

The adaptive significance of schooling as an anti-predator defence in fish

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Recent experiments have demonstrated the adaptive advantages of schooling behaviour during predator defence. Fish in schools benefit from increased vigilance and, as a consequence of inspection behaviour, predator recognition and assessment is improved. Information about advancing predators can be obtained from other school members without each fish needing to independently confirm the extent of the danger. Schooling behaviour and inspection behaviour may inhibit attack by predators, and, if schools are attacked a variety of tactics, ranging from the confusion effect to the flash expansion, serve to protect individual members.

There are however a number of constraints on the evolution of schooling and associated anti-predator mechanisms. For instance, conflicting selection pressures, such as the need to forage, mate and avoid predation, can operate simultaneously. Selection pressures acting on immature and adult fish may be discontinuous necessitating a period of increased vulnerability when individuals switch tactics. Schooling may not be an equally appropriate defence against all predators and the phylogenetic origins of populations or species can lead to additional genetic constraints. It seems probable that behavioural ecologists will increasingly focus on how interactions between such constraints govern the evolution of behaviour.

1. Introduction

In 1962, Evelyn Shaw commented that 'In spite of all the indications that schooling is an effective adaptation, no student has been able to show why it is so effective'. Since that time considerable

effort has been devoted to exploring the functional significance of schooling behaviour. There have, for instance, been suggestions that schooling is associated with hydrodynamic advantages (Pitcher 1986) and there is good evidence that foraging is more efficient when fish feed in social

groups (see for example, Morgan 1988a). In most cases however it appears that schooling has evolved as a defence against predation. A classic experiment by Neill & Cullen (1974) demonstrated that both cephalopod and fish predators are at a disadvantage when attacking schools of fish. A much greater success rate per attack is achieved if single fish are targetted. The anti-predator function of schooling is particularly evident when intra-specific variation in behaviour is examined. In both guppies, *Poecilia reticulata* (Seghers 1973, 1974) and minnows, *Phoxinus phoxinus*, (Magurran 1986a, 1989; Magurran & Pitcher 1987) schooling tendency is greater and associated anti-predator behaviours are more effective in populations experiencing high levels of predation.

This paper begins by examining the ways in which schooling functions as a defensive mechanism. Both passive and active modes of defence are explored and the role of schooling, from the initial detection of a predator through to the execution of coordinated evasive actions in the event of an attack, is analysed.

Although schooling occurs widely in teleosts, not all fish with the ability to form polarised and synchronised schools, or even more loosely organised shoals, do so on all occasions. One explanation is that schooling behaviour, which relies on cooperation, is incompatible with other activities that involve an element of conflict, such as competition for mates or food. Furthermore, despite its antipredator advantages, schooling is not always the best defensive tactic. Schooling may be additionally limited by genetic and developmental constraints. The consequences of such factors are examined in the second section of the paper.

2. Anti-predator advantages of schooling behaviour

2.1. Vigilance

Ambush predators, such as pike (*Esox lucius*), hunt by stealth. In the wild, pike remain stationary for long periods of time (Diana et al. 1977) and are often found in dense vegetation in shallow water. Their hunting strategy can be divided

into three main phases (Neill & Cullen 1974; Hart & Connellan 1984; Clarke 1986; Magurran & Pitcher 1987). First, pike orient to nearby prey. Then, using their pectoral fins for propulsion they stalk slowly towards their victim. Finally, when the prey is within close range the pike strikes using an acceleration lunge (Webb & Skadsen 1980). In such encounters the predator is at a clear advantage if it remains undetected by the prey until the last moment of the attack (Webb 1982). To this end, esocids have evolved a body form which, though sub-optimal for locomotion, is difficult for prey fish to detect in cross-sectional silhouette (Webb 1986).

The increased vigilance of larger groups offers a potential counter-defence in this evolutionary arms race (Bertram 1978, Dawkins & Krebs 1979, Lazarus 1979). In the first study to demonstrate such an advantage in fish, Magurran et al (1985) found that larger schools of minnows detected an approaching model pike more quickly than small schools. Predator detection was inferred from the presence of inspection behaviour and skittering behaviour. Inspection behaviour takes place when a single fish, or a small group, leave the main school and approach a potential predator. Skittering is a Mauthner drive startle response (Guthrie 1980; Eaton et al. 1977; Eaton & Hackett 1984; Webb 1976) and is seen most commonly when predators are in the first stages of an attack sequence (Magurran & Pitcher 1987). Both behaviours were observed earlier in larger schools (Fig. 1). Interestingly, there was no group size difference in the point at which foraging ceased. Minnows in large groups slowly decreased their foraging rate and gradually increased their inspection and skittering rate for the duration of the predator's advance. By contrast, fish in small groups abruptly stopped feeding (presumably because they had previously not been aware of the danger) and initiated defence only when the predator was in close proximity.

Other investigations have shown that there is not always a direct relationship between reaction distance (sometimes called flight distance) and group size (see Ydenberg & Dill 1986 for a review). As Seghers (1981) pointed out, it is important to distinguish between detection distance, when the predator is first spotted, and reaction distance, when evasive action commences. The

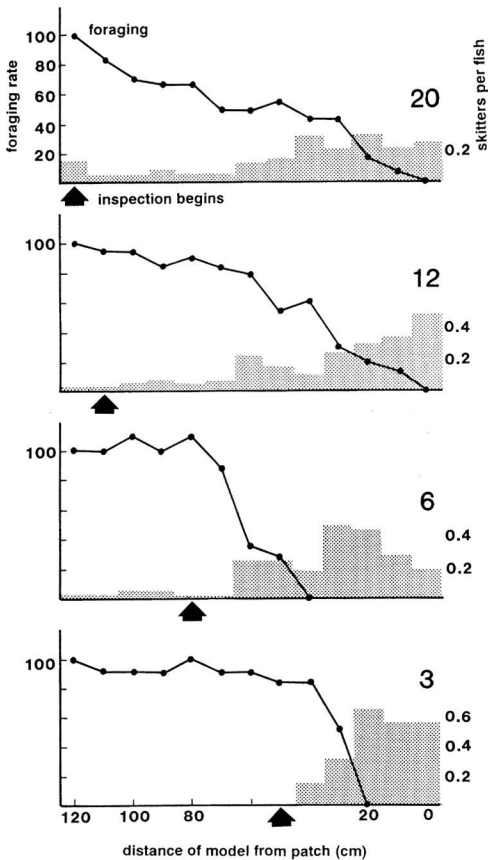


Fig. 1. Increased vigilance in larger schools. Four school sizes (20, 12, 6, and 3 fish) were tested and there were five replicates of each school size. The solid line shows the mean individual foraging rate (measured as seconds foraging) plotted against the approach of a 20 cm, realistically painted, model pike towards a feeding patch. Initial foraging rates are set at 100% to facilitate comparison between school sizes. Foraging rates declined sooner in the larger groups. The solid arrow shows the median distance of the pike when inspection began. Once again, this is earlier in larger schools. The stippled bars indicate the mean frequency of skitters per individual fish per trial. Although there was no significant difference in skittering rate per individual ($G=2.99$, $df=3$, $P>0.05$, G test; Sokal & Rohlf 1981) fish in the large schools were more likely to skitter earlier in a trial ($G=58.6$, $df=12$, $P<0.001$). See Magurran et al. (1985) for more details.

precise moment when predator detection occurs is difficult to measure accurately as it will not necessarily be indicated by a dramatic behavioural change. Nevertheless, careful monitoring of behaviours such as predator inspection or feeding rate can show that individuals are aware of potential danger.

Detection distance is a much more valuable measure of vigilance than reaction distance. Because of the increased protection afforded to members of larger groups flight may be postponed until the later stages of an attack by a predator. Furthermore, flight is not necessarily the optimal response in all circumstances (Ydenberg & Dill 1986). Detection distance (unlike reaction distance) does however increase with increasing school size (see also Godin 1986 and Godin et al. 1988).

2.2. Predator assessment

As soon as a potential predator has been detected further investigation is required in order to confirm its identity and assess its motivation. This is vital because not all large fish are necessarily dangerous, and, even if they are predators, they may not be motivated to feed. Given the proximity of predators and prey in the wild (Pitcher 1980), a prey fish which fled or hid at the slightest hint of danger would have little time left for other activities such as courtship or foraging. In addition, as mentioned above, esocids follow a body plan which offers few cues to prey fish viewing them from the front.

Inspection behaviour allows prey fish to obtain information on the morphology and behaviour of the predator. In a study comparing the reactions of minnows to four different types of predator model, which ranged from a realistic pike to a plain green cylinder (all with similar dimensions), Magurran & Girling (1986) showed that all approaching objects are initially inspected. Prey behaviour is modified following inspection. In the case of the realistic pike model, for instance, fish significantly reduced their foraging and formed a polarized school. With the unrealistic green cylinder, by contrast, minnows maintained a high foraging rate (Fig. 2). Although inspection is intrinsically a risky endeavor

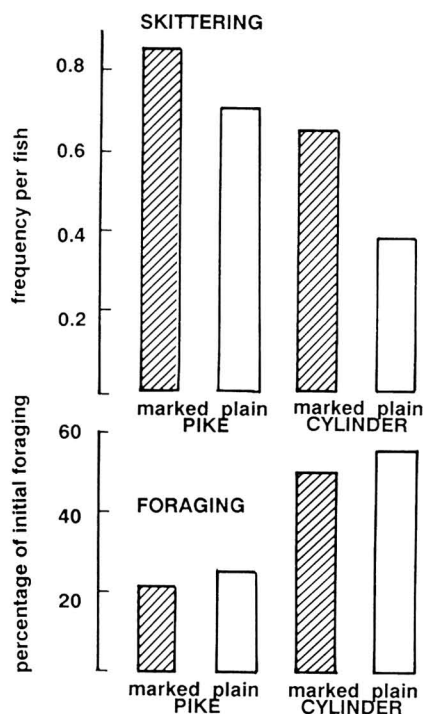


Fig. 2. Predator assessment. This experiment (see Magurran & Girling 1986) tested the reactions of minnows to four different types of model: a realistically painted pike (marked pike), a pike painted a uniform green (plain pike), a cylinder with pike markings (marked cylinder) and a plain green cylinder (plain cylinder). All models measured 21 cm long by 5 cm deep and 'stalked' towards a feeding patch. Minnows were tested in schools of 10 and there were eight replicates per model type. There was a significant difference in skittering rate per trial ($G=29.7$, $df=3$, $P<0.001$) with most occurring in the presence of the most realistic model. Foraging rates (the number of minnows foraging on the patch at the end of a stalk expressed as a percentage of the foraging level at the beginning of a trial, before the model appeared) declined more with the pike-shaped models than with the cylinder shaped models ($G=9.1$, $df=3$, $P<0.05$).

our (see below), inspecting fish minimise the danger by avoiding the 'attack cone' directly in front of the predator's mouth (George 1960; Magurran & Seghers, 1990a).

Licht (1989) has demonstrated that guppies can discriminate hungry and satiated predators while Coates (1980) showed that humbug dam-

selfish (*Dascyllus aruanus*) can distinguish predatory and non-predatory species.

Inspection behaviour may provide additional sensory information via the lateral line system. By swimming alongside a predator some assessment of its muscle tension and readiness to strike may be possible. This hypothesis remains untested though it is interesting to note that minnows approach a live pike much more closely if they are separated from it by a glass barrier.

2.3. Information transfer

Despite having excellent hearing, (von Frisch 1938, Hawkins 1986) there is no evidence that minnows or other fish use alarm calls to warn conspecifics of danger (Myrberg 1981; Magurran personal observation). Information about approaching predators is however transmitted using visual signals. This was demonstrated in an experiment in which *receiver* minnows behind a one-way-mirror were able to observe the reaction of *transmitter* minnows threatened by a stalking pike model (Magurran & Higham 1988). Although the *receiver* minnows could not see the pike model they stopped foraging and started hiding when the pike model came towards the feeding patch of the *transmitter* fish (Fig. 3). Thus, minnows can modify their own behaviour on the basis of information obtained from individuals which have seen a predator. It is not known whether transmitter fish attempt to manipulate the behaviour of individuals not yet aware of the predator's presence or whether receiver fish simply respond to behavioural cues. Since the two groups of fish benefit in such circumstances from merging in a tightly packed school it may be that both manipulation and passive information transfer are involved.

Smith & Smith (1989) also found intraspecific and interspecific information transfer about predators in two species of gobies, *Asterropteryx semipunctatus* and *Gnatholepis anjerensis*.

If a direct attack takes place, the speed of evasive tactics can be increased if individuals respond to the flight response of their colleagues rather than to the advance of the predator itself (Treherne & Foster 1981; Webb 1980; Potts 1984).

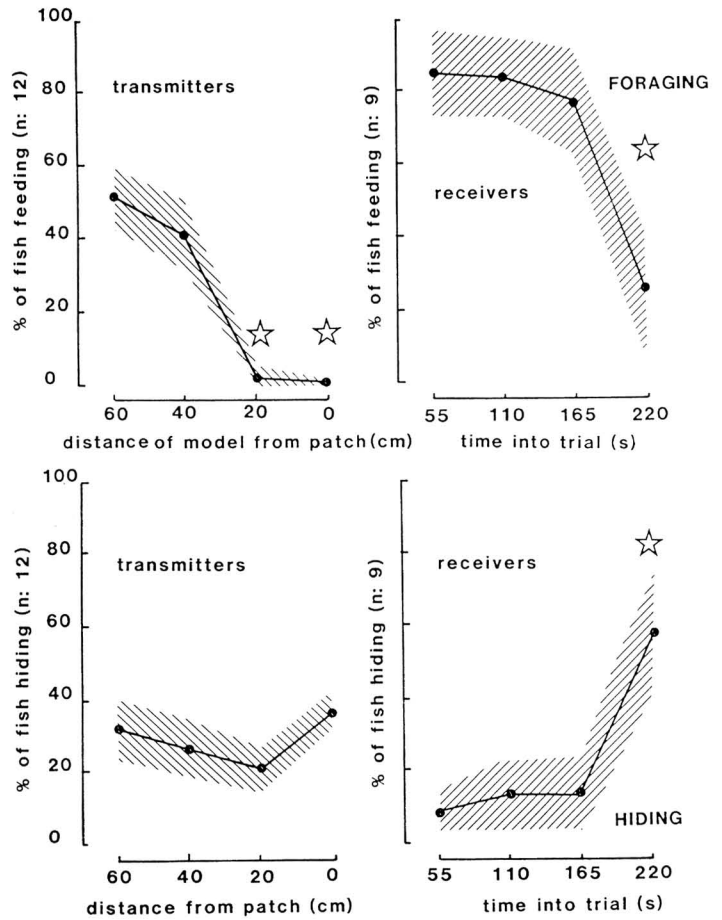


Fig. 3. Information transfer. y-axis: the percentage of minnows feeding (top) or hiding (bottom); x-axis: the distance of the pike model from the patch or (in the case of the receiver fish) the equivalent time into the trial. There were 12 replicates. Means and 95% confidence limits are given. Stars indicate those points that an LSR (least significant range test: Sokal & Rohlf 1981) has shown to be significantly different ($P < 0.05$) from the initial one.

2.4. Predator inhibition

Since the attack success of predators is increased if prey remain unaware of their presence (Webb 1982) prey fish could gain an advantage by 'signalling' to the predator. The predator may then choose to redirect its attack at another group of unenlightened fish. George (1960), who studied the anti-predator behaviour of mosquitofish, *Gambusia patruelis*, suggested that inspection behaviour, in conjunction with other behaviours such as surface swimming, deterred attacks by chain pickerel, *Esox niger*. Motta (1983) has described a number of cases of apparent mobbing by coral reef fish while Dominey (1983) has

argued that blue gill sunfish (*Lepomis macrochirus*) approach esocid predators in order to mob them.

The predator inhibition potential of inspection behaviour was tested in an experiment in which pike were able to view minnows through a one-way-mirror. When the pike's compartment was darkened the minnows were unaware of the pike's presence although the pike was able to observe the behaviour of its prey. In this situation the minnows foraged continuously and did not display inspection behaviour. By contrast, when the pike's compartment was illuminated the one-way-mirror functioned as clear glass and both predator and prey could see each other. Foraging

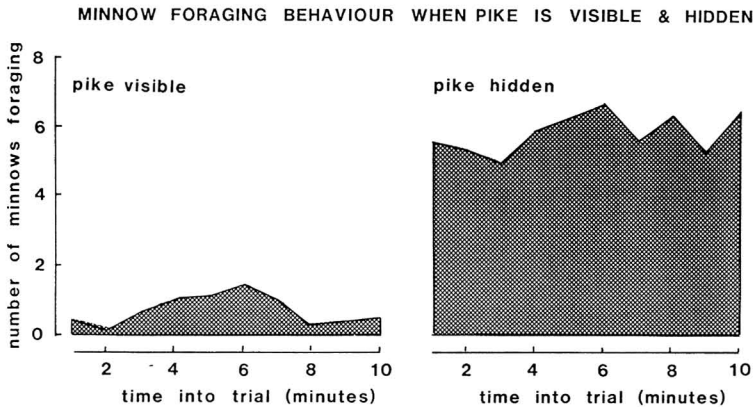


Fig. 4. Reduced foraging in the presence of a predator. Minnows (tested in schools of 10) significantly reduced ($F_{1,8} = 40.0$, $P < 0.001$, one-way ANOVA; Sokal & Rohlf 1981) their foraging level when they were able to view a live pike through a glass barrier.

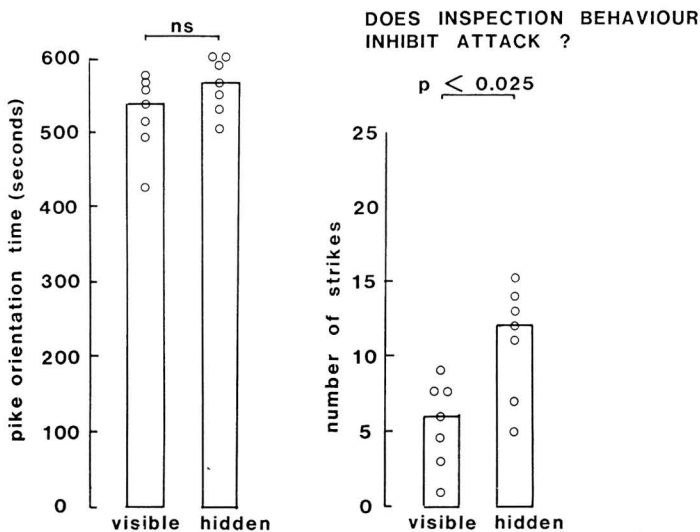


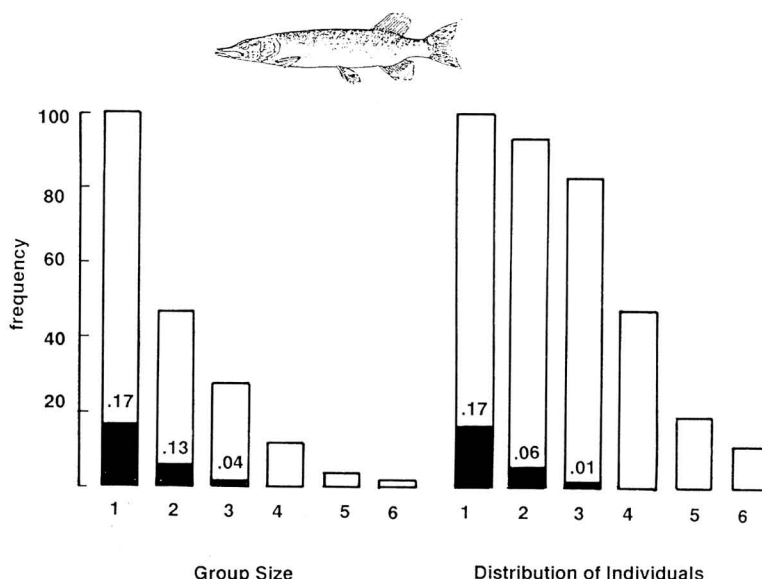
Fig. 5. Pike behaviour in the presence of inspecting minnows. Although pike did not significantly reduce the length of time (median number of seconds) that they spent orienting (Wilcoxon Matched Pairs Signed Ranks Test, $T=5$, $n=7$, $P > 0.05$) they did make fewer strikes ($T=1$, $n=7$, $P < 0.025$) at minnows which were inspecting them from the other side of a glass barricade. Seven pike were tested in the experiment.

diminished when the pike was visible (Fig. 4) and inspection commenced. The mean inspection rate was 2.6 ($SD=1.14$) inspections per minute. In both conditions the pike oriented towards the prey and attempted to capture them by striking at the glass (Fig. 5). Although pike orientation time was not affected by the change in minnow behaviour, the attack rate was reduced when the minnows switched from foraging to inspection behaviour (Fig. 5). This reduction in attack rate could have occurred either because there were fewer target prey (instead of feeding directly in front of the pike the minnows approached and retreated during inspection) or as a

direct consequence of the inspection behaviour itself. The experiment does not distinguish these two possibilities but does show that the attack behaviour of pike is mediated by the behavioural response of the prey.

These findings suggest that predator inhibition is a subsidiary function of inspection behaviour and that, at best, inspection behaviour will serve to limit rather than eliminate predatory attacks. However, even this small benefit may offer an important adaptive advantage in dangerous circumstances. Other studies have shown that approaching or displaying to a predator does not necessarily cause that predator to abandon its

Fig. 6. The frequency distributions of groups sizes (left) and individuals amongst groups (right) during inspection. Although most inspections were carried out by solitary minnows (left) individuals were as likely to inspect as members of a group of two as they were on their own (right). The shaded areas reflect the number of attacks directed at each group size. The figures superimposed on the graph list the probability of groups (left) being attacked and of individuals (right) being the victim of an attack.



attack. Caro (1986a,b) for instance concluded that the main function of stotting by adult and sub-adult Thomson's gazelles, *Gazella thomsoni*, is to inform the predator that it has been detected. This may lead the predator to redirect its attention towards less wary prey. The same function has been suggested for tail-flagging in white-tailed deer, *Odocoileus virginianus* (Bildstein 1983).

Figure 6 demonstrates that inspection can be a risky enterprise. In the majority of inspections a single minnow approached the predator and the probability of these solitary fish being 'attacked' by the predator was 0.17. When the dilution effect of larger group sizes is taken into account (Fig. 6) it becomes evident that individual fish are as likely to inspect the predator as members of a pair as they are as solitary fish. The benefits of inspecting with a companion are clear because the probability of being the victim of an attack drops to 0.06 when fish are in pairs (see Fig. 6). Pairs also approach a predator more closely and presumably gain greater information as a result (Milinski 1987). Milinski (1987, 1990) has shown how the reciprocal cooperation required in pairwise inspections can be achieved through the cooperative strategy of TIT FOR TAT. Lazarus & Metcalfe (1990) offer alternative ex-

planations to explain the occurrence of 'cooperation' during inspection. Given the advantages of inspecting in groups of two or more it is difficult to explain why solitary inspections occur at all. Yet solitary inspections are common, even when fish are directly confronted by an attacking predator (Magurran & Pitcher 1987). One possibility is that cooperation is difficult to achieve and that in the absence of a cooperative alliance, individuals are forced to inspect alone.

2.5. Evasion tactics

If all preliminary measures fail, and the predator escalates its attack, a range of defensive manoeuvres can be adopted. So long as all school members are of a similar size (Theodorakis 1989) and appearance (Ohguchi 1981, Landeau & Terborgh 1986) the confusion effect makes it difficult for the striking predator to select a single target. The behaviour of the prey fish is matched to the attack strategy of the predator. In minnows, for example, (see Fig. 7) inspection takes place primarily when a predator is present in the vicinity, but not actively hunting. Intermediate responses, including skittering, group jumps and fast avoids (Fig. 7) come into play when the pike

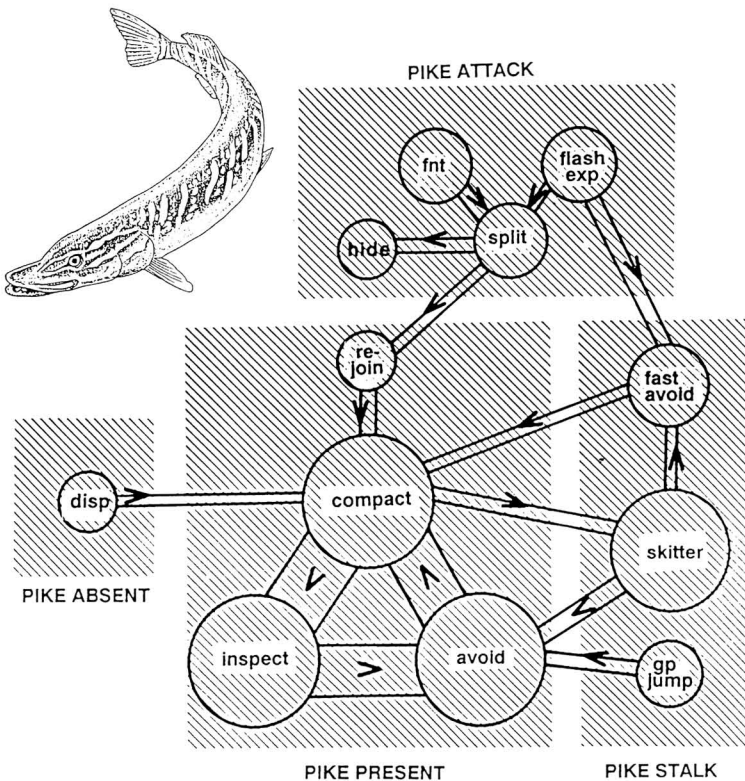


Fig. 7. Escape tactics of minnows. This figure summarises a sequence analysis of minnow predator evasion tactics during an attack by a live pike. Minnows were in schools of 20 and there were 12 replicates. The areas of the circles reflect the frequencies of the behaviours and the significant transitions ($P < 0.01$) are also shown. The behaviours are classified according to the stage of the attack sequence in which they are most likely to occur: pike absent; pike present but not actively hunting; pike stalking; and pike attack, involving a direct strike at the minnows. — Fnt = fountain; flash exp = flash expansion; gp jump = group jump; disp = dispersed. See Magurran & Pitcher (1987) for details.

is actively stalking. Tactics such as the fountain (when the school splits and reforms behind the predator) or flash expansion (when the school 'explodes' with individuals rapidly swimming in all directions) are generally reserved for the final stages of attack (Magurran & Pitcher 1987). These behaviours (fountain and flash expansion) are selected randomly (Fig. 7) making it difficult for the predator to predict the response of the prey. Such manoeuvres however often lead to the breakup of the school and isolated individuals are especially vulnerable to subsequent attacks by the predator (Magurran & Pitcher 1987, Parrish 1989).

The selfish herd effect (Hamilton 1973) implies that peripheral individuals are at a greater risk of capture than individuals at the centre of a school. In a recent examination of this idea Parrish (1989) has shown that, contrary to expectation, the central members of schools of 25 Atlantic silversides, *Menidia menidia*, suffered

more attacks from black seabass, *Centropomus striata*, than fish at the edge of the school. This arose because the predators attacked the dense school centre more frequently than its periphery. Central individuals were also disadvantaged when the school split during an attack.

3. Schooling as an inappropriate defence

Although schooling offers a valuable defence against many types of predator it is not necessarily the optimal tactic in all circumstances. Fishing boats with sophisticated sonar systems can easily locate and remove entire schools. Seals, whales and dolphins often herd schools of prey and schools can be particularly visible to hunting birds such as auks, gannets, terns and pelicans (Pitcher 1986). These predators tend to be large in relation to individual prey. An interesting case

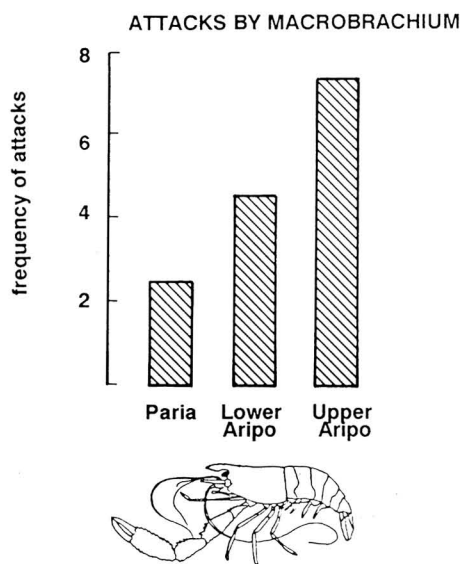


Fig. 8. The attack behaviour of a piscivorous prawn. The prawn, *Macrobrachium crenulatum*, directed significantly more attacks at guppies from the Lower and Upper Aripo rivers than it did at guppies from the Paria River in Trinidad ($F_{2,17} = 7.76$, $P < 0.01$). Attack rates over a 15 minute period are shown. There were six replicates per population. See Magurran & Seghers (1990a) for more details.

where the predator is proportionally smaller, and has a much simpler nervous system, than the birds and mammals mentioned above is the freshwater prawn *Macrobrachium crenulatum*. This prawn is abundant in a number of Trinidadian streams, especially those draining the northern slopes of the Northern Range mountains, and appears to be an important predator of guppies (Endler 1978, 1983, Magurran & Seghers 1990a). Guppies in rivers where *M. crenulatum* occurs in high densities, such as the Paria River, do not show a strong schooling response and are easily captured by fish predators, such as the pike cichlid, *Crenicichla alta*, (Seghers 1973, Liley & Seghers 1975). These Paria fish however exhibit well developed attack cone avoidance when inspecting *M. crenulatum* and are attacked less often than schooling fish (Fig. 8) (Magurran & Seghers 1990a). Since *M. crenulatum* use ol-

factory and tactile cues in addition to vision when locating prey, schooling may be disadvantageous. Furthermore, there is also the intriguing possibility that relatively unsophisticated predators, such as *M. crenulatum*, are not vulnerable to the confusion effect.

Unfortunately, there do not appear to be any rivers in Trinidad where guppies are exposed to heavy predation from both prawns and fish predators. A fascinating study would be possible in circumstances where fish are sympatric with predators which have very different hunting methods and where schooling is a good defence against one set of predators but a disadvantage when dealing with another set.

4. Developmental constraints

Predator avoidance is often well-developed from birth or hatching but there are many examples of cases where the ability to avoid predators improves. This may be linked directly to the maturation of the nervous system or to other morphological changes (Blaxter 1986, Huntingford 1986). For instance, Bailey & Yen (1983) showed that predation by the carnivorous marine copepod *Euchaeta elongata* on larvae of the Pacific hake, *Merluccius productus*, depends on larval swimming behaviour (Fig. 9). Predation rates are initially low because early-stage yolk-sac larvae are inactive swimmers and come in contact with few predators. As the larvae become more mobile the rate of encounter with the copepod predators increases. At this point their escape behaviour is poorly developed and mortality rates are high. Older larvae which have better developed swimming and evasion behaviour, are less prone to predation.

The improved escape ability of older individuals is not solely a result of increased strength or a more mature nervous system. Experience of being chased or attacked may lead to improved avoidance responses in subsequent encounters with predators (Dill 1974). For instance, Goodey & Liley (1986) found that the ability of guppies to survive in the presence of a piscivore was related to the cannibalistic attacks they had received as juveniles. The schooling behaviour and inspection behaviour of minnows is also en-

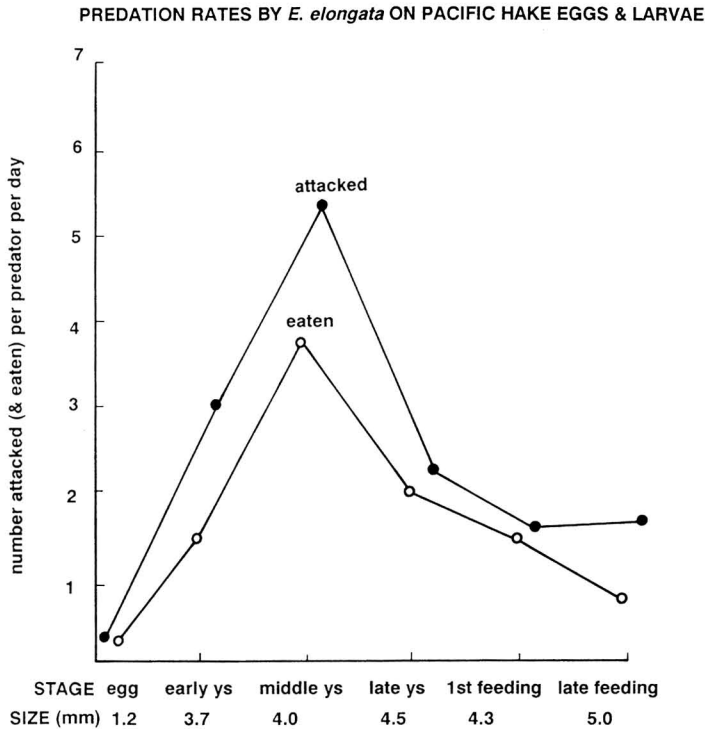


Fig. 9. Predation rates by the copepod, *Euchaeta elongata*, on eggs and larvae of the Pacific hake. Redrawn from Bailey & Yen (1983).

hanced as a consequence of early experience (Magurran 1990).

Changes which accompany development, for instance an increase in size, change in morphology, modification of behaviour or acquisition of defence skills, may protect individuals from one set of predators but lay them open to attack by another. For example, large guppies are difficult for Hart's rivulus, *Rivulus hartii*, to capture but are preferentially selected by another piscivore, the pike cichlid (Liley & Seghers 1975). Larvae of clupeoid fishes must run the gauntlet of attack by predatory invertebrates and even cannibalistic siblings (Blaxter & Hunter 1982). As adults, a different suite of predators is encountered. Up to 73% of adults in a stock of northern anchovies (*Engraulis mordax*) may be consumed annually by predators which include 29 species of marine birds and 27 species of fish.

Evidence that the selection pressures operating on adult and juvenile fish are discontinuous comes from observations on the schooling behaviour of newborn wild guppies (Magurran &

Seghers 1990c). Adult guppies from the Lower Aripo river in Trinidad suffer heavy predation from characin and cichlid predators (Seghers 1973; Liley & Seghers 1975) and form well developed schools. Newborn Lower Aripo guppies, like the adults, also form cohesive and polarised schools. Barrier waterfalls have prevented the upstream migration of the fish predators, and, as a consequence, adult guppies in the Upper Aripo portion of the river have a much lower schooling tendency than their downstream counterparts (Seghers 1974, Breden et al. 1987). However, newborn Upper Aripo fish are excellent schoolers. It may be that juvenile schooling in both Upper and Lower Aripo guppies serves as a protection against cannibalism. In the Upper Aripo population schooling tendency diminishes as the fish increase in size.

Switching between anti-predator strategies during development may entail a short-term increase in vulnerability. Newly hatched minnows initially remain hidden under pebbles in the stream or lake bed (Magurran 1986b). Once the

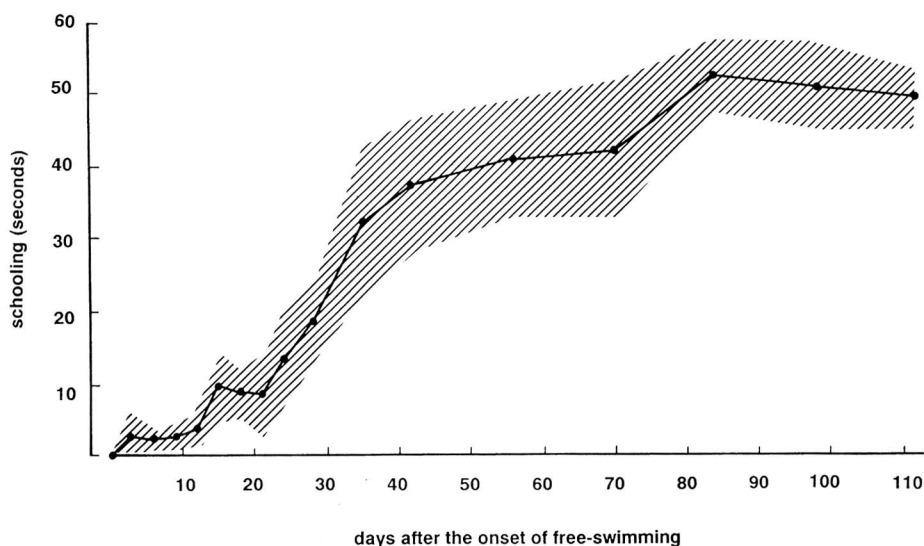


Fig. 10. Development of schooling behaviour in the European minnow. Fish were threatened by a small hand net and the schooling behaviour of focal individuals (expressed as number of seconds that the fish formed part of a cohesive school) scored for 60 seconds. 24 separate fish were scored on each recording day. Time (in days) is measured from the onset of free-swimming. 95% confidence limits are indicated. See Magurran (1986b).

yolk-sac is absorbed the larvae are forced to hunt for food and thus are more liable to predatory attack. Although schooling behaviour is present as soon as larvae become free-swimming it is not until three weeks have elapsed that the fish begin to adopt this behaviour when threatened and it is only after five weeks that the majority of fish school (Fig. 10) (Magurran 1986). There is some evidence that the onset of schooling is mediated by the development of the lateral line system (Cahn et al. 1968, Jorne-Safriel & Shaw 1966; Shaw 1970).

5. Genetic constraints and the inheritance of behaviour

Genetic constraints, including pleiotropy and epistasis (Rose et al. 1987, and see also Trexler 1990 for a fuller discussion), may interact with natural selection during evolution (Endler 1985, Loeschke 1987). Although this area is potentially of great importance, very little research on

the role of genetic constraints has been undertaken. The phylogenetic basis of behaviour is also frequently ignored. Nevertheless, past histories and previous predation regimes may have played an important role in moulding the behaviour of present day populations. A recent biochemical analysis (Carvalho, Shaw, Magurran & Seghers unpublished data) has, for instance, demonstrated striking genetic variation among Trinidad guppy populations with some genetic identities falling below the value normally expected for conspecific populations of fish ($I < 0.90$, Ferguson 1980). This genetic variation has almost certainly arisen as a consequence of divergent ancestry and may explain why certain populations exhibit considerable behavioural divergence, even when ecological conditions are similar.

There is good evidence that inheritance plays an important role in determining the type of predator evasion behaviour employed (Magurran 1990). For example, both guppies (Seghers 1974) and sticklebacks, *Gasterosteus aculeatus* (Giles

1984) exhibit anti-predator behaviour even when raised without exposure to predators or other threatening situations. The observation that there are quantitative (and heritable) differences in the anti-predator responses of different populations within a given species (including guppies (Seghers 1973, 1974) minnows (Magurran 1990) and sticklebacks (Giles & Huntingford 1984)) underlines the fact that the tendency to school will be influenced by the genetic factors.

An additional complication arises from the finding that the interaction between inheritance and experience can vary between populations. Magurran (1990) found that laboratory-reared minnows, derived from a population sympatric with pike, increased their anti-predator response (in particular their inspection behaviour) following exposure to a stalking model pike. Minnows taken from a population where pike are absent, raised under identical conditions and given the same experience, also adjusted their behaviour as a consequence of early experience, but to a lesser extent. Population variation in the predisposition to respond to early experience similarly occurs in three-spined sticklebacks. Tulley & Huntingford (1987) showed that normal fathering leads to a greater enhancement of the escape response in fish from populations that are exposed to high levels of predation in the wild. This phenotypic plasticity (Via 1987) is adaptive as it facilitates the fine-tuning of the anti-predator response to meet local conditions.

6. Behavioural tradeoffs

The time and energy that fish and other animals devote to activities such as foraging, reproduction and territorial defence are often reduced when there is a severe risk of predation (Sih 1980, Milinski 1986, Power 1987, Helfman 1989). The exact nature of the tradeoff depends on the balance between risk of capture by the predator and the benefits derived from continuing the behaviour (Dill 1987, Sih 1987, Pitcher et al. 1988). Such tradeoffs can vary between populations (Fraser & Gilliam 1987). Most studies to date have investigated tradeoffs between predator defence and foraging, though there is also

recent research indicating that guppies exhibit risk-sensitive courtship behaviour when exposed to predators (Endler 1987, Magurran & Seghers 1990b). Sargent (1990) shows how stochastic dynamic programming can be used to explore the consequences of trading off conflicting demands such as foraging, predator avoidance and reproduction in different ways.

Helfman (1989) has demonstrated how prey fish adjust their anti-predator behaviour to match the level of risk. He terms this phenomenon 'threat-sensitivity' and shows that a greater avoidance response will be observed when predators are larger, approach more closely or exhibit more threatening behaviour. Other activities, such as intraspecific competition, will occur most frequently when the risk of attack by a predator is small.

Many species of fish are adept at switching between polarised schools and loosely organised (even competitive) aggregations. Magurran & Bendelow (1990) found that white cloud mountain minnows, *Tanichthys albonubes*, form well developed schools when they first encounter an unfamiliar environment. These schools however rapidly break up when males begin to display and defend the clumps of weeds that are used as spawning sites. Morgan (1988b) showed that aggressive interactions amongst bluntnose minnows, *Pimephales notatus*, increased as hunger levels increased but decreased in the presence of a predator. Such flexibility is an important asset in a situation where there is a variable risk of predation and where the benefits of predator defence must be weighed against other needs. It is clear evidence for threat sensitivity (Helfman 1989) and shows that individual fish are skilled at constantly reassessing their environment and adjusting their behaviour accordingly.

7. Future prospects

Optimality theory has tended to lead behavioural ecologists to view the genome as a blank sheet on which natural selection writes the optimal solution for a particular problem. Yet there are many reasons why an 'optimal response' may not be observed when episodes of an individual's life

are studied in isolation. Each behaviour, such as schooling as a means of predator defence, cannot operate independently from other activities. Fitness depends not just on successful courtship, or adequate food finding or on skillful predator defence, but on a combination of these and other needs. The ability to perform a given behaviour or to opt for a particular tactic is a product of both inheritance and experience and not all members of a species will be equally equipped to employ every behaviour. Selection pressures are not continuous through space, time, or even the duration of an individual's life.

Dill (1987) has predicted that behavioural tradeoffs, particularly in the context of predation risk, will receive further attention from aquatic ecologists. In addition, he has pinpointed behavioural flexibility (where animals adjust their behaviour to changing conditions) and decision making, as other expanding areas of study. This review has demonstrated why these themes should play a major role in any analysis of anti-predator behaviour. Other topics that are likely to be extensively studied include the effects of developmental and evolutionary constraints on behaviour. An allied area, which has received little attention to date, is genetic architecture and its consequences for the inheritance and evolution of behaviour. The techniques of quantitative genetics need to be applied to a much wider range of species (particularly vertebrate species) and greater emphasis placed on behaviours with a clear functional significance. Closer consideration of the consequences of historical events could also prove invaluable. This approach might well consider the behavioural legacy of predation on previous generations, rather like the 'ghost of competition past' recognised by Connell (1980). Naturally occurring population differences in behaviour are an important asset in all these endeavours.

Dill (1987) warns about the dangers of predicting significant developments in behavioural ecology. It seems clear however that the functional and evolutionary approach, which is increasingly being adopted in investigations of anti-predator behaviour, will greatly enhance our understanding of the behaviour patterns we observe in the natural world.

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