FISH REPRODUCTION

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Introduction

Two characteristics of fish – that they are cold blooded and that many species continue to grow after reaching sexual maturity and throughout most of their life span – have profound effects on their reproductive ability. The ambient temperature influences the rate of development and growth, the time to reach sexual maturity and the life span. Fish living at high latitudes or in deep water usually grow more slowly, reach sexual maturity later and have longer life spans than their low-latitude counterparts. The seasonality of temperature change in high latitudes causes seasonal patterns of growth and has a role (with daylength) in determining spawning time. Some of these influences may be less clear in species such as tuna that have ocean-wide migrations during their life histories.

General Life Histories

In most fish species fertilization is external, there is no sexual dimorphism (the sexes look alike) and the large number of eggs produced annually by a female (its fecundity) develop and hatch and the larvae grow without parental protection. Sexual dimorphism is more likely to occur when fertilization is internal or elaborate courtship behavior takes place. In some species the fish are hermaphrodite, usually changing from one sex to another during their lifetime. Self-fertilization is rare. The generation time (age at first spawning) varies from a few weeks in small tropical species to several years in large temperate and deep-water species. Most species spawn several times during their lifespan (iteroparity), a few such as the Pacific salmon spawn once and then die (semelparity).

Typically, teleost (bony fish) eggs are 1–2 mm in diameter (**Figure 1**) and hatch after a few days, the time for incubation being dependent on ambient temperature (**Figure 2**). The larvae at hatching are a few mm long (**Figure 3**) and have a prominent yolk sac containing an endogenous supply of nutrients that they utilize until they reach the first-feeding stage. They are then large and well-developed

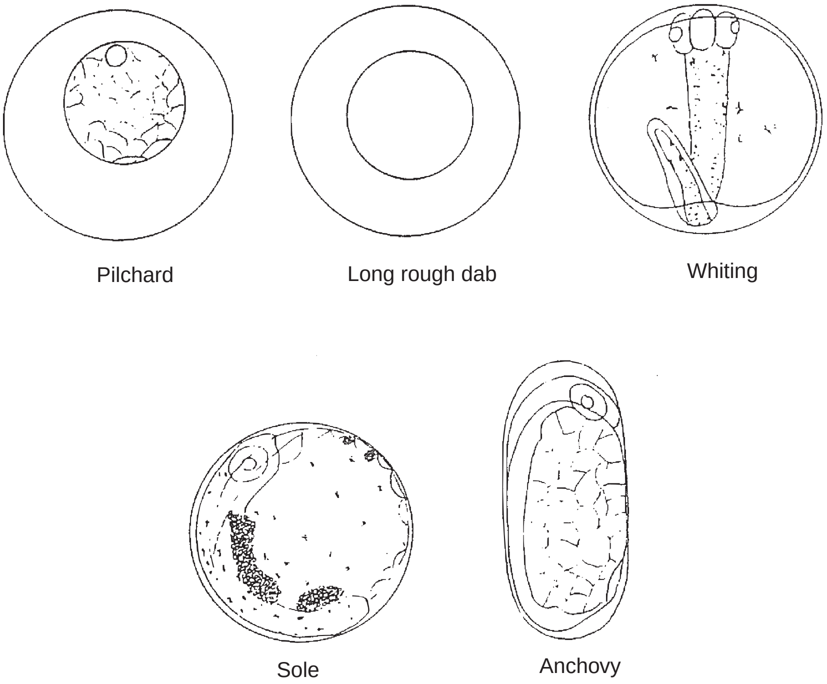

Figure 1 Free-living (oviparous) fish eggs of various species at different stages of development (diameter about 1 mm). (Reproduced with permission from Bone *et al.*, 1999.)

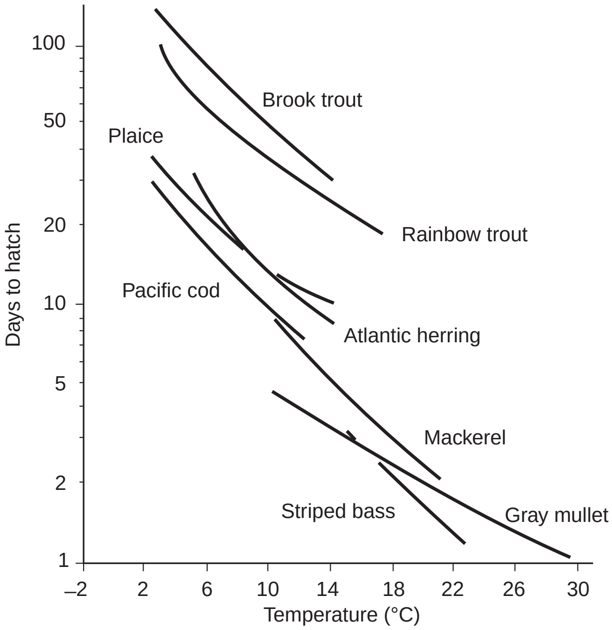

Figure 2 Time from fertilization to hatching of various species depending on temperature. (Reproduced with permission from Bone *et al.*, 1999.)

enough to search for an exogenous supply of live food in the microzooplankton of the surrounding water. After a period of days to months, depending on species and temperature, the larvae metamorphose into juveniles, i.e. immature stages of adult-like form.

Such a typical early life history has many exceptions. Some teleosts and all elasmobranchs (cartilaginous sharks and rays) have internal fertilization and the eggs of many but not all species develop within the female, which produces live young. Other species guard their eggs or young in one way or another.

This article elaborates on the themes of spawning season, fecundity and egg size, spawning behavior and parental care, egg and larval development and behavior, the underlying theme being the range of 'reproductive strategies' that have been adopted by fishes.

Spawning Season

The time of spawning is synchronized with ambient conditions by temperature and daylength. In high latitudes spawning is most often associated with cycles of productivity in the plankton and the presence of food of appropriate size for larvae when they first start to feed. A 'match' between the presence of first-feeding larvae and their microzooplanktonic food is one key to their survival, the other

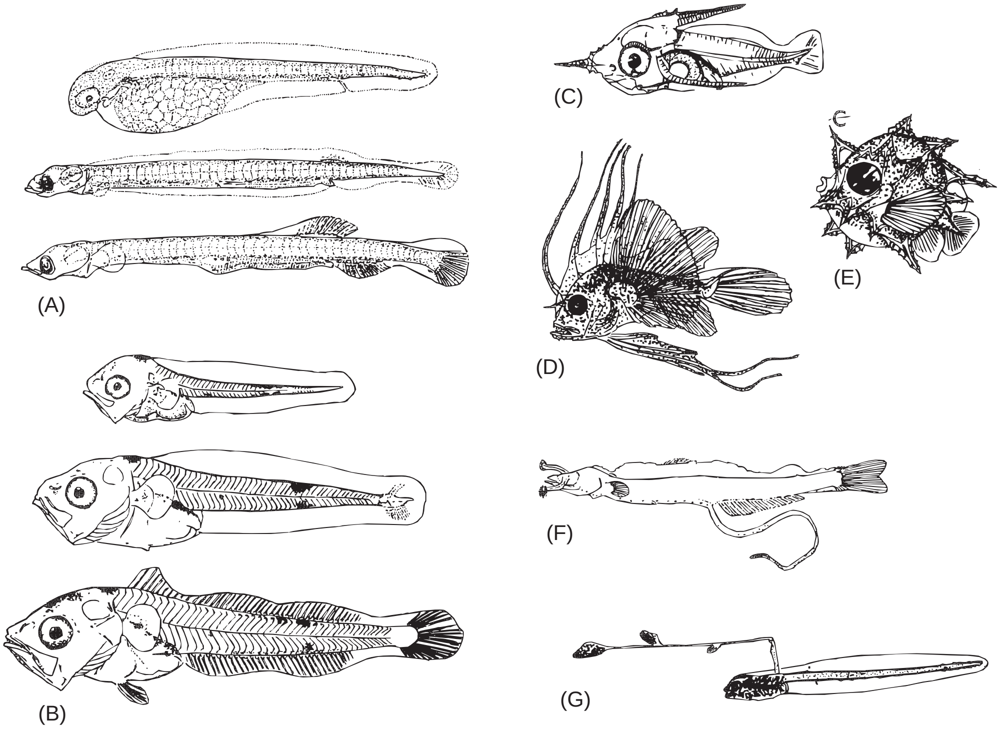

Figure 3 Teleost (bony fish) larvae. (A) Three stages in the development of northern anchovy (*Engraulis mordax*). (B) Three stages in the development of hake (*Merluccius productus*). (C)–(G) more unusual larvae: (C) *Holocentrus vexillarius;* (D) *Lophius piscatorius;* (E) *Razania laevis;* (F) *Myctophum aurolaternatum;* (G) *Carapus acus.* Drawings not to scale. (Reproduced with permission from Bone *et al.*, 1999.)

being a ‘mismatch’ with their predators. Spring spawning is most common and some species such as cod produce all their eggs in one batch over a few days (single-batch spawning) whereas others such as the plaice produce several batches of fewer eggs over several weeks. The reproductive strategy is clear. The single-batch spawner takes a ‘gamble’ on all its offspring reaching first-feeding when the food supply is of suitable size and quantity; the multiple-batch spawner ‘hedges its bets’ with the prospect of at least one (smaller) batch matching the available food, whose abundance can vary in space and time.

In low latitudes, the seasonality of temperature (and daylength) is less marked, but other environmental factors such as monsoon conditions or wind-induced upwelling may influence spawning season. Some tropical species spawn year round whereas others follow the limited seasonality, both types producing many small batches of eggs over the year. In deep water with a stable temperature regime, seasonality may be imposed by the descent of nutritive particles (fecal material and dead bodies) from the surface, where seasonal cycles of production prevail.

Fecundity and Egg Size

Their relationship can be summarized as follows:

1. Given that there is limited space within the body cavity of a female, species with high fecundities have small eggs and those with low fecundities have large eggs.
2. Fecundity within a species increases with age (size) of the female (**Figure 4**). This has important implications for overfishing since the loss of large fish means a disproportionate reduction in total egg production by a stock. In this way fecundity can also be looked on as the lifetime production of eggs by a female.
3. Fecundity is highest in species that release their eggs into open water and lowest in those species that bear their young alive or show parental care.
4. Within a species, egg size decreases in multiple-batch spawners as the spawning season progresses (**Figure 4**). In the particular and unique case of the herring, which has many physiological races with characteristic spawning times throughout the year, fecundity and egg size are inversely related on a seasonal basis (**Figure 5**).
5. Larger eggs produce larger larvae at hatching with more yolk and a longer period of endogenous feeding, larger body size at first-feeding and probably a better chance of survival in relation to feeding and predation.

Reproductive strategies such as generation time, breeding once or several times in the lifespan, spawning season, single vs. multiple-batch spawning, egg size vs. fecundity and parental vs. no parental care lead to the concept of k and r strategies. A k-strategy is where low fecundity, large eggs and

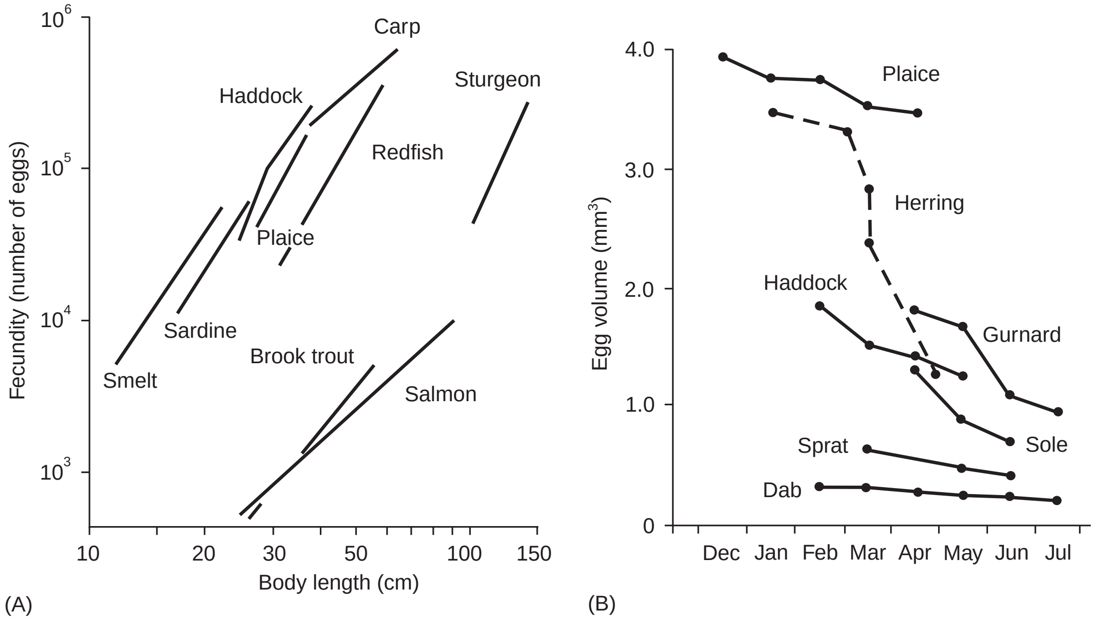

Figure 4 (A) The fecundity of various species depending on their length. (B) The size (volume) of fish eggs as the spawning season progresses. (Reproduced with permission from Bone *et al.*, 1999.)

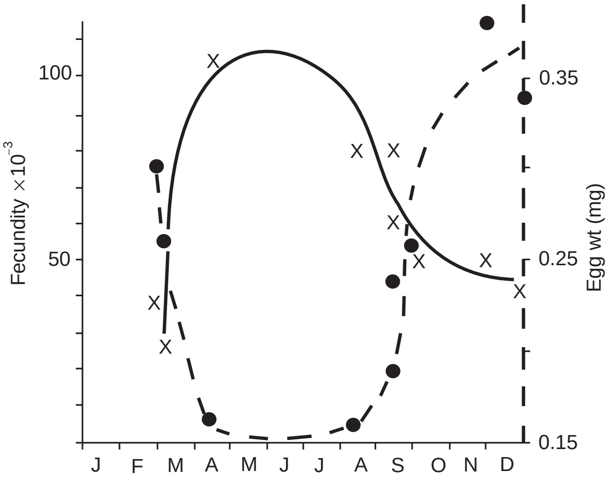

Figure 5 The inverse relationship between egg size (dry weight, ●) and fecundity (×) in the herring from various seasonal spawning races. (Reproduced with permission from Bone *et al.*, 1999.)

a long development period are favored in stable but crowded environments; r-strategists have high fecundity, small eggs and a short developmental period suited to less stable, less crowded environments in order to exploit the opportunities for expansion.

Spawning Behavior and Parental Care

Although inshore or littoral species restrict their ranges to small areas over their life span, many marine species make seasonal migrations for spawning, feeding and overwintering. Often the juveniles occupy nursery grounds inshore and move into deeper water as they grow.

The annual concentrations of many commercial species make them vulnerable to exploitation. They are typically r-stategists having oviparous (free-living) eggs that are released in large numbers into the water and left to fend for themselves. It is important that this release should not be too random, in order to maximize fertilization. Some degree of courtship or forms of signaling between males and females is known to occur in many species. For example, vocalization occurs when haddock are spawning and visual signals are known to play a part in the spawning of herring. Because it is difficult to maintain and breed many of the larger oceanic species in captivity, we are ignorant of much of their behavior

The k-strategists often have some form of courtship or mating interaction that may range from the elaborate behavior of the male stickleback to ensure the female lays her eggs in his nest, to internal fertilization of some live-bearing teleosts and all elasmobranchs. The teleosts have modified fins as an intromittent organ and the male elasmobranchs have claspers. Some elasmobranchs then lay and abandon their large horny eggs (e.g. the oviparous mermaid's purses of rays and sharks, **Figure 6**) attached to the substratum. Incubation can take several months. More commonly ovoviviparity occurs in which the large eggs develop independently within the female's 'uterus' and are produced alive. More common still is viviparity where the developing young derive nourishment directly from the mother, as in the smooth dogfish and many shark species. In the ovoviviparous species, the embryos usually depend on their own yolk supply or they eat other eggs (intra-uterine cannibalism or oophagy). In some ovoviviparous rays a nutritive uterine milk is secreted and protrusions from the uterine wall extend into the mouth cavity of the embryos. The viviparous sharks have a form of placenta to transfer nutrient to the young. All these species produce quite small numbers of young, less than 50 or so, but some are as long as 30 cm at birth. The viviparous basking shark produces young 150–180 cm long.

The advantage of both ovoviviparity and viviparity is obvious – the young are large and well-formed

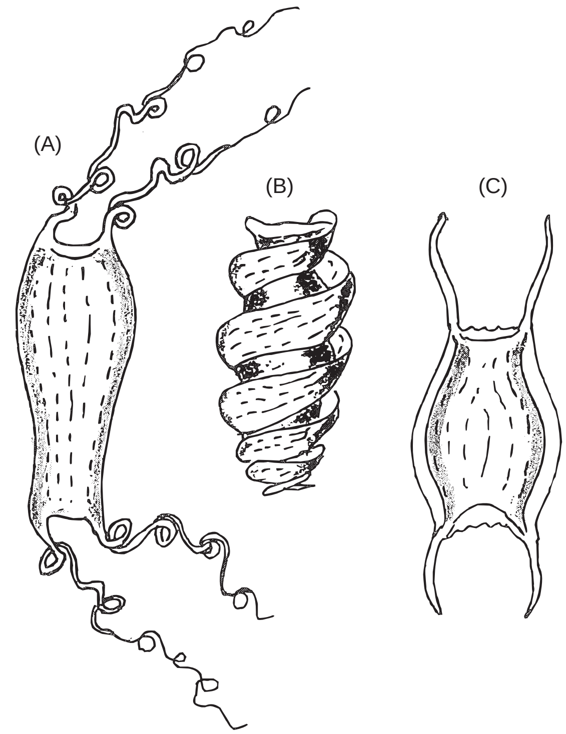

Figure 6 Egg cases of oviparous elasmobranchs. (A) spotted dogfish (*Scyliorhinus* sp.) 11 cm long without tendrils; (B) Port Jackson shark (*Heterodontus phillippi*) 9 cm long; (C) ray (*Raia* sp.) 12 cm long. (Adapted from Norman JR (1931) *A History of Fishes.* London: Ernest Benn.)

at birth and so more independent of their environment. The disadvantage lies in the fact that if the mother is eaten, all the young are lost.

Parental protection takes several forms: the nests of sticklebacks already mentioned, the pouches of seahorses and pipefish and the mouth-brooding of the male catfish. Many intertidal species protect their young. These survival mechanisms all suffer from the concentration and so the increased vulnerability of the young. It has to be said that the most successful species in terms of numbers or biomass are the r-strategists.

Egg and Larval Development

The eggs of r-strategists are small, round and transparent with a fairly tough egg membrane or chorion which protects them against wave action. However, anchovies have ellipsoidal eggs and in some gobies they are pear-shaped. With the exception of a few species such as the herring, capelin and most littoral species the eggs are buoyant and move passively with the currents. Development is meroblastic, the embryo developing at the animal pole as a blastodermal cap that overgrows the yolk and invaginates to form a gastrula (**Figure 7**). As the neurula develops the embryonic axis becomes visible as a head with prominent eye cups and a body of segmented muscle (the myotomes). As the body grows a tail is formed, the heart starts to beat and the embryo can be seen to move within the chorion. At hatching, part of the chorion is softened by hatching enzymes. In most oviparous teleosts the larva is a few millimeters long at hatching; it is very transparent and neither the mouth nor gut is fully formed. During yolk resorption over the next few days the mouth and gut develop and become functional. At first-feeding the larvae are predators of the microzooplankton (young stages of many invertebrates and especially crustacea) and use vision to feed. The larvae must obtain adequate food within a few hours to days if they are not to die of starvation. Feeding behavior usually takes the form of stalking, the larvae approaching the prey, bending into an s-shape and darting forward to engulf it. Some degree of suction may also be involved. The locomotor organs comprise a primordial finfold. Being so small the larvae are in a 'viscous' locomotor regime and swim in an eel-like or anguilliform style.

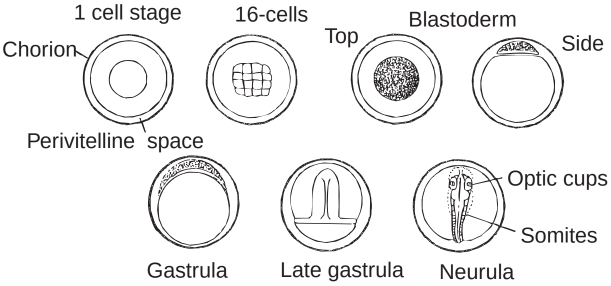

Figure 7 Development of a typical teleost egg (diameter of egg about 1 mm). (Reproduced with permission from Bone *et al.*, 1999.)

As the larvae grow the median (anal and dorsal) fins appear, but the most significant event is flexion when the posterior tip of the body turns upward and a caudal or tail fin develops. This greatly improves locomotor performance, which includes both capture of prey and escape from predators. Flexion and increasing size tend to bring the larvae into the 'inertial' locomotor regime occupied by the adults.

The sensory systems are fairly well known. The embryo may move within the chorion when stimulated by light, the eye cups being visible early on in the development of the neurula stage. At hatching the eyes may or may not be pigmented but are always functional at first feeding. At this time they usually have a pure-cone retina giving good acuity for perceiving food particles. The rods, which are designed to perceive movement, develop later. Large nasal pits containing a high density of cilia are present on the upper surface of the snout and taste buds can be observed in the pharyngeal area. Prominent over the head and body are free neuromast organs, consisting of bundles of hair cells each with cilia at the tip invested by a gelatinous cupula. The neuromasts, which are vibration receptors, proliferate during development and some of them become arranged in linear series to form the head and trunk lateral line. Little is known about the development of the inner ear, but there is a great interest in the otoliths which contain daily growth rings that can be used for determining the age of the larva. The development of the sense organs is of particular interest in terms of survival because the early larvae are poorly equipped and only later does the full suite of sense organs become available to make the larva maximally aware of its environment.

In the youngest larvae a liver and pronephric kidney is present but the gut is often a straight or coiled tube and develops into different regions later. The circulation may include an extensive blood supply to the yolk sac to help mobilize the yolk in endogenous feeding. The blood is a colorless fluid, the red pigmentation of hemoglobin appearing later often near metamorphosis. In the earliest stages respiration is cutaneous and gills appear later in the larval stage. It seems likely that development occurs in such a way as to keep the larva as transparent as possible as an antipredator device, but increasing

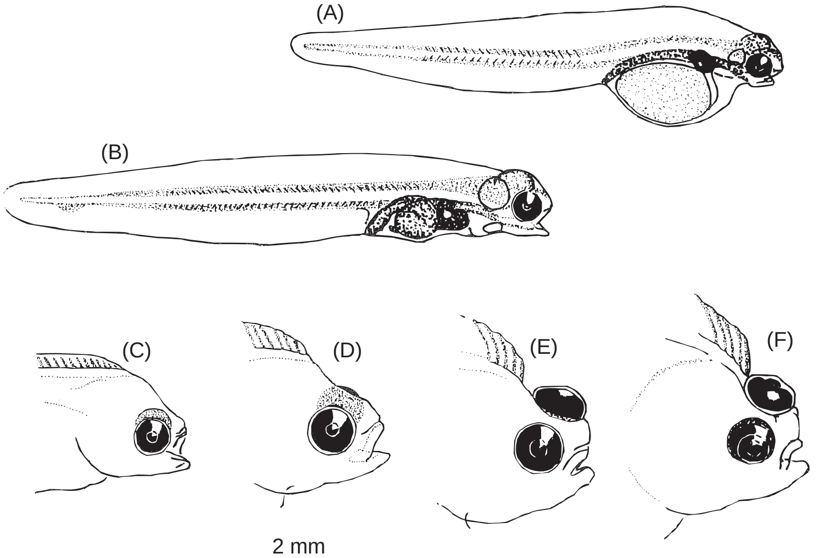

Figure 8 Larval stages and metamorphosis in the plaice: (A) yolk-sac larva; (B) first-feeding larva; (C)–(F) eye movements during metamorphosis. (Reproduced with permission from Bone *et al.*, 1999.)

size and thickness of the muscle tissue eventually makes the larvae more conspicuous, the eye being the most difficult organ to camouflage. Undigested food also makes the larva more conspicuous.

After a larval period of days to weeks, metamorphosis takes place as the larvae assume the juvenile stage, which is usually in the form of a miniature adult. The body thickens, pigment and scales appear in the skin and the blood turns red; behavior also changes. In flatfish, such as plaice, the larva is bilaterally symmetrical; at metamorphosis the eye on one side moves across the head and the juvenile lies on one side (**Figure 8**). Metamorphosis is not so clear in elasmobranchs and viviparous teleosts; the young hatch or are born at an advanced state of development, although some may still retain a yolk sac.

Behavior

While searching for food the larvae may move continuously or have periods of rest. Having a higher specific gravity than seawater, they then sink. Larvae are at the mercy of small-scale turbulence as well as larger scale wind-induced, tidal and residual currents that influence their distribution. These are important dispersion mechanisms that often bring the larvae inshore to nursery grounds. Within this imposed movement the larvae search for food and make predatory feeding movements. As the larvae grow the gape of the jaw increases, allowing larger food to be eaten; the searching speed and volume of water searched also increase. Light has some influence on behavior and larvae show changes in their vertical distribution by day and night especially as they get bigger. This may also be a dispersion mechanism allowing them to exploit currents at different depth horizons.

Antipredator mechanisms of small larvae seem to consist usually of showing little or no response to predatory attacks so depending on their transparency to remain inconspicuous; as they grow they respond by a fast-start mechanism that is mediated via giant nerve fibers in the spinal cord (Mauthner cells). The evasion strategy is to make a fast-start escape response, taking a few hundred milliseconds, at a very close response distance to the predator, so preventing it from reprogramming its attack.

At and after metamorphosis the juveniles adopt different defense mechanisms. Many species come together in schools or aggregations that make it difficult for the predator to select a target. Others, such as flatfish (**Figure 9**), seek cover on the sea bed where they adapt to the color of the background or bury in the substratum. Camouflage is achieved by the deployment of pigment cells (chromatophores) in the skin that adapt the fish to its background using countershading or color-matching mechanisms. Silvery-sided fish have reflecting layers of guanine crystals on their flanks that act as mirrors.

Despite millions of years of evolution, the mortality of fish during the early life history is enormous. Small, soft-bodied organisms are ready prey for a vast suite of predators. There is a premium on fast growth to reduce predation by smaller predators. High mortality is compensated by various reproductive strategies as described above. It has even been

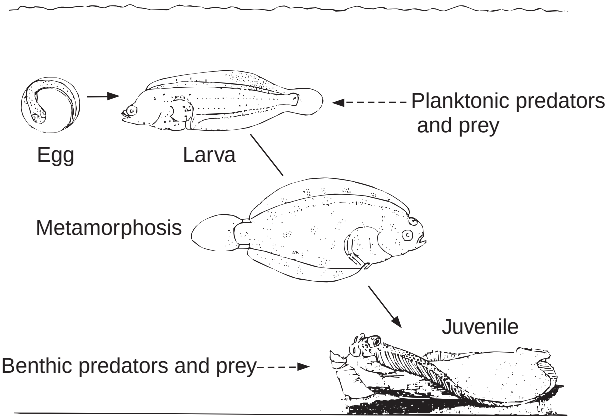

Figure 9 Life history of the plaice with a planktonic larva and bottom-living (benthic) juvenile and adult. (Reproduced with permission from Bone *et al.*, 1999.)

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,