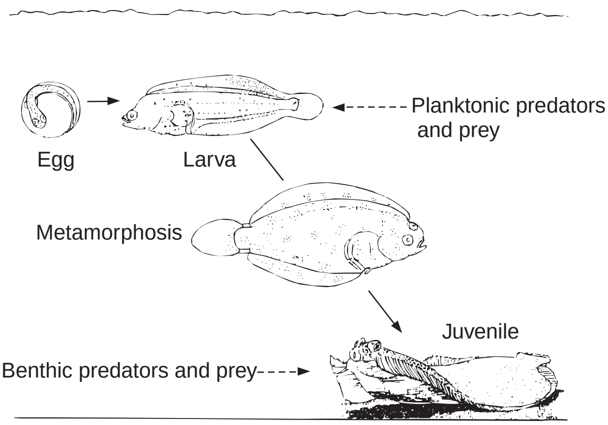

Figure 9 Life history of the plaice with a planktonic larva and bottom-living (benthic) juvenile and adult. (Reproduced with permission from Bone *et al.*, 1999.)

suggested that the production of large numbers of young provides an additional food supply, the faster growers cannibalizing their slower-growing siblings.

See also

Fish Larvae. Fish Predation and Mortality.

Further Reading

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FISH SCHOOLING

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Introduction

Wheeling and turning in synchrony, flashing iridescent silver flanks, fish in a school have been a source of inspiration to poets and naturalists since ancient times. But, to understand schooling behavior, scientists ask 'How?' and 'Why?' questions to address both form and function (**Table 1**). Schooling ('form'), is brought about by an integrated physiological system of muscles, nerves, and senses ('how?') that has evolved under natural selection ('why?') because of benefits to survival ('function'). This article surveys our knowledge of the physiological mechanisms that cause schooling behavior, the behavioral and ecological rules that govern its evolution, the implications of schooling for scale, pattern, and process in the ocean, and the impacts of schooling on human fisheries.

Definitions

Most of the 24 000 known species of bony fish form cohesive social groups known as 'shoals' at some stage of their life history. Social groups occur because animals choose to stay with their own kind to gain individual benefit, whereas grouping for extrinsic reasons such as food, shelter from water currents or oxygen availability is known as aggregation. The term 'school' is restricted to coordinated swimming groups, so schooling is one of the behaviors shown by fish in a shoal; there can be others, such as feeding or mating (**Figure 1**). The tendency to form shoals or schools varies both between and within species, depending on their ecological niche and motivational state respectively. For example, many species of fish shoal for part of the time (e.g. mullet, squirrelfish, cod), while other species adapted to fast swimming (e.g. mackerel, tuna, saithe), or rapid maneuvering around a reef (barracuda, seabream), generally school most of the time. Some species (e.g. minnows and perch in fresh water, herring and snappers in the sea) opportunistically switch between shoaling and schooling to maximize survival,

Table 1 Matrix, pioneered by the Nobel Laureate ethologist Niko Tinbergen, showing 'How?' and 'Why?' questions in relation to form and function in fish schooling behavior

	How?	*Why?*
Form	Swimming hardware, sensory inputs, neural decision mechanisms	Evolutionary shaping of schooling hardware (linked to below)
Function	Finding and eating food; hiding from or escaping from a predator	Trade-offs between schooling costs and benefits to evolutionary fitness (linked to above)

or – strictly speaking – evolutionary fitness. At one time, species that schooled a lot were termed 'obligate' schoolers while those that schooled part-time were termed 'facultative' schoolers, but these terms have been replaced by 'frequent' and 'occasional' schoolers.

The School Rules and School Size

In contrast to early work on fish shoals that emphasized the collective actions of the whole group as though they were some kind of super-individual, insight into fish shoaling and schooling has come from examining the costs and benefits to individuals. Constantly, from second to second, shoaling fish take decisions to join, leave, or stay with the group (JLS). This provides a flexible 'online' response to the environment, which can change rapidly, for example when a food source is found or when a potential predator appears. Because of differences among individuals in opportunity and motivation, the tensions and conflicts underlying such a system are evident even in the most impressive phalanx of mackerel, which will break ranks to feed, or among schooling herring, which segregate by hunger level.

The size of the group is one important elective adjustment that is made to adjust individual payoffs in a shifting regime. But adjustment of shoal size to the prevailing food/predation regime is possible only if fish shoals both split and meet so that they have the opportunity to merge and exchange

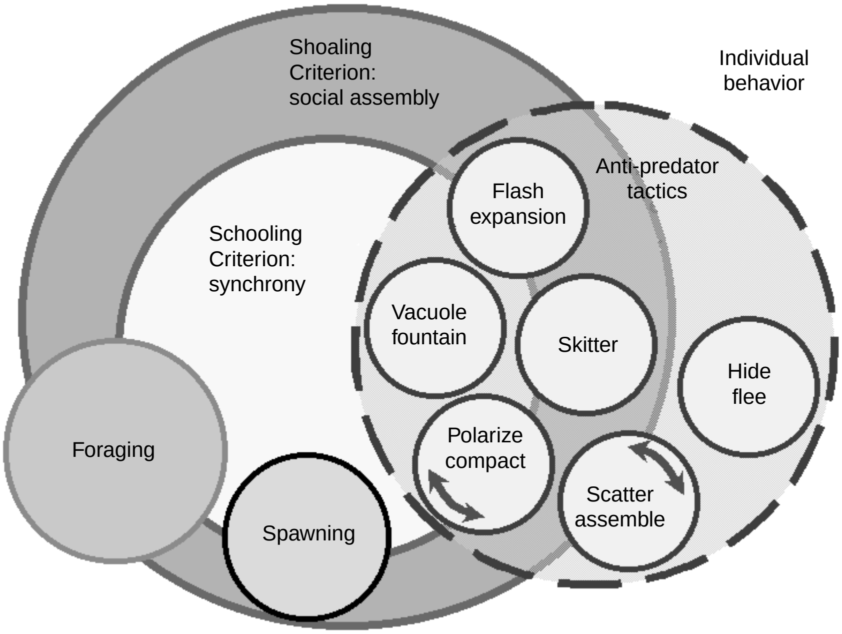


Figure 1 Fish schooling and shoaling behavior (Venn diagram). Criteria for these two behaviors are indicated. Three other behavior categories are superimposed: feeding, spawning and anti-predator behavior; some examples of behaviors in the latter category are also shown. (Concept from Pitcher, 1993.)

members. Such shoal meetings, long observed in laboratory experiments, have recently been measured in the wild.

Are there rules that govern how fish pack in a school? Mathematicians can prove that the maximum packing of spheres in 3-D is in layers of offset hexagons, but fish do not do this. As fish join a group, they adopt a roughly equal distance from neighbors. Hence three fish form a triangle, four a pyramid and so on. Experiments with minnows, herring, saithe, and cod show that schools are like roughly stacked pyramids, about 15% less dense than the maximum. However, fish in schools do not behave like rigid crystal lattices, and the most useful finding from this work is that fish in a school tend to occupy a water volume of approximately one body length cubed, with neighbors about 0.7 of a body length apart. This value, recently validated using sonar on wild herring schools, shifts with swimming speed and timidity, but generally does not change with school size.

There are many reports that fish of similar size shoal together. For example, wild mackerel and herring choose school neighbors within a 15% band of their own length. Recent observations from the wild support laboratory experiments showing that this choice is not merely because smaller fish cruise more slowly and fall behind, but because competition for food and coordinated escape from predators favor size-sorting.

Senses and Schooling

Vision is the predominant sense used in schooling, but swimming fish also use the lateral line, the ‘distant touch’ sense. Olfaction and hearing are more important in assembly of shoals, or their break-up when food is detected.

Experiments show that schooling fish use vision to join other fish, mirror images of themselves, or fish behind transparent barriers, although their behavior shows that they can distinguish these different kinds of visual images from the real thing – perhaps this is where other senses become important, and perception is mediated through central integration by the brain. In fact, many schooling fish species have visual display signals such as colored spots, longitudinal stripes along the flank, or even spots on fins or gill covers that can be raised or lowered at will. These schooling signals act as visual cues for JLS decisions.

In herring, which have a particularly well-developed lateral line system over the head, velocity changes are communicated by very rapid pressure waves from the accelerations of neighbors. Surgically cut lateral line nerves hamper minnows in their coordinated escape maneuvers from predatory pike. The roles of vision and lateral line were teased out in experiments where saithe were temporarily blinded with opaque blinkers. Blind fish were able to join and swim with a school when repeatedly passed by intact saithe swimming in a large annular tank. Saithe with cut lateral line nerves were also able to do this. The two sensory-deprived types of fish schooled differently; blind fish kept more precise distances to neighbors, while fish with no lateral line kept neighbors at 90°, where they could better detect velocity changes. Not surprisingly, cutting the lateral lines of blind saithe eliminated schooling. The work shows that the lateral line sense is critical to synchronization of acceleration and turning in schools.

Food, Predators, and Schooling

Predators and food are the keys to understanding what shoaling is for and why it has evolved. The functions of shoaling in foraging and in providing anti-predator advantage have been investigated with carefully controlled and replicated experiments in large laboratory aquaria, and in recent years these investigations have been extended to the wild using high resolution sonar or scuba diving.

One of the advantages of foraging in a larger group is that randomly located food items are located more rapidly. Moreover, in larger groups, fish spend more time feeding and are less timid. Furthermore, when the amount or quality of food changes, shoaling fish switch to a better location more efficiently in larger groups. All these effects are achieved by modifying JLS decisions after subtle observation of the behavior of other fish. If some individuals succeed in finding food, other fish copy their moves, including sampling new feeding patches. The benefits of foraging in a shoal get larger as the numbers in the group increase to a few dozen, but improvement becomes progressively less as shoal numbers get larger and the law of diminishing returns comes into play. Costs of competition for food get larger as shoal size increases, and such intra-school competition seems to help segregate size classes of fish in the wild, since large fish win in contests for food items.

As well as switching among food patches, some species of shoaling fish like clupeids and some cichlids can actually switch feeding methods. For example, schooling herring can filter-feed using their gill rakers, swimming with mouths and gills open, or alternatively, can bite at larger food organisms. The switch between the two feeding methods occurs when the density of small food is high enough to sustain the faster swimming speed and energy consumption of filter feeding. When food density is close to the threshold, individuals make different estimates of the switch point so both types of feeding can occur in a school.

Often used in ecology, the theory of the 'ideal free distribution' predicts that individuals will distribute themselves among food patches in proportion to the reward encountered, so that all individuals have the same average intake rate. But alternative strategies in competition for food or differences in perceived predation risk affect the JLS decisions of individual fish and result in distributions that differ from this theory. More modern theory, supported by experiments, is based on trade-offs between predation risk and food reward.

Although food is vital to survival and breeding, and hence is an important component of fitness, avoiding being eaten is even more critical: the Life/Dinner Principle. Shoaling fish try to reduce the success of predator attack through tactics of avoidance, dilution, abatement, detection, dodging, mitigation, confusion, inhibition, inspection, and anticipation. Predation events occur rapidly, and are not very frequent for a human observer. In the wild they are hard to observe at all, whereas in the laboratory, there is a worry about introducing artifacts. Fortunately, many laboratory and field experiments investigating anti-predator functions in fish shoals have successfully employed protocols in which dummy predators approach test shoals. This protocol has the advantage of being replicable, and most shoal responses appear realistic in the early stages of a simulated attack.

Fish shoals tend to have an oblate spheroid shape that may reduce their envelope of visibility but, unlike the situation in air, there is only a minor advantage of shoaling as a defense against detection by a searching underwater predator. The scattering of light under water means that the distance at which a shoal may be detected is almost the same as for an individual fish. And in fact, detection is not so important, because fish in shoals are often accompanied closely by many of their predators, like big game herds in the Serengeti.

Apparently, fish in a group have a clear advantage over singletons through being less likely to be the one selected as a victim by an attacking predator. Logically, this benefit should be in proportion to the reciprocal of group size, the 'attack dilution effect'. But to check if dilution may cause shoaling to evolve, we must compare the risk to individual fish that adopt solitary or grouping strategies. In both cases, the joint probability of being in the group attacked by a predator, and of being the victim picked out of the group is identical (because the dilution probability within groups is exactly balanced by the attack probability among groups). However, a singleton joining a larger group decreases its risk. But having joined, individuals in the now enlarged group bear an increased risk, but have no way of reducing it by leaving – unless they exclude newcomers, a behavior not observed in fish schools. This is termed the 'attack abatement' effect, and is an example of an evolutionarily stable strategy (ESS).

In larger shoals, experiments show vigilance to be a major anti-predator advantage. Fish detect a threat earlier because of the many eyes in the group. It is important to observe fish closely in these experiments; recording alarm or flight is not sufficient, because fish may choose to stay feeding when a predator approaches as they are less nervous, or more confident of successful escape. In experiments with minnows, counting two subtle behaviors were the key: 'skitters' are rapid alarm signals, and 'inspections' are approaches towards the predator (discussed in more detail below). In larger shoals, both of these behaviors were more frequent earlier in a predator attack. In another experiment, a clever protocol demonstrated a faster reaction of neon tetras to a randomly located light flash.

In a wide range of fish shoals, experiments have generally shown a declining success of attacks by fish, cephalopod, mammal, and bird predators as shoal size increases. Moreover, fish separated from the shoal are more likely to be eaten, and predators may learn not to attack larger groups. All of these phenomena derive from a large repertoire of anti-predator tactics performed by fish in shoals ranging from sandlance to tuna. Fish select tactics from the repertoire partly at random, to counteract predator learning, and partly according to the likelihood of an attack. Many fish can tell by olfaction when predators are nearby, and can pick up subtle visual cues as to their state of attack readiness and hunger.

Compaction, where fish reduce distance to neighbors and become more polarized, allows fish to take advantage of coordinated escape tactics. Compact groups may glide slowly out of predator range (**Figure 1**), taking advantage of cover provided by weed or rock. A 'pseudopodium' of fish may join two sub-schools like a thin neck along which individual fish may travel, so that one potential target next to the predator shrinks while the other enlarges surreptitiously. In the 'fountain maneuver' fish initially flee in front of the predator, turn, pass alongside in the opposite direction, and then turn again to reassemble behind the predator. This serves to relocate a target out of attack range. Tightly packed balls of fish, seen in response to severe attacks by cetacean, bird, and fish predators on schools, inhibit or deflect attack, like the 'silver wall' caused by highly polarized schooling fish suddenly changing direction in unison. And there are a few reports of 'mobbing' in fish; inhibition of predator attack by physically pushing it away. Information about approaching danger travels rapidly across compact polarized schools, termed the 'Trafalgar effect' because of its resemblance to the flag signaling system invented early in the nineteenth century by the British Navy. Impressively, the message can move among schooling fish two to seven times faster than the approach speed of the predator.

Predators attacking prey, like humans operating radar screens, become less accurate as the number of potential targets increases. This is known as the 'confusion effect', and probably results from overloading the peripheral visual analysis channels of the brain (the midbrain optic tectum in fishes). Confusion could also be cognitive, as in a dog unable to choose between several juicy bones. Two tactics in the anti-predator repertoire of shoaling appear to be designed specifically to exploit predator confusion. First, 'skittering' (see above) may confuse predators attempting to lock-on to a target. Secondly, 'flash expansion' (**Figure 1**) occurs when fish in a polarized compact school rapidly accelerate away from the center, like an exploding grenade (a behavior brought about by the 'Mauthner system' of rapid nerve fibers). One disadvantage of flash expansion is being found alone by the predator afterwards, and so there is a premium on rapid reassembly, or hiding if refuges are nearby.

One of the most interesting discoveries among anti-predator tactics in fish shoal is 'predator inspection' behavior. 'Inspecting' fish leave the shoal and swim towards an approaching predator, halt for a moment and then return to the group. It is clear that inspection carries a real risk of being eaten, and inspectors behave to try to minimize this risk. How can such evidently dangerous behavior have evolved? Clever experiments, where fish can see school fellows but not an attacking predator, have demonstrated transfer of information from inspecting fish about an impending attack. Strikes by pike on minnows are anticipated after inspectors return to a shoal, and predators may be inhibited in their attack by seeing inspections. (A counter-intuitive suggestion that inspection invites attack, giving prey an advantage in controlling how attack occurs, has received no experimental support.) The repetition rate of inspections may code for the degree of danger. Moreover, fish perform inspections in larger groups as risk increases, so dilution of danger during inspection may be a way of mitigating the costs. It seems that the sheer advantages of information about the predator derived from inspection may outweigh the risk of getting eaten. Under this theory, inspection behavior has evolved because, although noninspectors will get some of the benefit through transfer of information concerning risk, fish that inspect can act on more accurate information about the predator.

An alternative view states that, although inspectors are more likely to die than noninspectors, the behavior has evolved because genes coding for inspection increase in the population through kinship or in some other way. If fish in shoals were genetically related (see below), inspection behavior could evolve to save kin in the shoal. A second way in which altruistic inspection behavior might evolve is revealed by game theory. 'Tit-for-tat' is helping another at cost to oneself immediately after receiving benefit from the same move by the other player. A series of elegant experiments involving mirrors and companion inspectors revealed that tit-for-tat may be implicated in the evolution of inspection behavior. But, at present, it is not clear which of the two competing theories for the evolution of inspection behavior is correct.

Recent studies into the ways in which fish trade-off feeding and predator risk have led to productive insights of the evolution of shoaling behavior. For example, shoaling fish foraging on patches which were either safe or where predators might appear, altered feeding in almost perfect proportion to risk and food: a 'risk balancing' trade-off (see **Figure 2**). Elegant experiments demonstrate that hunger

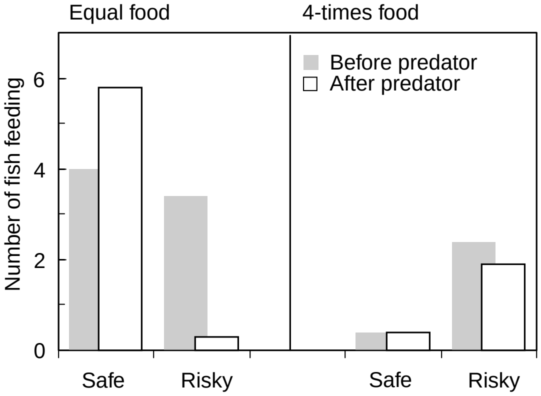


Figure 2 Results of an experiment demonstrating a risk balancing trade-off between food and risk of predation in schooling minnows offered food on two feeding patches. Number of fish feeding were counted before and after fish saw a diving bird at the risky feeding patch. When four times as much food was present, the fish accepted the risk and fed. (Data from Pitcher *et al.* 1988.)

increases risky behavior. Even more complex sets of trade-offs occur in the wild, and involve motivational factors such as mating, hunger, food availability, competition, and perceived predator risk. As yet, few such complex circumstances have been investigated with experiments that test theoretical expectations.

Successful predators on fish schools employ a number of clever devices to counteract the schooling prey's defenses. For example, predators may attack shoals from below at dawn and dusk, when the prey are silhouetted and dim light gives predators' eyes an advantage. This 'twilight hypothesis' was confirmed in experiments with a dummy pike and shoaling minnows. Nevertheless, minnows can compensate using inspection behavior to shift feeding to a safer location.

Many predators on shoaling fish are considerably larger than their fish prey and one common anti-schooling technique employed by tuna, sawfish, bluefish, marlin, swordfish, thresher sharks, and dolphins is to disrupt a prey school and split off individuals that may subsequently be pursued without confusion costs. Central positions in the school might be safer, simply because they are not on the edge where predators arrive first. Nevertheless, specialized predators like jacks attack the centre of schools at high velocity. Stripe-and-patch patterns on bird and cetacean bodies and flippers may serve to disrupt schools through the 'optomotor response'. One ingenious experiment showed that rotating striped penguin models depolarized anchovy schools. Some predators herd their prey in one way or another. For example, humpback whales blow bubble rings and rise to the surface to engulf entire schools of capelin. Other fish shoal predators themselves school and hunt in packs. For example, schools of sailfish may herd prey in rings formed by their large raised dorsal fins. Barracuda, jacks, tuna, yellowtail, and perch are species that hunt in schools.

A Genetic Basis for Behavior in Fish Schools

What are the origins of JLS dynamics and the impressive switches among the spectrum of behaviors seen in individual fish that shoal? Do these adaptive behaviors have a genetic basis or are they learned in some way from experiences in early life? Either of these mechanisms can produce adult animals with adaptive behavior.

This question has been addressed in elegant experiments that raised groups of fish from the egg. Minnows were collected from two locations in Britain; one a river in England where minnows lived with pike, the other a river in Wales where pike were absent. Previously, it had been found that fish from the wild population living with pike had more effective anti-predator behavior. The fish were spawned in aquaria, and the eggs from each location were divided into two batches. From each location, one batch experienced a test with a model pike at 3 months old, while the other batch had a sham test. When adult at 2 years old, all four batches of minnows were tested with model pike. Adult minnows grown from the population that lived with pike, and had seen the pike model when juvenile, performed better than individuals which had not seen the pike, suggesting that they had learned from their early encounter. Conversely, minnows from the non-pike population were not able to learn from early experience. These results suggest that both genes and learning are important, but that there is a genetic basis to what can be learned, an example of the 'innate schoolmistress' – the genetic programming of animals' learning agenda.

Some Other Functions of Schooling

A number of other advantages of shoaling have been documented. For example, shoals of sticklebacks have a lower per-individual incidence of ectoparasites and the fish formed larger shoals in the presence of the ectoparasite.

Fish swimming in schools may make better estimates of the right direction in which to swim. For example, directional changes appropriate to either good or poor conditions of food, salinity, temperature or oxygen, spread through schools of migrating herring. A wave of turns passes through the school to fish that have yet to encounter the new good or bad conditions themselves: a behavior termed 'synchrokinesis'.

Swimming in a school may bring energy saving through some sort of hydrodynamic advantage involving the chain of rotating vortices set up by fishes' tails (these vortices are the main mechanism producing thrust in fish swimming.) Experiments with saithe, cod, and herring produced no support for hydrodynamics when quantitative predictions from theory were tested using tens of thousands of frames of film. And there is a more serious objection to the theory. Since only fish behind the leaders get energy savings, leaders would choose to fall back to get it, and so we would see continuous jostling for position, something that is not observed. Many experiments report lower oxygen consumption in larger shoals, but on its own this is not sufficient to prove hydrodynamic advantage, because fish are calmer in larger groups. However, recent experiments reporting energy saving from slower tail beats in fish at the rear of a school lend support to the hydrodynamic theory of fish schools.

Schooling, Fisheries and Pattern in the Ocean

The application of knowledge about fish shoaling lies in its impact on human fisheries. More than 60% of the world's fisheries are for species that are frequent schoolers, and nearly all species shoal to some extent. Modern commercial fishing gear, such as mid-water trawls and mechanized purse seines, have been designed to exploit schooling fish; entire schools of tuna, mackerel, or herring may be caught by a purse seine, which may be over a kilometer in diameter. Purse seine technology has itself replaced a clever device for catching schools of giant bluefin tuna that was in use in the Mediterranean since the time of the ancient Greeks. The 'tonnare' fishery consists of kilometers of long guide fences leading to traps constructed from sisal rope, representing a preindustrial technological solution to catching schools of giant 3 m long fish migrating along the coastline at 20 knots. Today there is only one 'tonnare' fishery left, operated annually for tourists in Sicily.

The most important applied aspects of shoaling behavior are population collapse and range reduction. In both of these phenomena, shoaling can cause spatial problems that are hard to correct by intervention from management. The behavioral adaptations of pelagic fish in feeding, spawning, migration, and schooling are driven by the opportunity to exploit transient high levels of planktonic production: the highest plankton production levels are intrinsically patchy. Planktivorous fish constantly move in groups to minimize predation risk and get foraging advantages, to seek out these ephemeral food sources. This is an oceanographic perspective on why schooling and JLS dynamics have evolved, fitting pelagic fishes to their niche by determining their ocean distribution.

Unfortunately, there is a mismatch between human fisheries and this behavior. On an annual timescale, the mismatch generates volatility, range, and stock collapse. On a timescale of decades, the human response to uncertainty in pelagic fisheries has been to develop ever more effective levels of fish catching technology (see **Figure 3**).

When fish populations collapse from natural changes in habitat, from unsustainable levels of human harvest, or from an unholy alliance of both of these factors, two linked phenomena generally occur; stock collapse and range collapse. Stock collapse is defined as a rapid reduction in stock abundance, and is distinguished from short-term

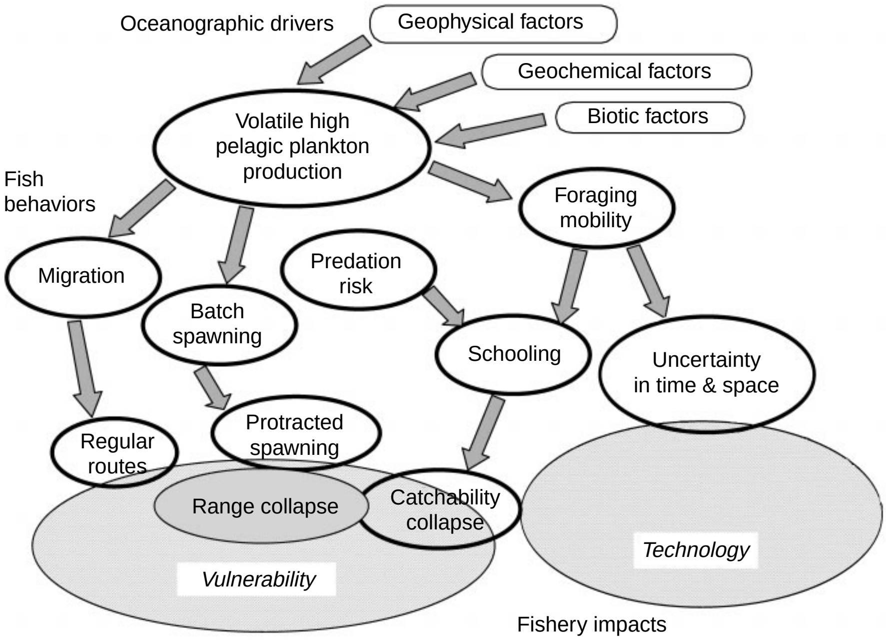


Figure 3 Diagram showing the factors that may have brought about the evolution of fish schooling, and the mismatch of these factors with human fisheries. For further details, see text. (Redrawn from Pitcher 1995.)

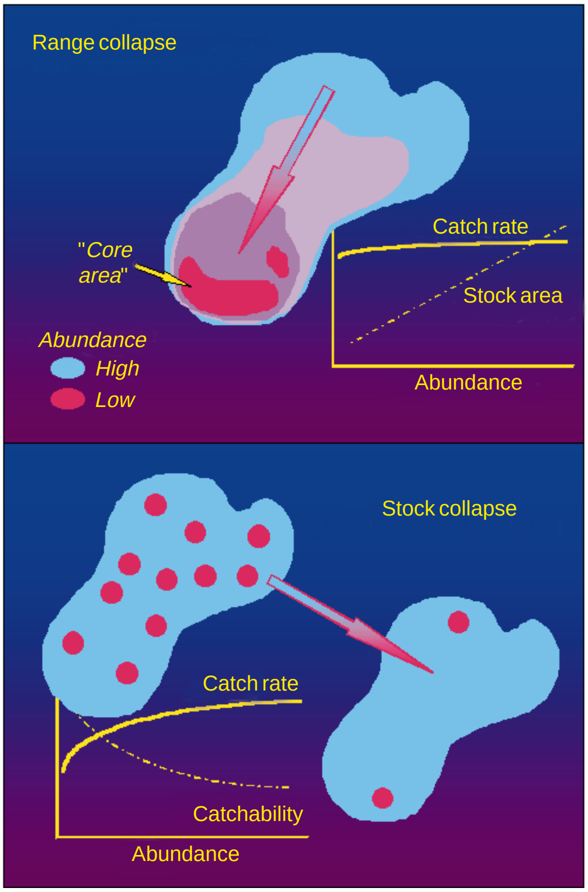


Figure 4 Diagrams illustrating range (top) and stock (lower) collapse in schooling fishes. Inset graphs plot catch-per-unit-effort (= catch rate), population range, and fish catchability against fish population abundance.

natural fluctuations. Range collapse is a progressive reduction in spatial range. Although some seek environmental correlates of collapse, sufficiently powerful mechanisms driving stock collapse can be generated by the impact of harvest on fish population dynamics and fish behavior. Range collapse makes a stock collapse more serious because the concentration of remaining fish into a reducing area makes fish easier to locate and concentrates the fishing power of a fleet built with profits from a previous era of higher abundance (see **Figure 4**).

Catchability is the proportionality coefficient between fishing effort and population abundance. In a collapse event, schools stay the same size as before and so the catch rate within a school stays high. Also, schools, rather than individual fish, are located by fishing vessels. These two factors mean that catchability increases as range decreases, until the last school is caught. For schooling fish, the catch rate, conventionally used to predict abundance, stays constant as population abundance declines, bring about a rapid collapse (see **Figure 5**). Acting together, these forces can cause a great reduction in abundance and this is thought to be the mechanism behind disastrous collapses in many fisheries, such as the Monterey sardine in the 1950s, the NE Atlantic herring in the 1970s, and the Newfoundland cod in the 1980s, all of which had profound economic consequences.

In one of the most powerful theories underlying range collapse, known as the 'basin' model, spatial collapse is driven by environmental forces through competition among fish for optimal habitat. An alternative model is based on the shoaling behavior of fish where leaving and joining behavior adjusts school size to local conditions (see **Figure 6**). Schools need to be proximate for such meetings. When a population is greatly reduced by fishing, schools that do not have encounters with others move faster until they do, and this process concentrates schools in an area of ocean. The process proceeds until the spatial collapse is complete. In practice, both basin and school size adjustment mechanisms may operate. The size-adjustment hypothesis raises the prospect of obtaining cheap diagnostics of impending collapse by monitoring the behavioral and spatial parameters of shoaling fish.

The model that best describes schooling over a fish's life history is analogous to that of the metapopulation, where groups comprised of essentially random individuals assemble for periods of their life history and then split up. School formation and dissolution is on a more rapid timescale, occurring within each phase of the life history; termed 'metasociality'. A pelagic schooling species like herring is made up of meta-populations that assemble to breed on spawning grounds, are advected by ocean cur-

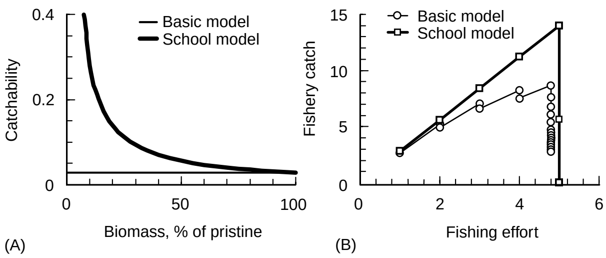


Figure 5 Graphs showing two alternative models of fisheries for schooling species subjected to severe depletion causing a collapse. 'Basic model' is the classic 'surplus production' model used in assessing fisheries; 'school model' takes account of school dynamics as described in the text. (A). Catchability plotted against stock biomass. 'Basic model' assumes constant fish catchability; in 'school model' catchability increases as biomass falls. (B). Simulated annual fishery catch plotted against fishing effort showing a rapid collapse in schooling fish. (Data from Pitcher 1995.)

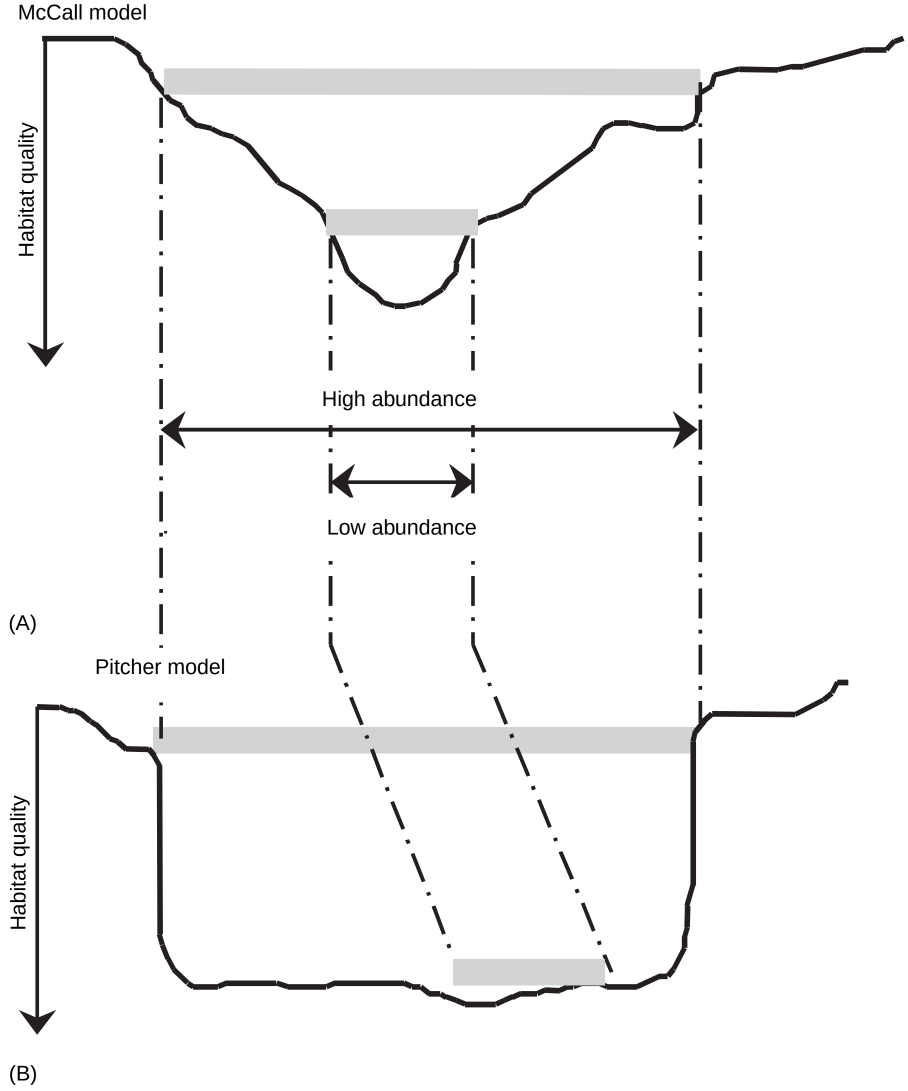


Figure 6 Diagrams illustrating two alternative models for range collapse in schooling fishes. Basins represent spatial distance in horizontal dimension, habitat quality (reversed) in vertical dimension. Thick shaded bars represent the fish population at high and low abundances. (A) Basin model proposed by Alex McCall, where the depleted population collapses to the best quality habitat as individual fish compete for resources. (B) School size adjustment model proposed by the author, where the depleted population collapses to a random location as schools maintain their size in relation to local conditions by packing in a mesocale pattern that allows exchange of members. (After Pitcher 1997.)

rents as larvae, and then, as juveniles and adults, adopt a dynamic schooling regime during their feeding migrations. Individuals join and leave schools according to their perception of an ever-changing mix of predator and feeding trade-offs. So at each stage and on each timescale, individuals are shuffled by the behaviors that have evolved to maximize fitness.

But, at each level, these processes are not totally random. Three types of ocean processes (upwellings, gyres, and fronts) act as retention zones for fish larvae and allow long-term persistence of ocean fish populations. Moreover, homing to the natal area is a widespread basic trait in bony fishes (the obvious examples such as salmon are but extreme cases). In herring, there is a genetic basis for spawning at a particular time of year and for homing to a general spawning area, but in both Atlantic and Pacific herring it is unclear how much homing there is to precise spawning localities. These have very important implications for fishery management, since locally based populations require more precautionary management to sustain local fisheries and preserve genetic diversity. Genetic studies have generally failed to show much evidence for local stocks, but many argue that local populations were wiped out long ago by inshore herring fisheries.

Evidence is emerging to support the idea of fidelity of fish to a shoal. Early work on freshwater perch and reef grunts in the wild suggested this, but experiments in many laboratories never proved consistent allegiance to particular schools. Recoveries of tagged tuna from fisheries did not support school fidelity either. However, recent work on yellowfin and bluefin tuna (and white sharks) in Hawaii and Australia using sophisticated archival and acoustic tags has demonstrated regular homing to very precise coastal locations after days and even months elsewhere. Here, it looks like schooling predators repeatedly cruise a huge range looking for food, while minimizing their own predation risk, so high school fidelity may be more a consequence of this behavior than any active choice of particular individuals to swim with, which is what would be required for fidelity to be regarded as a trait intrinsic to fish schools.

There is almost no evidence of genetic relatedness in fish schools. Isozymes and mitochondrial DNA among individual fish sampled have been sampled from the same schools in the wild several times, but no close genetic ties were found. In fresh water, minnows and sticklebacks in the same watershed often have closer genetic affinity, but there is no link to schools. The lack of kinship is not surprising theoretically as it would have to provide a major selective advantage to outweigh the benefits of having a flexible school size that can respond rapidly to local predator/food trade-offs through JLS decisions. This makes some unpublished work on anchovy and sardine schools sampled with purse seines at night in the Adriatic Sea even more intriguing. Fish were taken when two fishing vessels were about 5 km apart and had set their purse net within 20 minutes, so the same fish school could not have swum to the other vessel. Comparisons based on DNA fingerprinting showed that anchovies within each school were more closely related than between schools. This was not the case for sardines, perhaps reflecting the higher mobility and range adopted by this species.

The dynamics of schooling decisions of young herring on their spring feeding migration in Norwegian waters were studied with a very high resolution scanning sonar originally designed to detect small floating nonferrous mines. The machine could track and resolve individual herring in schools at 300 m range. Herring schools could be sampled using a precisely controlled mid-water trawl so that ages, stomach samples, and other fish swimming with the herring were measured. The findings were dramatic. Herring schools were found to be accompanied by a mix of predators, rather like game herds on the Serengeti. Cod and haddock swam with the herring, picking off prey from time to time, and causing minor changes to school structure, but not dispersal of the school. Saithe swept in to attack as a fast-moving school, causing the herring to bring their last line of defense into play – a rapid dive to 200 m. Driving the research vessel at them causes herring to dive like this. Moreover, there was a dynamic regime of school splitting and joining as herring schools distributed throughout this region of ocean encountered each other. On average an ‘event’ in a herring school occurred every 5 minutes; school encounters occurred every 15 minutes and splitting and joining events occurred every 30 minutes (see **Figure** 7). Events that were tentatively distinguished as predation happened every 25 minutes. Moreover, the sonar enabled the visualization of school formations such as ‘rings’ and ‘pseudopodia’ previously only studied with light. The overall conclusion was that herring school decisions were shaped by trying to minimize predation.

The distribution of older herring migrating northward in much deeper water 200 miles offshore appears to be limited by the southern edge of the polar front. They feed initially on copepods overwintering with eggs in deep layers, and then on euphausids near the surface at night as the spring bloom begins. Here there are no fish predators swimming with the herring schools. The herring exhibit a marked nightly vertical migration, often dispersing into loose shoals when they reach the surface to feed, whereas in the day they are found in exceptionally deep, dense, nonfeeding schools at around 300 m or more (see **Figure** 8). The sonar revealed night attacks on the herring by fin whales, causing great school compaction and rapid diving. On the surface, about a dozen fin whales were seen in the area. It was calculated that even a few fin whales cruising the Norwegian Sea might have a major impact on the evolution of herring behavior. For example, 12 fin whales could easily search the whole Norwegian Sea during a 6 month season. In this population, herring live to 12–15 years of age, each year taking part in the spring and summer feeding migration after spawning, and then assembling in a fiord in northern Norway to overwinter. Now, an individual herring has to meet a feeding fin whale only once in this life history to die. In fact, the chances are that it will meet fin whales at least once per year, and hence 10 times during its life. Such selection pressure seems sufficient to shape the behavioral schooling decisions that drive the ocean movements of herring.

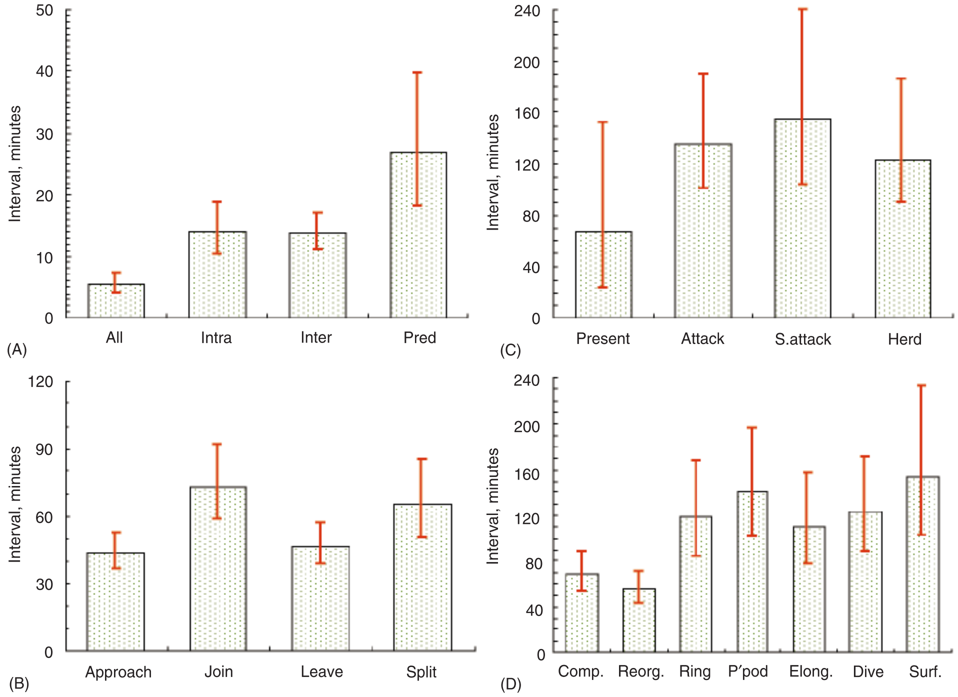


Figure 7 Mean frequency intervals (columns), and 95% confidence limits (bars), for 15 recorded behavioral events scored for herring schools observed with high-resolution sonar in the Norwegian Sea. (A): total of all events, and for intra-school, inter-school, and predator categories of behavior. (B): Four inter-school behaviors. (C): Four putative predator interaction behaviors. (D): Seven intra-school behaviors. (Data from Pitcher *et al.* 1996.)

In fact, ecologists have recently come to believe that much of the spatial behavior of fish is driven in very profound fashion by attempts to minimize predation: schooling represents one of these strategies. Manipulation of cover and food in experimental lakes has revealed that fish choose habitats as refuges and feed only when hunger and reward provide a beneficial trade-off with the risk of being eaten themselves. Where cover is absent, as in pelagic and open ocean habitats, schooling is the best defense. Modeling of predator–prey interactions in ecosystem simulation models has taken advantage of this finding. Refuge behavior produces more realistic and stable dynamics than classical Lotka-Volterra equations.

The spatial pattern of fish in the ocean depends on the type of behavior associated with shoaling. The following analysis assumes that frequent challenges to school membership arise from the actions of predators, the detection of food, and physical process in the ocean. It assumes that depletion is brought about mainly by overfishing, although

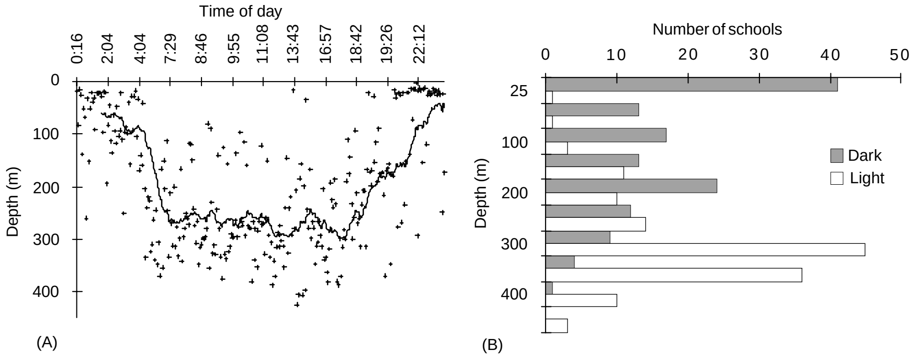
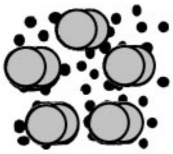
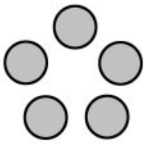
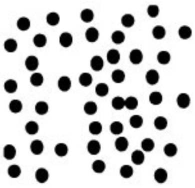
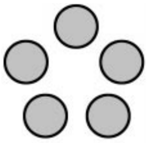
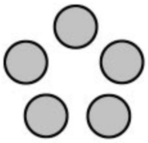
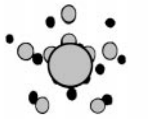
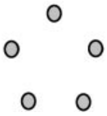


Figure 8 Diurnal changes in vertical distribution of herring recorded by echosounder in the Norwegian sea. (A) Depth distribution of herring schools – line is running average. (B) Number of schools with depth zone at day and night. (Data from Mackinson *et al.* 1999.)

Table 2 Analysis of the implications of various fish shoaling traits for distribution dynamics on the ocean, especially range collapse and resilience to fishing

Social behavior regime		*Shoal*	*Cannibal*	*Fidelity*	*Relatedness*
	Undepleted				
	Depleted				
Shoaling		Shoaling	No shoaling	Smaller shoals	Smaller shoals
Ecology	Range	Collapse	Patchier	Reduced	Patchier
	Refugia	Few	Many	Some	Many
Behavior	Join	High	Low	High	Low
	Stay	Low	Low	High	High
	Leave	High	Low	High	Low
Fishery	Resilience	Fragile	Resilient	Less fragile	More resilient
	Rebuild time	Slow	Fast	Medium	Faster

Rows 1 and 2 show schema representing school size and distribution before and after a severe depletion event. For further details of the four columns, see text.

population may also be reduced by environmental changes.

With normal shoaling, as described above, range collapse can occur, so that rebuilding of populations is from a small number of refugia (**Table 2**). The probabilities of 'join' and 'leave', decisions of individual fish probabilities are high while 'stay' is low, in order to adjust group size to local conditions. This leads to populations fragile to overfishing and slow to rebuild. On the other hand, nonshoaling piscivorous fish, like cannibalistic hake, space out rather than school, and 'join', 'leave', and 'stay' decisions are all of low probability. Hence such fish tend not to exhibit range collapse, serious depletion results in patchy abundance throughout the range, and rebuilding is fast because it can occur from many refugia. In other words, these species exhibit resilience in the face of depletion or environmental perturbations. In support of this idea, hake species differ in their degree of cannibalism, and this seems to be reflected in their relative resilience. The two strategies are summarized in the first two columns of **Table 2**.

Genetic relatedness (column 4 in **Table 2**) within schools implies high fidelity, so that only the 'stay' decision probability is high. Under this behavioral regime, schools shrink with population depletion and there is no reason for schools to be near each other, so that range collapse is less likely and there are more refugia from which the population may rebuild. This implies that resilience is higher, while the opportunity to adjust to local conditions is lower. A documented collapse and rebuilding of anchovies in the Adriatic Sea in the 1980s may fit this scenario.

A behavioral regime of high intrinsic fidelity within schools (column 3 in **Table 2**) would shift 'join',

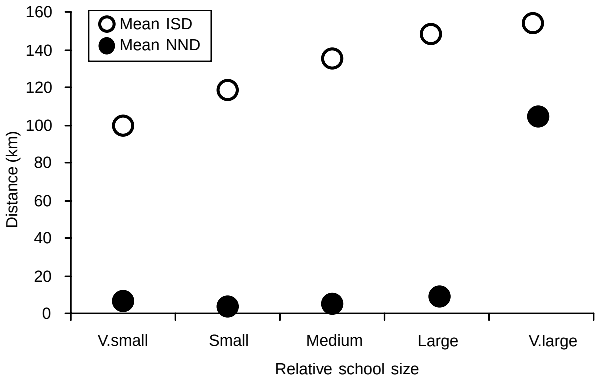


Figure 9 Relationships between average distance to nearest neighbor school distance (NND), average inter-school distance (ISD), and school size for echosounder data on herring in the Norwegian sea. (Data from Mackinson *et al.*, 1995.) The results show a mesoscale pattern of school patches in the ocean for all except very large herring schools.

'stay', and 'leave' decisions to high probability, so that, as the number of fish reduced, schools would shrink. However, schools might stay close together so that members could reassemble with their former schoolmates. Under this regime, fragility and rebuilding time would be intermediate. Measurements of the mesoscale distributions of fish shoals can distinguish among the hypotheses above. One attempt at measuring the patchy ocean distribution of herring schools is shown in **Figure 9**.

See also

Fish Feeding and Foraging. Fish Locomotion. Fish Predation and Mortality. Fisheries Overview. Mesopelagic Fishes.

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FISH VISION

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Introduction

The eyes of all vertebrates are built to a common plan, with a single optical system focusing radiation on a light-sensitive retina lining the posterior part of the eye (**Figure 1**). It is, none the less, impossible to describe a general fish eye. Fish inhabit almost every conceivable optical environment, from the deep sea where darkness is punctuated only by brief bioluminescent flashes to the sunlit surface waters, from the red peat lochs of Scotland to the green coastal waters of the English channel and the blue waters of a tropical lagoon (**Figure 2**). Fish therefore live at all levels of illumination and are exposed to many different spectral environments. The fish