoal may be fastest when all fish are alert. Inattentive fish may cause small but fatal delays.

Theory 1: the selfish herd theory

Hamilton (1971) suggested that shoal aggregation occurs as a side-effect of fish seeking protection behind each other's backs. He postulated the selfish herd theory: fish surround themselves by as many neighbours as possible so that a predator (that attacks the first prey it encounters) attacks a shoal mate first (*image 2*).

Several studies have tried to find empirical support for the selfish herd theory by determining if mortality rate by predation is higher in the shoal's periphery than in its centre (*table 1*). Most studies find that the periphery is indeed the most dangerous area. Only one study found the opposite (Parrish 1989). She describes how black seabass split up shoals of 25 Atlantic silversides by ramming into the centre. Central fish suddenly found themselves in the periphery. The author notes, however, that had the shoal been larger, the predator may have attacked a more peripheral part, since its main goal probably was to split off a piece of the shoal. Still, predator tactics like these make central positions less attractive: the optimal shoal position may in part depend on the predator's hunting strategy (Parrish 1989).

Problems proving the selfish herd theory

Stankowich (2003) shows that the studies in table 1 are difficult to compare, because they differ in their definitions of 'periphery' and 'centre'. He also argues that the selfish herd principle is not required to explain their results. He suggests that the increased predation rate in the shoal's periphery could be caused by a predator's active selection: it may prefer specific phenotypes that commonly reside in the periphery, e.g. smaller, younger or hungrier fish.
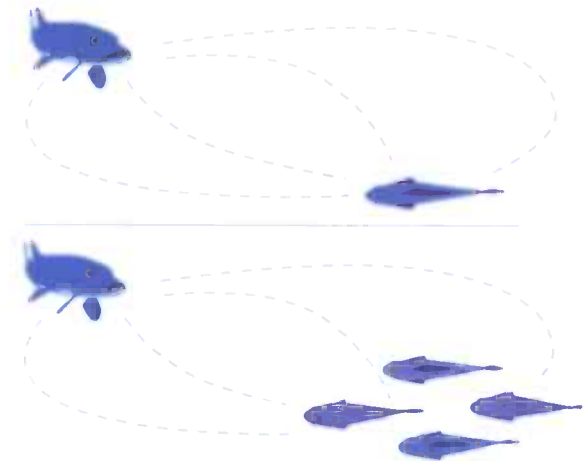

Image 2: according to the selfish herd theory fish try to minimize the number of search trajectories leading from the predator to oneself. By aggregating, many trajectories will lead to shoal mates instead.

Table 1: mortality by predation in shoals' centre and periphery (excerpt from Stankowich 2003)

Article	Prey species	Predation rate periphery > predation rate centre?
Krause & Tegeder 1994	Three-spine sticklebacks	Periphery>Centre
Krause 1993	Minnows	Periphery>Centre
Barber & Huntingford 1996	Minnows	Periphery>Centre
Parrish et al 1989	Flat-iron herring	Centre = periphery
Parrish 1989	Atlantic silversides	Periphery<Centre

Table 2: predators preferences for shoals

Article	Predator species	Prey species	Preference for attacking (larger) shoals?
Morgan & Godin 1985	White perch	Banded killifish	Preferred shoal over solitary fish
Krause & Godin 1995	Blue acara cichlids	Trinidadian guppies	Preferred larger over smaller shoal
Botham et al 2005	Pike cichlids, blue acara cichlids	Trinidadian guppies	Preferred shoal over solitary fish
Botham & Krause 2005a	Wolf fish	Trinidadian guppies	Preferred shoal over solitary fish

Image 3: according to the dilution effect per capita predation risk decreases with shoal size
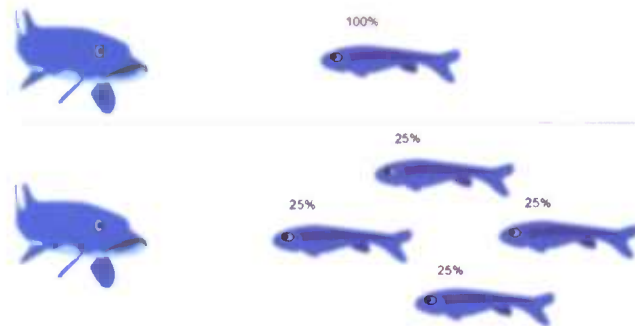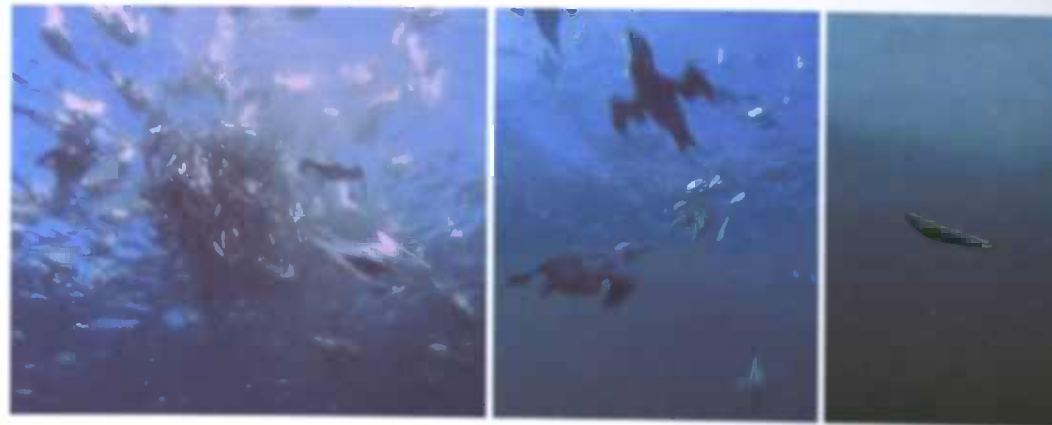

100%

25%

25%   25%

25%

Image 4: a herring school is vanquished by yellowtail rockfish and birds (from *BBC's The Blue Planet*).

Theory 2: the dilution effect

Many studies find that shoaling fish enjoy a lower predation risk, than solitary fish (Krause & Godin 1995: guppies). This benefit is often explained with the *dilution effect*. This effect indicates that chances to be attacked decrease with shoal size (Krause & Ruxton 2002). E.g. if a predator is looking for prey and runs into a solitary individual, this fish has a 100% chance of being attacked. If the predator runs into a shoal of 100 fish, and still only requires one prey, then the chance of one member being attacked is reduced to 1% (*image 3*). The existence of the dilution effect is supported by findings that fish prefer to join the largest shoal, i.e. the shoal having the most members, in the vicinity (Krause 1998b: creek chubs; Tegeder & Krause 1995: threespine sticklebacks; Hager & Helfman 1991: fathead minnows).

There are several conditions that have to be met for the dilution effect to work (Krause & Ruxton 2002):
- a predator must not, once it has found the shoal, eat all its members.
- a shoal of N individuals must not be N times more detectable or attractive than a solitary fish. Godin (1986) showed that the first condition was

met at least for banded killifish. However, there are cases in which predators reduce shoals of millions of fish to nothing (The Blue Planet: herring attacked by aerial and aquatic predators, *image 4*). As for the second condition: shoals may increase as well as decrease detection by predators. Decrease, because a randomly swimming predator has to find a localized clump in a large water column, increase, because a larger group is more conspicuous (Krause & Ruxton 2002). For decreased detection there is little evidence. Many predators live in the vicinity of their prey: they know exactly where to find food at all times and detection is independent of shoal size (Magurran & Pitcher 1987: pike hunting minnows; Seghers 1974: various predators hunting guppies). On the other hand there is much evidence for increased detection (Monadjem et al 1996, Remsen 1991: predatory birds; Magurran 1990a: freshwater prawns).

Predators also seem to be attracted towards prey aggregations (*table 2*). They may be drawn towards the increased activity and movement of large prey numbers (Krause & Godin 1995). Predators can sense activity with their lateral line system.

The lateral line system gives fish an idea of hydrodynamic pressures in their direct vicinity. It has a reach of a few body lengths only (Pitcher 1993). For some predators this sytem is crucial for directing the final strike (Pohlman et al 2004: catfish; Reist 1983: pike). To sabotage this strike an individual prey may 'freeze': becoming completely motionless and often sinking to the bottom, for up to tens of seconds (Pollock 2001; Smith 1997a). Freezing is commonly observed (e.g. Pollock 2003: fathead minnows; Brown and Smith 1998: rainbow trout, Savino 1989: bluegills; Lehtiniemi 2005: threespine sticklebacks).

Tegeder & Krause (1995) observed how, at a critical distance from the larger of two shoals, half the threespine sticklebacks chose the smaller one.

Northern red-belly dace chose the smaller of two shoals shoal if the larger one was too close to a predator. This preference changed when shoal size difference became large enough (Ashley et al 1993).

Blue acara cichlids were not attracted by shoal size, but by shoal conspicuousness: they preferred to attack the larger of two prey shoals, but when it was immersed in cold water, and as a result less conspicuous than the smaller shoal, their preference switched (Krause & Godin 1995).

Image 5: on seeing an enormous amount of similar fish predators become confused and unable to single out one prey (from *BBC's The Blue Planet*)

Table 3: many predators have a reduced capture success when attacking prey in shoals

Article	Prey species	Predator species	Reduced capture success with larger shoals?
Neil & Cullen 1974	Various prey (max. shoal 20)	Various predators	Yes
Morgan & Godin 1985	Banded killifish (max. shoal 20)	White perch	No
Landeau & Terborgh 1986	Silvery minnows (max. shoal 15)	Largemouth bass	Yes
Parrish 1993	Flat-iron herring (>> 100.000)	green jack and black skipjack	Yes
Krause & Godin 1995	Trinidadian guppies (max. shoal 16)	Blue acara cichlids	Yes
Krause et al 1998a	Creek chub (max. shoal 13)	Rock bass	No
Turesson & Brönmark 2004	Roach (max. shoal 16)	Perch	Yes
Turesson & Brönmark 2004	Roach (max. shoal 16)	Pikeperch	No
Turesson & Brönmark 2004	Roach (max. shoal 16)	Pike	No

Image 6: Krakauer's network (1995) simulates how a vertebrate may process spatial information. One could interpret 'input' as the image formed on the hunter's retina; 'transport' as the neurons connecting eyes to brain, and 'output' as the spatial image formed in the brain. Cube 1 receives information from the left part of the visual field, cube 2 information from the left-center part of the visual field, etc. Using an algorithm, the network 'tries' to place the information received through cube 1 into cube '1; through cube 2 into cube '2, etc. The chance of success depends on the signal strength. Signal strength depends on contrast with the environment. Also, signal strength increases if the point/prey is focused on/targeted.
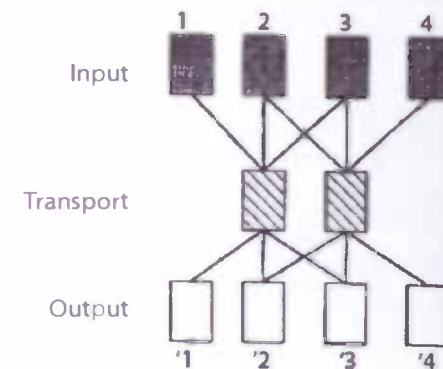
Theory 3: the confusion effect

Aggregated prey are eaten less, because they are surrounded by others. Being aggregated may provide them with second benefit: according to the confusion effect predators suffer a reduced capture success when attacking shoals instead of solitary fish. On seeing an enormous amount of similar fish predators become confused and unable to single out one prey (*image 5*). In support of this theory, many studies indeed found a reduced capture success for predators attacking larger shoals (*table 3*). Some benefits of the confusion effect overlap with those from the dilution effect: both are supposed to lead to a decreased per capita predation risk. Both should induce prey to join the largest shoal available. It is not easy to determine which effect, dilution or confusion, causes the greater part of these shared side-effects.

Krakauer (1995) designed a neural network simulation that could predict the confusion effect. He assumed that predators have a limited ability to process visual information. This could be caused, for example, by a limited amount of neurons connecting the eyes to the brain (*image 6*). Increased prey aggregations lead to larger amounts of similar visual information. More and more of this have to pass the same neurons, and visual resolution decreases.

Oddity effect

Krakauer' (1994) interpreted an odd-looking prey in a shoal as a localized increase of signal intensity. As a result, his simulation predicted that such prey was easier to target. Several studies found empirical support for this prediction: they found that 'odd' individuals in a shoal suffered higher predation risks (*table 4*). And others showed that fish preferred to be in shoals composed of similar individuals (Krause & Godin 1994: banded killifish: Wolf 1985: parrotfish and surgeonfish). Notwithstanding the results above, 'odd' individuals may still be safer in shoals than alone (Landeau & Terborgh 1986: silvery minnows).

Skittering/dashing

Fish may increase the confusion effect by *skittering* or *dashing* (Pitcher 1993). Skittering fish make rapid, jerky movements of several body lengths and, in this way, make it even more difficult for a predator to lock-on (Templeton & Shriner 2005: threespine stickleback; Dupuch et al 2004: northern redbelly dace; Pollock et al 2003: fathead minnows; Pitcher 1993 pp 389-391). Dupuch et al (2004) suggested that skittering may also serve to warn shoal mates of a detected predator.

Krause & Godin (1994) offered banded killifish, a choice of shoals. The killifish preferred to join a shoal composed of heterospecific, but similar sized individuals to either a larger or a conspecific shoal.

Wolf (1985) described how parrotfish and surgeonfish, after detecting a predator, left their shoal if their conspecifics constituted a minority.

Magurran & Pitcher (1987) described how minnows, after detecting pike, inspected it, judged it dangerous and then skittered.

Table 4: increased predation rate of 'odd' individuals

Article	Predator	Prey	Increased predation?
Theodorakis 1989	Largemouth bass	Fathead minnows Bluntnose minnows Stoneroller minnows	Yes
Landeau & Terborgh 1986	Largemouth bass	Silvery minnows	Yes
Ohguchi 1978	Threespine sticklebacks	Water fleas	Yes

Milinski & Heller (1978) suggested that the attention-consuming aspect of foraging drives three-spine sticklebacks to switch to a lower-density food source when they detect a predator: the sticklebacks do not want to be confused by their own food, and deal with a predator at the same time.

Milinksi (1990) asked human test-subjects to pinpoint dots in three densities of two-dimensional swarms. Only at the highest density (8 dots/cm²) did the test-subjects' performance become hampered.

Problems proving the confusion effect

Not all studies in table 3 support the existence of the confusion effect. Both Neil & Cullen (1974) and Turesson & Brönmark (2004) studied pike. Neil & Cullen's found that pike suffers a reduced capture success when attacking larger shoals, Turesson & Brönmark did not. Turesson & Brönmark attributed this inconsistency to an alternative definition of 'capture success'. Neil & Cullen (1974) measured capture success as number of captures / number of prey encountered. Since attacking prey in shoals automatically leads to a very high encounter rate, this does not seem like a fair measure. Turesson & Brönmark measured number of prey captured / number of prey attacked. But perhaps the confusion effect makes pike hesitate to attack in the first place. Once it manages to lock on it may get the same success rate.

There is another problem with studies trying to find evidence for the confusion effect. They often use small shoals of prey (table 3). Turesson & Brönmark (2004) offered pike shoals composed of up to 16 prey, and found no evidence for the confusion effect. Magurran & Pitcher (1987), on the other hand, offered pike shoals composed of up to 50 prey. The latter did not look at pike's capture success rate, but they did describe how pike sought to disrupt the schools and pick off stragglers, a hunting strategy that may well serve to overcome the confusion effect (Magurran & Pitcher 1987). Many researchers probably use such small shoals, because of laboratory constraints such as tank size. But if the shoal is too small, a specialized, efficient predator such as pike may not be confused at all. Shoal sizes in the wild are usually quite a bit larger than 16, especially after fish have aggregated in response to a predator (table 5).

Table 5: shoal sizes of various species observed in the wild

Authors	Species	Shoal size
Misund 1991	Atlantic herring	10^4
Morgan & Godin 1985	Banded Killifish	2-200
Blaxter & Hunter 1982	Clupeoids (including herring, sardines and anchovies)	~100 to ~10^6
Dupuch & Magnan personal observations	Northern redbelly dace	50-300
Croft et al 2003	Trinidad guppies	Several-50

Size-segregation

Pressure exerted by predators may drive the commonly observed size-segregation in shoals (Wolf 1985; Pitcher et al 1985; Allan & Pitcher 1986; Parrish 1989; Theodorakis 1989; Svensson et al 2002; Wong et al 2005). Both the oddity effect and the selfish herd theory can cause it. The oddity effect predicts that one is safer from predation among similar individuals. Thus fish may align themselves with similar-sized individuals to be as inconspicuous as possible. The selfish herd theory suggests that the shoals centre is the safest place. In a struggle for the best shoal positions larger fish may beat the smaller ones, resulting in large fish in the centre and small fish in the periphery. Such a shoal organization has been observed (Krause 1994; Theodorakis 1989). If size-segregation indeed originates from anti-predator behaviour, one would expect it to increase when the shoal feels threatened. Only a few studies have tried to assess this (table 6). Three out of four studies show increased size-segregation in response to predation. One does not. Many shoals are size-segregated when no predator is present. This suggests that there are other reasons for size-segregation as well. Food-competition is often mentioned: small fish do not want to be in the same shoal as large fish because the latter are better competitors (e.g. Krause 1994; Theodorakis 1989). Hemelrijk & Kunz (2004) suggest an interesting alternative: size-segregation may arise by self-organization. Their model predicts that variations in repulsion area sizes (larger fish have larger repulsion areas than smaller fish) lead to a shoal structure in which larger fish reside in the periphery, and smaller ones in the centre. Such a shoal structure has only been observed with water insects (Romey 1997; Sih 1980). But if fish are given the additional tendency to avoid larger shoal mates more than smaller ones, the structure is reversed: larger fish appear in the centre, and smaller ones in the periphery (image 7).
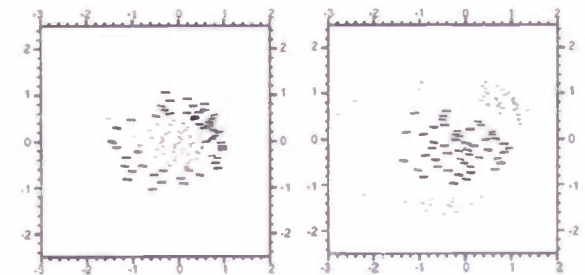

Image 7: left: differences in repulsion areas between large and small fish drive large fish to the periphery and small fish to the centre. Right: if small fish try to avoid large fish, this distribution is reversed (from Hemelrijk & Kunz 1994)

Table 6: increased size-segregation in response to predation

Study	Fish	Threat	Size-segregation?
Pitcher et al (1986b)	European minnows	Pike	Yes
Theodorakis (1989)	Bluntnose minnows	Largemouth bass	Yes
Theodorakis (1989)	Fathead minnows	Largemouth bass	No
Krause (1994)	Creek chub	Alarm cues	Yes

Inspection behaviour

While the major part of a shoal aggregates in response to a predator, some shoal members may approach it (E.g. Brown & Schwarzbauer 2001: glowlight tetras; Dugatkin & Godin 1992b: guppies; Magurran & Pitcher 1987: minnows; Milinski 1987: threespine sticklebacks) (*image 8*). This so-called *inspection behaviour* is described as a tentative and salutatory approach towards and withdrawal from the predator, either alone or in groups (Dugatkin & Godin 1992a; Pitcher 1992). I will first discuss why fish inspect. Then I will show how prey modify their inspection behaviour, based on the knowledge they gather.

Inspection to deter predators

Why would fish leave the safety of their shoal to approach a potential threat? Currently, an important reason for inspection is thought to be predator deterrence or *mobbing* (George 1960). The idea that inspection is a form of predator deterrence is supported by several studies showing that inspectors are less likely to be attacked than non-inspectors (Godin & Davis 1995: guppies; Magurran 1990a: minnows; Brown et al 1999: glowlight tetras).

Some species' inspectors exert physical displays in front of their predators: glowlight tetra inspectors flick their fins (Brown et al 1999; Motta 1983), and bluespotted goby inspectors increase their head-bobbing (Smith 1989). Such displays may discourage a predator even further (Motta 1983). Magurran & Pitcher (1987) showed that minnows in larger shoals inspect in larger groups. Possibly larger inspection groups are more unnerving to the predator. In contrast to birds, prey fish rarely chase their predators away (Dominey 1983) (*table 7*).

Inspection to gather information

Inspection may also serve to gather information about a threat. Many fish live in close association with their predators (Pitcher 1980: roach; Seghers 1974: guppies). Also, anti-predator responses are costly: fish have to stop foraging and mating (Lima & Dill 1990; Dill 1987). Therefore it may be inefficient to flee as soon as an odd shape is detected (Milinski 1993), and more rewarding to find out what the shape is, if it eats one's own species, and if it's hungry (Licht 1989; Magurran & Pitcher 1987). Some aspects of a threat can be determined from greater distances by olfactory cues. E.g. a predator's diet can be deduced from chemicals emitted by the predator (Brown & Schwarzbauer 2001; Smith & Belk 2001). Fathead minnows can even determine a predator's size by their odour alone (Kusch et al 2004). But other, important information, such as a predator's amount of hunger can only be determined visually and one must take a closer look (Smith & Belk 2001). Possibly, gathered information can be passed on to the shoal mates (Brown 2003, Brown & Godin 1999: glowlight tetras; Pitcher et al 1986: minnows).

Information gathering was originally thought to be the most important reason for inspection behaviour (hence the name *inspection*). To explain its evolution Milinksi (1987) designed his influential tit-for-tat model. He assumed that inspectors were facing a 'prisoner's dilemma'. He described a scenario in which two fish inspect together. Either one may stop co-operating (or defect) at any given moment.
- if both fish defect, neither gets information.
- if one inspects and one defect, the defector gets information without risk.
- if both inspect, both get information and share the risk.

Milinski (1987) suggested that fish resolve the di-

lemma, using a turn-based tit-for-tat strategy.

- During the first inspection visit both fish co-operate.
- During a subsequent visit, one fish or both fish may defect.
- If one fish co-operates and the other defects, the co-operating one may forgive, and co-operate again during the next visit, or it may retaliate and defect as well.
- If one fish defects twice in a row, the other fish will defect during the next visit.

For Milinski's model to work, fish must be capable of *book-keeping*: to remember previous behaviour of shoal mates and to base their decisions on this knowledge. Various studies confirm this (Dugatkin & Alfieri 1991: guppies; Milinski et al 1990: threespine sticklebacks).

However, evidence against Milinski's model is piling up. One of Milinski's major arguments for tit-for-tat was that sticklebacks, inspecting with a co-operating conspecific approached a predator more closely than sticklebacks inspecting with a defecting conspecific. However, Stephenson et al (1997) could reproduce this behaviour by assuming that two randomly swimming fish keep a close eye on the predator, while staying near each other at the same time. Also, the comparison of inspection behaviour with a prisoner's dilemma is based on the assumption that inspecting is danger-

ous for the inspectors. The reduced mortality rate of inspectors suggests otherwise.

Modification of inspection behaviour by predators

Inspectors assess risk from a distance and modify their inspection behaviour based on the knowledge they can gather. If they detect that the predator eats their kind they will take longer to initiate inspection (Brown & Godin 1999, Brown & Dreier: glowlight tetras), and maintain greater distances from the predator (Smith & Belk 2001: mosquitofish; Brown & Godin 1999: glowlight tetras). They will also show greater avoidance of the area around the predator's head (Brown & Dreier 2002, Brown & Schwarzbauer 2001: glowlight tetras; Brown et al 2001a: finescale dace). In this cone-shaped area, the *attack cone*, the predator is most likely to attack (Magurran & Seghers 1990a; Dugatkin & Godin 1992b; Pitcher 1992). But even in risky circumstances about a third of the inspections is aimed at the head (Brown & Dreier 2002: glowlight tetras; Brown et al 2001a: finescale dace). Brown & Schwarzbauer (2001) suggest that predator deterrence may only work if the predator is approached head-on. Also important information, like posture indicating satiation, may only be acquired at the head area.

Dugatkin & Alfieri (1991) showed that guppies retaliate against defectors: during a subsequent inspection visit the guppy that had previously co-operated now defects. Also, the distance from the predator at which it defects is similar to the distance at which its partner had defected during the previous visit.

Table 7: an overview of sightings of mobbing fish (excerpt from Motta 1983)

Article	Prey	Predator
Dominey (1983)	Colonial nesting bluegills	Snapping turtle
Eibl-Eibesfeldt (1962)	Redbelly yellowtail fusilier	Moray eel
Maksimov (1970)	Various tropical fishes	Various sharks
Fricke (1973)	Damselfish	Barracuda; triggerfish; octopus

Image 9: fish fleeing from a predator
(from *BBC's The Blue Planet*)

Table 8: commonly observed evasion patterns in fish schools

Image 11: some evasion
manoeuvres performed by schools
(adapted from Magurran & Pitcher 1987)

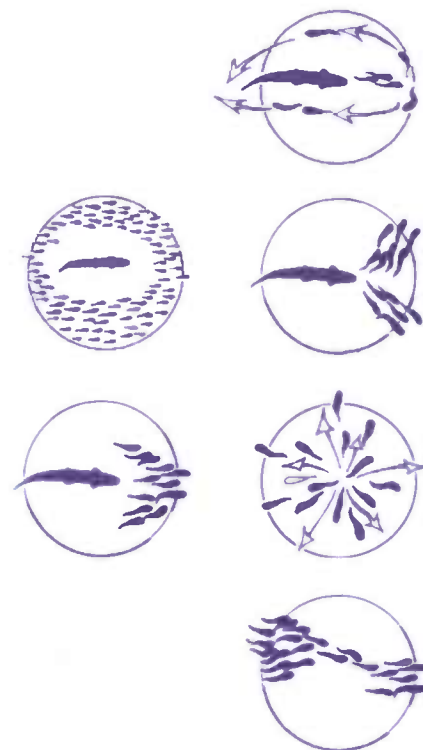| Manoeuvre	Article	Species
Fountain (evading fish turn around pursuing predator and rejoin the school behind it)	Magurran & Pitcher (1987)	Minnows
	Nursall (1973)	Spottail shiners
	Pitcher & Wyche (1983)	Sand-eels
	Nøttestad & Axelsen (1999)	Herring
Vacuole*: fish surround the predator	Pitcher & Wyche (1983)	Sand-eels
	Nøttestad & Axelsen (1999)	Herring
Split: school splits up into two or more subschools	Pitcher & Wyche (1983)	Sand-eels
	Nøttestad & Axelsen (1999)	Herring
	Magurran & Pitcher 1987	Minnows
Herd: school flees in front of predator	Pitcher & Wyche (1983)	Sand-eels
	Nøttestad & Axelsen (1999)	Herring
Flash expansion: school 'explodes' into all directions	Pitcher & Wyche (1983)	Sand-eels
	Magurran & Pitcher 1987	Minnows
Hourglass: school narrows in the centre	Pitcher & Wyche (1983)	Sand-eels
	Nøttestad & Axelsen (1999)	Herring

*Magurran & Pitcher (1987) did not see the minnows perform vacuole. They suggested that even the largest shoal they experimented with, a shoal of fifty, may have been too small to surround the predator pike.

Schooling and evasion patterns

When the predator attacks, a shoal of fish often flees en masse. It turns into an aggregated, polarized (all members facing the same way) swimming group, termed *school* (as defined by Pitcher 1993. Observed by e.g. Templeton & Shriner 2005: guppies; Ferrari et al 2005: fathead minnows; Brown et al 2004: glowlight tetras; Magurran & Pitcher 1987: European minnows) (*image 9*). Pitcher (1993) suggests that schooling may serve to increase the confusion effect: he describes how many schooling fish species are thin and silvery, so that they become almost invisible during synchronous turns. Schools may evade the predator by intricate predator evasion manoeuvres, such as *fountain*

and *flash expansion* (Pitcher 1993). How fish manage to perform these evasion manoeuvres is unclear. They may learn them (Kelley & Magurran 2003b), or they may emerge through self-organization. Vabø and Nøttestad (1997) showed that seemingly complex schooling patterns, such as *herd*, *vacuole*, and *fountain* could be simulated in a cellular automata by giving prey and predator agents a simple set of instructions (*image 10*).

Empirical studies on fish evasion manoeuvres are, unfortunately, rare. They are difficult to reproduce in the laboratory, especially when the 'predator' is an immobile model (Kelley & Magurran 2003b). Recent-

ly, new techniques using high-resolution multi-beam sonar systems were developed to study schools in the wild (Nøttestad & Axelsen 1999). Hopefully this will revive research on the subject. For an overview of the most commonly observed manoeuvres, see table 8 and image 11.
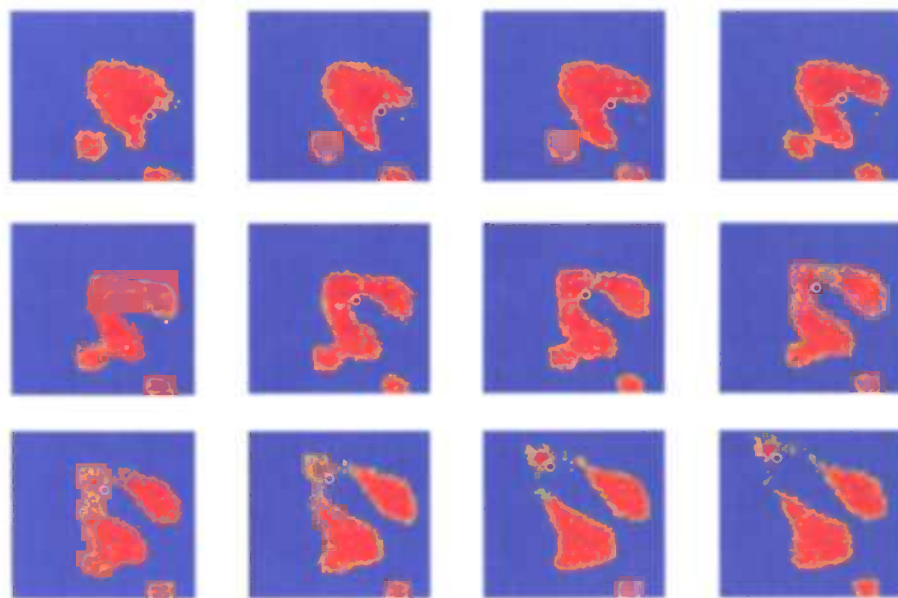
Image 10: a schooling pattern produced by Vabø and Nøttestad (1997). The red clumps are the prey, the black dot is the predator. Predator an prey were given a simple set of rules. Prey:
1   Be attracted to a shoal mate in sight;
2   Swim in the opposite direction from a predator in sight; (predator repulsion is far stronger than shoal mate attraction)
Predator:
1   Follow prey for a limited amount of time, then switch to 2;
2   Attack single individuals for a limited amount of time, then switch to 1.

How predators deal with shoaling prey

Until now, I have mainly discussed the prey's side of predator-prey interactions. In this chapter I will focus on how predators cope with their prey's anti-predator tactics. I will start by debating if and how predators select their prey. Then I will describe two strategies by which predators capture shoaling prey.

Brook trout

Northern pike

Largemouth bass

Predator preferences

In chapter 3 I explained how the confusion effect results in reduced capture success rates for predators attacking larger shoals. Still, predators are attracted to larger shoals. How can such an unbeneficial attraction have evolved? Possibly, predators want to have a choice of prey. From large shoals they can pick small, tasty, easy-to-swallow, or easy-to-catch prey. This explanation is only possible if predators actively select their prey, a topic that is still under debate.

Studies on predator preference have mainly focused on the selection of specific prey sizes and prey morphologies, not on selection of specific shoal sizes. Still, the findings of these studies may shed some light on how predators select their prey.

Selection of small fish

Researchers often find that predator diets consist of smaller prey than what the optimal foraging theory (*OFT*) predicts (e.g. Hoyle & Keast 1987: largemouth bass; Gillen et al. 1981: tiger muskellunge). The OFT theory suggests that a predator will prefer prey that gives him the largest energy intake (Charnov 1976; Schoener 1971). Might this inconsistency arise from active selection? I will give three alternative explanations. Firstly, several studies show that larger prey

are more difficult to catch, partly due to larger swimming speeds (Domenici 2001; Scharf et al. 1998; Ellis & Gibson 1997; Juanes & Conover 1994; Folkvord & Hunter 1986). This explanation is supported by studies showing that predators catch more large prey in confined laboratory tanks than in open water (Johansson 2004: pike cichlid; Christensen 1996: perch, but see Nilsson & Brönmark 2000: pike). Secondly, the inconsistency could arise by small fish being the first ones that predators encounter, because they often reside in the shoal's periphery (Krause 1994; Theodorakis 1989). And thirdly predators may more often lose large prey to fellow predators due to longer handling times: kleptoparasitism is common amongst fish (Arnegard & Carlson 2005; Hoyle & Keast 1987; Nilsson & Brönmark 2000; Major 1978).

Selection of fish without armour

Predators disproportionately often eat prey without armour (Hoyle and Keast 1987: largemouth bass; Lyons 1987: walleyes; Reist 1980: northern pike). Again this preference can be explained without a predator's active preference. Armoured fish have longer handling times (Gillen et al 1981; Wahl & Stein 1988) or may not be palatable at all (Bosher et al 2006).

Krause et al. (1998a) found that the leader of a prey shoal was attacked far more often than fish in other positions.

Several studies show that a predator's gape size determines maximum ingestible prey (Hambright 1991: largemouth bass; Nilsson et al 2000: pike, Scharf et al 2000: various predators).

Crucian carp can increase its body depth, a change that takes about six weeks, when it is confronted with chemical cues of predators (Brönmark and Petterson 1994), making it too large to swallow.

Mathis & Chivers (2003) described how threatened brook sticklebacks preferred to join fathead minnow shoals instead of conspecific shoals. They showed that yellow perch preferred the less armoured minnows as food and concluded that in spite of the oddity effect sticklebacks were safer in shoals of dissimilar individuals.

Active selection

There is evidence for active prey selection as well. Krause & Godin (1996) showed that blue acara cichlids prefer to attack unwary prey. Arnegard & Carlson (2005) described how nocturnal mormyrid fish first probe their prey electrically. Next, they either attack or move on to another prey. The authors could not determine what factors induced mormyrid fish to abandon their first prey. They suspected that prey size may be a factor. There is also evidence that predators prefer to attack prey they are familiar with (Warburton & Thomson 2006: silver perch; Nshombo 1994: Plecodus straeleni). In an evolutionary sense it would be strange if predators didn't have a close look at their prey before they attacked. It's not beneficial to keep locking-on to, and invest energy into the pursuit of prey that is hard to catch or digest. If smaller prey are indeed easier to catch and easier to swallow, predators may learn this in the course of their lives and thus passive choice becomes active choice.

Warburton & Thomson (2006) observed how silver perch preferred to attack a prey species it knew to a novel species. Over time this preference changed.

Co-operative hunting

By schooling, prey may try to confuse their predators. But these predators do not sit idly by, letting themselves be confused. Turesson & Brönmark (2004) suggested that, in an evolutionary arms-race between predator and prey, co-operative hunting may be a predator's response to schooling. Major (1978) describes how groups of co-operatively hunting jacks aligned into U- or V-shaped attack formations to split up schools of Hawaiian anchovy (*image 12*). In contrast to attacks by individual jacks, co-operative attacks often succeeded.

Once the school has been disrupted, the prey may seek refuge in the vegetation (Magurran & Pitcher 1987: minnows; Savino 1989: bluegills). Flushing prey out of their hiding places poses an additional challenge. In this, co-operative hunting may prove a valuable tactic as well: Annet (1998) describes how a hunting group consisting of both largemouth bass and bluegill sunfish spread out around some vegetation. One predator dashed into it and flushed out all the prey, so that the others could get their fill. It seems that hunting co-operatively with heterospecifics is not unheard of. Another fine example of this was given by Bshary et al (2002). He described how red sea coral groupers and lunartail groupers looked for giant moray eels. Once an eel was found, a grouper would shake its body to wake it up. Grouper and moray eel would then search for prey together. While the moray eel sneaked through holes (inaccessible to the grouper), the grouper would wait outside to catch any escaping prey. The authors even observed how a grouper, after waiting for two minutes for an escaped prey to come out again, fetched the moray eel and led it to the escapees hiding place.

The cohesiveness of hunting packs varies per species. Electric mormyrid fish remain together for days. Even when two hunting packs meet there is little member exchange (Arnegard & Carlson 2005). They may even have a specialized electrical communication system to separate pack mates from unfamiliar conspecifics (Arnegard & Carlson 2005) Largemouth bass, on the other hand, stay together for an average time of seven minutes (Annet 1998).

In many cases the distinction between co-operative hunters and predators that steal each other's food (*kleptoparasitism*) becomes irrelevant. Major (1978) describes how a ramming attack into a school is initiated by one jack. This leader usually catches the prey. But if it misses, this prey is often caught by a fellow pack hunter. Though kleptoparasitism is disadvantageous for the robbed predator, it is advantageous for the robber. As such, it may be a reason for predators to hunt 'co-operatively'. Arnegard & Carlson (2005) could find no co-operative hunting techniques with packs of mormyrid fish, but kleptoparasitism was common. These fish left their pack as soon as they caught prey to eat in peace. If they didn't, their prey got stolen twelve out of thirteen times (Arnegard & Carlson 2005).

Kleptoparasitism may be one of the main considerations for short handling times: Major (1978) described that if a predator caught a prey 'wrongly' oriented, and had to disgorge it repeatedly, its pack mates would abandon their own chases and try to get part of the prize.
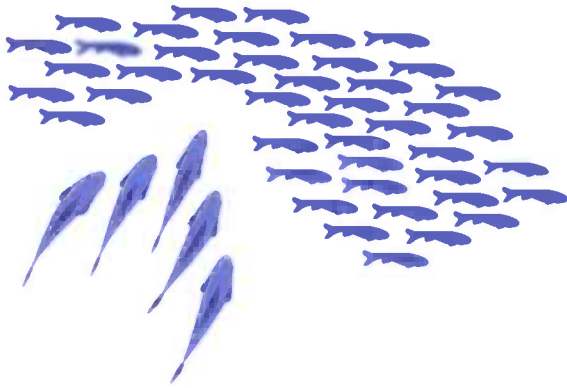

Image 12: jacks ramming into a school of prey.

Magurran & Pitcher (1987) describe how pike tried to flush out minnows from beneath rocks by directing jets of water at them.

Many predator species have increased growth rates when they hunt near conspecifics (Arnegard & Carlson 2005: mormyrid fish; Foster et al 2001: Australian salmon; Eklöv 1992: perch), but many other species suffer from it (Botham & Krause 2005b: blue acara cichlid; Eklöv 1992: pike).
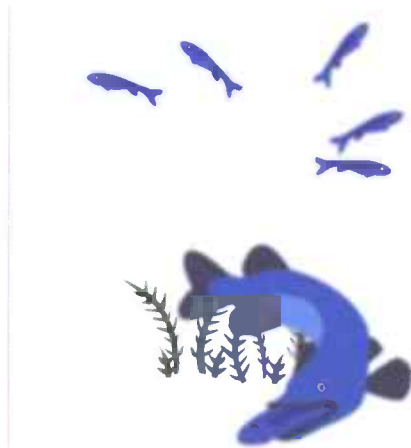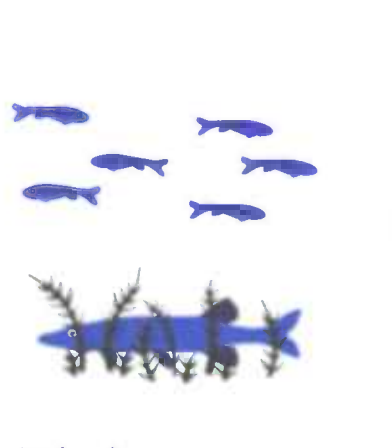
Image 13: a predator ambushing its prey

Ambushing

Co-operative hunting is not the only strategy predators use to outwit their prey. Many predators are ambushers: they lie motionless at the bottom and launch surprise attacks on prey moving overhead (Holliday 2003: pike; blue acara cichlid (Krause & Godin 1995: blue acara cichlid; Arnegard & Carlson 2005: mormyrid fish). Webb (1982) describes how pike has evolved a cryptic shape that makes it hard to see. Ambushed prey don't have time to perform anti-predator behaviour, such as aggregating, skittering or schooling (Godin & Smith 1988: guppies; Milinski & Heller 1978: threespine sticklebacks). Also, a fish that is aware of danger can anticipate the moment of a predator's strike. The exact tell-tale signs are unclear, but may involve an unnatural stillness in the predator's body (Magurran & Pitcher 1987: pike hunting minnows). Turesson & Brönmark (2004) showed that pike's first surprise attack had a far higher success rate than any subsequent attacks. And Krause & Godin (1996) showed that the ambusher blue acara cichlid prefers to attack unwary prey. The deterring aspect of inspection behaviour may be especially effective with ambushing predators: if such a predator spots the inspector, it may conclude that its cover is blown and search for other prey.

When pike hunts near conspecifics a size-hierarchy is formed in which larger pike hold larger territories that are closer to the prey (Eklöv & Diehl 1994; Eklöv 1992)

How predator-prey interactions are modified by learning

Heavily predated fish populations inspect predators more often, in larger groups and from greater distances, than less-predated conspecifics (Magurran 1986: minnows; Seghers 1974: guppies). After an inspection they are less likely to recommence foraging.

Every organism is endowed with a set of genes that enables it to cope with its environment. But in a single lifetime genes cannot adapt to novel environmental challenges, such as changes in the habitat or new predators. It is therefore likely that any organism that hasn't gone extinct possesses the ability to learn so that it may adjust its behaviour to the specific needs of the time and place In which it was born. Many researchers find slight differences in antipredator behaviour between fish that live in predator-dense areas, and conspecifics that live in environments where predators are rare. This has led them to believe that at least part of fish's antipredator behaviour can be fine-tuned by learning (reviewed in Kelley & Magurran 2003b). The fitness advantage of good learning abilities is clear: experienced fish have higher survival rates (Mirza & Chivers 2000: brook trout; Mathis & Smith 1993a: fathead minnows).

Unfortunately, learning by predators is studied far less extensively than learning by prey. As a result, this chapter mainly deals with the latter. I will start by discussing two well known learning mechanisms in fish: learning by alarm cues and social learning.

Alarm cues and learning by personal experience

Alarm cues are secreted by *club-cells*, large secretory cells in the epidermis. These cells lack an opening at the skin surface and release their contents only when the skin is damagaed (Pitcher 1993).

Image 14: fish aggregate in response to alarm cues
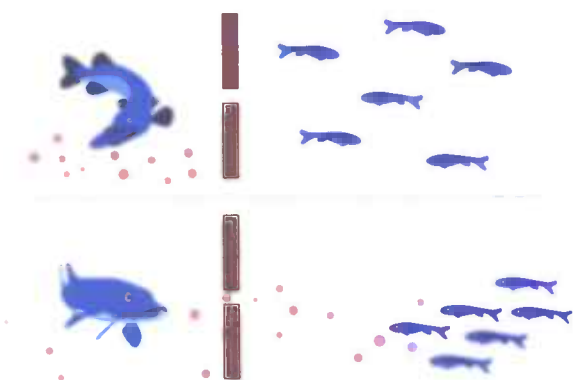
European and fathead minnows acquire predator recognition (either visual or chemical) after a single exposure to predator odour accompanied by conspecific alarm cues (Magurran 1989; Mathis & Smith 1993b)

Many fish species, when injured by a predator attack, release chemical compounds called *alarm cues*. Alarm cues have been found in many families, including ostariophysans, salmonids, gobies, pecilids, sticklebacks, percids, cottids, cichlids and centrarchids (Chivers & Smith 1998), but not in swordtails (Pfeiffer 1977). The chemical nature of alarm cues is still under debate (Mirza & Chivers 2001a). Brown et al (2000) showed that a nitrogen oxide group may act as the chief molecular trigger in ostarlophysans.

It is not entirely clear how a fish benefits from sending alarm cues. Chivers et al (1996) found that, by emitting alarm signals when wounded by pike, fathead minnows attract other pike that try to steal the prey. The authors show that the ensuing struggle between the predators increases the minnow's survival probabilities. It is dubious if this phenomenon is enough reason for alarm cues to evolve so universally.

Alarm cues are greatly beneficial to the victim's shoal mates, however: while killing or digesting a meal, predators emit its alarm cues. Their faeces are labelled by them as well. The conspecifics of the predator's meal pick up their own alarm cues, realize that this predator eats their kind, and learn to avoid it (Wisenden et al 1994, Mathis and Smith 1993a,b; Brown et al 1995: fathead minnows) (*image 14*).

Predator recognition

It is as yet unclear if fish need alarm cues to learn to recognize their predators. Some species do (Chivers et al 1995: brook sticklebacks and, Chivers & Smith 1994: fathead minnows, learn to recognize northern pike), but others seem to recognize their predators by predator odour alone (Vilhunen & Hirvonen 2003: arctic char recognizes brown trout; Berejikian et al 2003: chinook salmon recognizes northern pike; Mirza & Chivers 2002: brook char).

Risk assessment

At low concentrations alarm cues may not elicit any behavioural response in fish. This does not mean they are unaware of danger. Brown et al (2004) observed how glowlight tetras, in the presence of sub-behavioural threshold concentrations of a chemical stimulus, responded more strongly to a frightened conspecific than when no chemicals were present. And fathead minnows learned to recognize yellow perch by sub-behavioural threshold concentrations of alarm cues (Brown et al 2001b), but not when no alarm cues were present.

At higher concentrations, the alarm cue concentration is often correlated to the intensity of a fish's anti-predator behaviour (Dupuch et al 2004: northern redbelly dace; Kusch et al 2004: fathead minnows;

Wisenden et al 2004: glowlight tetras), and to its future risk assessment of a predator (Ferrari et al 2005: fathead minnows). Alarm cue concentration may be an indicator of predator distance, since its concentrations are diluted within the space covered (Dupuch et al 2004). In confined laboratory tanks, alarm cues dissolve far slower than in the wild (Wisenden et al 2004). This partly explains why fish, that are exposed to alarm cues, respond stronger in the laboratory than in the wild (Wisenden et al 2004: glowlight tetras; Irving & Magurran 1997: minnows). Alarm cues may also provide information about the direction of a threat: Krause (1993) set up a current in a laboratory tank that transported alarm cues. The redbelly dace responded by swimming 'downstream'.

Little is known about how fish react when conflicting information about a predator is given. Ferrari & Chivers (2006) found that fathead minnows adopt a worst-case-scenario strategy if conflicting information about the seriousness of a threat is offered. Dill (1974) showed that the first few predator encounters of a naïve zebra danio determine the greater part of the intensity of its anti-predator behaviour.

Response to heterospecific alarm cues

Alarm cues are highly conserved in many species (e.g. Schutz 1956: various species; Mirza & Chivers 2001a). Not surprisingly recognition of alarm cues of related fish is common (Smith 1999). More interestingly, fish may respond to alarm cues of non-related species: brook sticklebacks were shown to respond to alarm cues of fathead minnows and vice versa (Pollock et al 2003; Wisenden et al 1994). This sensitivity to non-related alarm cues is probably learned. Brown (2003) suggests four non-mutually exclusive mechanisms by which fish may acquire recognition of heterospecific alarm cues:

1. Fish may learn from heterospecific demonstrators (Mathis et al 1996).
2. Fish may be exposed to a mixture of conspecific and heterospecific alarm cues. This could happen in mixed species shoals (Smith 1999).
3. Fish may detect heterospecific alarm cues in the dietary cues of a predator, which they already know and avoid, or which also emits conspecific alarm cues (Mirza & Chivers 2001b: fathead minnows and brook sticklebacks).

How did alarm cue production evolve?

There are some great benefits for the shoal mates associated with alarm cue production. So this mechanism may have evolved as a result of some form of group selection. Alternatively current research focuses on family ties within schools. Possibly the sender itself may not benefit, but its family will.

Brown & Dreier (2002) showed that predator-naïve tetras only avoided a predator's head area if this predator was paired with alarm cues, but once the tetras had learned to recognize the predator they always avoided the head area.

Social learning

Predator-naïve guppies from a low-predation site, adjusted their time spent in schools and their inspection behaviour to high-predation site demonstrators (Kelley et al 2003).

Brown (2001) showed that fish learned to use escape routes far sooner if they had time to get to know their environment. In many studies fish are kept in one tank and placed in another for the experiment itself. In these studies, the time that a fish needs to learn to use an escape route is partly invested in overcoming the problems of an unfamiliar environment.

Ferrari et al (2005) observed that predator-naive fathead minnows did not learn to recognize brook char from an experienced demonstrator, that was exposed to alarm cue concentrations, too low to elicit a behavioural response.

Reader & Laland (2000) showed that female guppies learned a route towards food much faster than males. And fishes that were food-deprived were faster to learn than their less hungry conspecifics.

Entire shoals were shown to adjust their anti-predator behaviour to that of a few experienced conspecifics, or even heterospecifics. (Conspecific - Pitcher et al 1986: minnows; Magurran & Higham 1988: minnows; Brown et al 1999: glowlight tetras. Heterospecific - Krause 1998b: creek chub demonstrators, threespine stickleback observers; Mathis et al 1996: brook stickleback demonstrators, fathead minnow observers). Kelley et al (2003) showed that the behavioural differences between fish from high-predation and fish from low-predation sites may arise by *social learning*.

Learning from conspecifics or heterospecifics has been observed in various taxa and seems to be at least as important as learning by personal experience. Cultural transmission of gained knowledge across the shoal is much faster than each member having to acquire the knowledge by personal experience (Brown 2003). Brown & Warburton (1999) found that the transfer speed of new knowledge increases with shoal size in rainbowfish. As such, social learning may be an important reason for fish to live together. Brown et al (1997) showed that a population of 80.000 fathead minnows acquired predator recognition of northern pike within 2 to 4 days. Transfer speed of knowledge seems to be influenced by sex, motivation and age (Reader & Laland 2000).

In addition to recognition of a predator, fish may also learn the amount of risk associated with it. They will adjust the intensity of their anti-predator responses (schooling, time spent hiding, freezing, etcetera) to that of their demonstrators (Ferrari et al 2005: fathead minnows; Vilhunen et al 2005: Arctic char; Kelley et al 2003: Trinidadian guppies). To see if fish can also learn less common anti-predator behaviour, several studies examined fishes' ability to learn escape routes. Sugita (1980) showed that guppies avoid an electric shock by following a demonstrator into the safe one of two boxes. Brown & Laland (2002) found that naïve fish, which were accompanied by a demonstrator, took the 'right' escape route from a model predator far more often than a group without demonstrator. How do fish decide from whom to learn? Vilhunen et al (2005) showed that for social learning to occur with arctic char, the demonstrators had to be a minority, and Swaney et al (2001) found that guppies learn from familiar individuals faster than from unfamiliar ones. Brown (2003) argued that glowlight tetra inspectors may set the example for their shoal mates. In this way the entire shoal may acquire predator recognition, while only a few fish have to approach the predator. Nonetheless, inspectors probably gain more knowledge about a predator than non-inspectors (Brown & Godin 1999).

Brown & Godin (1999) showed that only glowlight tetras that had inspected a tetra-fed predator learned to both visually and chemically recognize it. The shoal acquired only chemical recognition.

Ontogeny

Little is known about the ontogeny of fish anti-predator behaviour (Kelley & Magurran 2003b). Possibly fry are far more sensitive to predator encounters than adult fish. Magurran (1990b) observed how minnows that were exposed to a pike model in childhood performed more inspections 2 years later. In many species, fathers guard their newly hatched offspring for several days:

- Three-spined sticklebacks: for about 10 days (Tulley & Huntingford 1987);
- Paradise fish: for about five days (Miklosi et al 1997).

Miklosi et al (1997) suggest that this period may be a key-period in the development of anti-predator behaviour. During this time the father chases the young when they stray, catches them in his mouth and spits them back into the nest. These experiences may provide early anti-predator training (Tulley & Huntingford 1987). Raising by the father can lead to strongly increased anti-predator behaviour (Tulley & Huntingford 1987, Benzie 1965: three-spined sticklebacks; Miklosi et al 1997: paradise fish).

To be able to assess the learning abilities of fish, one must take ontogeny into account. Walling et al (2004) caught young and old three-spined sticklebacks from a perch sympatric population. Since the older ones did not show stronger developed anti-predator responses than the younger ones, the researchers conclude that experience is of little importance for the development of anti-predator responses. But if anti-predator responses are mainly learned in childhood, these conclusions may be incorrect.

Genetic or learned

Many researchers ask themselves which anti-predator behaviour in fish is embedded within the genetic material and which behaviour is learned. To me this distinction between genetic and learned seems problematic. For example: the urge to school when in danger may be genetic, but to repress this urge when the predator is a bird may be learned. Genes set the boundaries for behaviour that can be fine-tuned by learning.

Learning by predators

Several studies suggest that predators specialize on specific prey types. From this type they learn life style and anti-predator behaviours (Warburton & Thomson 2006: perch; Nshombo 1994: Plecodus Straeleni). Bosher et al (2006) showed that largemouth bass became sensitized to spined catfish: after it had to disgorge prey several times (because of the spine) it began to disgorge catfish from which the spines were clipped as well. One would expect that largemouth bass would learn to avoid catfish altogether. Catfish was the only prey species available. Perhaps, if the predator would have had a choice, it would have switched to another prey type.

Paradise fish that had been raised by their fathers showed higher fleeing and backing frequencies towards a predator than did orphaned fish (Miklosi et al 1997).

Warburton & Thomson (2006) showed that silver perch's capture success of an unfamiliar prey increased over time, suggesting that it developed improved search and handling skills.

Nshombo (1994) described how hunting techniques of the predator *Plecodus straeleni* varied with sex, size and even individuals. He noted that many predators specialized on one or several prey species (this also varied per individual). He attributed this specialization on the predators getting to know their prey's life style and anti-predator behaviours.

Conclusions

There are more fish species than all other vertebrates combined. Also, the few species that are most commonly researched (guppies; minnows; sticklebacks; pike), and are often supposed to represent fish in general are largely chosen because they live nearby, or because they are easy research subjects, not because they are such great examples of 'typical fish' (Svensson et al 2000). Therefore caution should be exercised in drawing general conclusions on fish behaviour.

There are, however some research topics, which transcend even the fish taxa as a whole, such as living in groups. As of yet, researchers are unsure how advantages relate to disadvantages. They cannot easily be compared (since they influence one another) (Krause & Ruxton 2002): the dilution effect only functions if shoal delectability doesn't increase proportionally to shoal size. Odd-looking individuals benefit less from the confusion effect than common-looking ones. Shoaled fish may confuse predators, but they seem to attract them at the same time. Therefore it is hard to assess if the advantages of group life outweigh the disadvantages. Since it is so common, one must assume that it has been advantageous at one point in time. But predators evolve too. Many studies describe how they utilize sophisticated hunting techniques to split up schools and pick off stragglers

(Parrish 1993, Parrish 1989: black skipjack; Magurran & Pitcher 1987: pike; Major 1978: black seabass). Possibly, an increasing ability of predators to cope with schools will drive their prey back towards solitary life (Eklöv 1992).

Inspection implies the counterintuitive behaviour of approaching one's predator. Such behaviour seems dangerous, yet several studies showed that inspectors were in less danger than their shoal mates! Possibly the predator gets confused by the unexpected behaviour, but since inspection is quite common, one would expect the predator to get used to it. Alternatively, the inspectors may often consist of a phenotype that is hard to capture, e.g. large, healthy fish.

During my study of the literature I regularly encountered passages or studies that noted the significant influence of laboratory conditions on fish behaviour. Braithwaite & Salvanes (2005) found that North Sea cod reared in arid laboratory tanks do not develop the same learning skills and tendency to explore as conspecifics reared in more natural conditions. Anti-predator responses were shown to be more intense in the laboratory than in the wild (Wisenden et al 2004: glowlight tetras; Irving & Magurran 1997: minnows). As mentioned before, increased concen-

trations of alarm cues may explain this. Alternatively, fish may be stressed: they cannot flee, and since they are often alone when exposed a predator, they are unable to shoal (Smith 1997).

The effects of laboratory conditions may make behaviour of laboratory fish difficult to compare to that of their wild counterparts. An increasing amount of researchers points out the importance of natural conditions for research (Brown 2001; Irving & Magurran 1997). The drawback of such studies is that the researcher can control less variables. However, since laboratory conditions seem to add other variables, such as confined spaces and unfamiliar environments, this benefit is reduced. Personally, I found studies performed under (near-)natural conditions such as the excellent studies by Arnegard & Carlson (2005), Parrish (1993) and Major (1978) more informative.

Since researchers established that fish are social, clever creatures, research has focused on topics such as fish character and social networks in shoals. Hopefully these studies will provide new insight into fascinating aspects of fish behaviour, such as inspection behaviour and co-operative hunting.

Vilhunen (2003) describes how brown trout, exposed to pikeperch odour tried to swim away. After it found that it could not escape (because it was in a laboratory tank) it started to freeze and dash about.

Appendix: Fish names and families

English name	Latin name	Dutch name	Order	Family
Arctic charr	Salvelinus alpinus	Arctische zalmforel	Salmoniformes (Zalmachtigen)	Salmonidae (Zalmen)
Atlantic herring	Clupea harengus	Atlantische haring	Clupeiformes (Haringachtigen)	Clupeoidae (haringen)
Atlantic silversides	Menidia menidia	Getijdenaarvis	Atheriniformes (Aarvisachtigen)	Menidiinae (Koornaarvissen)
Australian salmon	Arripis trutta	Australische zalm	Perciformes (baarsachtigen)	Carangidae (Horsmakrelen)
Banded killifish	Fundulus diaphanus		Cyprinodontiformes (Tandkarpers)	Fundulidae (Killivisjes)
Black sea bass	Centropristis striata	Zwarte zeebaars	Perciformes (baarsachtigen)	Serranidae (Zeebaarzen)
Black skipjack	Euthynnus lineatus	Gevlekte tonijn	Perciformes (baarsachtigen)	Scombridae (Makreelachtigen)
Blue acara cichlid	Aequidens pulcher	Blauwe acara	Perciformes (baarsachtigen)	Cichlidae (bonte baarzen)
Bluegills	Lepomis macrochirus	blauwkeel zonnebaars	Perciformes (baarsachtigen)	Centrarchidae (Zonnebaarzen)
Bluespotted goby	Asterropteryx semipunctata	Sterrengrondel	Perciformes (baarsachtigen)	Gobiidae (zeegrondels)
Bluntnose minnow	Pimephales notatus		Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Brook charr	Salvelinus fontinalis	Bronforel	Salmoniformes (Zalmachtigen)	Salmonidae (Zalmen)
Brook stickleback	Culaea inconstans	Beekstekelbaars	Gasterosteiformes (Stekelbaarsachtigen)	Gasterosteidae (Stekelbaarzen)
Brown trout	Salmo trutta	Zeeforel	Salmoniformes (Zalmachtigen)	Salmonidae (Zalmen)
Catfish	Silurus glanis	Meerval	Cypriniformes (karperachtigen)	Siluridae (Echte Meervallen)
Chinook salmon	Oncorhynchus tshawytscha	Quinnat	Salmoniformes (Zalmachtigen)	Salmonidae (Zalmen)
Coalfish	Pollachius virens	Koolvis	Gadiformes (Schelvissen)	Gadidae (Kabeljauwachtigen)
Cod	Gadus morhua	Kabeljauw	Gadiformes (Schelvissen)	Gadidae (Kabeljauwachtigen)
Creek chub	Semotilus atromaculatus		Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Crucian carp	Carassius carassius	Kroeskarper	Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Darter	Etheostoma blennioides	Grondbaars	Perciformes (baarsachtigen)	Percidae (Echte baarzen)
European minnow	Phoxinus phoxinus	Elrits	Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Fathead minnow	Pimephales promelas	Amerikaanse dikkop-elrits	Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Finescale dace	Phoxinus neogaeus		Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Flatiron herring	Harengula thrissina		Clupeiformes (Haringachtigen)	Clupeoidae (haringen)
Glowlight tetras	Hemigrammus erythrozonus	Vuurneon	Characiformes (Karperzalmachtigen)	Characidae (karperzalmen)
Green jack	Caranx cabal	Groene jack	Perciformes (baarsachtigen)	Carangidae (Horsmakrelen)
Hawaiian anchovy	Encrasicholina purpurea	Hawaiiaanse anchovis	Clupeiformes (Haringachtigen)	Clupeoidae (haringen)
Jack	Caranx ignobilis	Jack	Perciformes (baarsachtigen)	Carangidae (Horsmakrelen)
Largemouth Bass	Micropterus salmoides	Forelbaars	Perciformes (baarsachtigen)	Centrarchidae (Zonnebaarzen)
Lunartail grouper	Variola louti	Wijnrode tandbaars	Perciformes (baarsachtigen)	Serranidae (Zeebaarzen)

English name	Latin name	Dutch name	Order	Family
Minnow: see European minnow				
Moray eel	Gymnothorax javanicus	Reuzemurene	Anguilliformes (Palingachtigen)	Muraenidae (murenen)
Mormyrid fish	Mormyrops anguilloides	Nijlsnoek	Osteoglossiformes (Beentongvissen)	Mormyridae (Olifantsvissen)
Mosquitofish	Gambusia affinis	Koboldvisje	Cyprinodontiformes (Tandkarpers)	Poeciliidae (Levendbarende tandkarpers)
Northern pike	Esox lucius	Snoek	Esociformes (snoekachtigen)	Esocidae (Snoeken)
Northern redbelly dace	Phoxinus eos		Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Paradise fish	Macropodus opercularis	Paradijsvis	Perciformes (baarsachtigen)	Osphronemidae (Echte goerami's)
Perch	Perca fluviatilis	Rivieraars	Perciformes (baarsachtigen)	Percidae (Echte baarzen)
Pike: see northern pike				
Pike cichlid	Crenicichla frenata		Perciformes (baarsachtigen)	Cichlidae (bonte baarzen)
Pikeperch	Sander lucioperca	Snoekbaars	Perciformes (baarsachtigen)	Percidae (Echte baarzen)
Rainbow trout	Oncorhynchus mykiss	Regenboogforel	Salmoniformes (Zalmachtigen)	Salmonidae (Zalmen)
Red sea coral grouper	Plectropomus pessuliferus	Panter forelbaars	Perciformes (baarsachtigen)	Zeebaarzen (Serranidae)
Redbelly yellowtail fusilier	Caesio cuning		Perciformes (baarsachtigen)	Cichlidae (bonte baarzen)
Roach	Rutilus rutilus	Blankvoorn	Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Rock bass	Ambloplites rupestris	Steenbaars	Perciformes (baarsachtigen)	Centrarchidae (zonnebaarzen)
Sand-eel	Ammodytes sp.	Zandspieringen	Perciformes (baarsachtigen)	Ammodytidae (zandspeiringen)
Scale-eater	Plecodus straeleni		Perciformes (baarsachtigen)	Cichlidae (bonte baarzen)
Silver perch	Bidyanus bidyanus	Zilverbaars	Perciformes (baarsachtigen)	Terapontidae (Tijgerbaarzen)
Silvery minnow	Hybognathus nuchalis		Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Spottail shiners	Notropis hudsonius		Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Stroneroller minnow	Campostoma anomalum		Cypriniformes (karperachtigen)	Cyprinidae (Karpers)
Swordtail	Xiphophorus birchmanni	Zwaardstaart	Cyprinodontiformes (Tandkarpers)	Poeciliidae (Levendbarende tandkarpers)
Three-spined stickleback	Gasterosteus aculeatus	Driedoornige stekelbaars	Gasterosteiformes (Stekelbaarsachtigen)	Gasterosteidae (Stekelbaarzen)
Tiger muskellunge	Esox masquinongy	Maskulonge	Esociformes (snoekachtigen)	Esocidae (Snoeken)
Trinidadian guppy	Poecilia reticulata	Guppy	Cyprinodontiformes (Tandkarpers)	Poeciliidae (Levendbarende tandkarpers)
White perch	Morone americana		Perciformes (baarsachtigen)	Moronidae (Moronen)
Wolf fish	Hoplias malabaricus	Wolfvis	Characiformes (Karperzalmachtigen)	Erythrinidae (Roofzalmen)
Yellow perch	Perca flavescens	Gele baars	Perciformes (baarsachtigen)	Percidae (Echte baarzen)
Zebra danio	Danio rerio	Zebravis	Cypriniformes (karperachtigen)	Cyprinidae (Karpers)

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