# Reproductive Physiology in Fishes

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Judith Betsy and Stephen Kumar

**Abstract**

Natural selection, which is the basic of theory of evolution as proposed by Charles Darwin and Alfred Wallace, is widely accepted as the central paradigm in biology. Any individual who performs better at surviving and reproduction alone will be selected by nature, which leads to the concept of survival of the fittest. Hence reproduction is an important criteria any individual should possess so that their genes will be disproportionably represented in the next generation. Thus, studying reproduction and the physiological mechanism behind reproduction becomes very essential. In this chapter, different types of reproduction and fertilization in fishes, spawning dynamics, mating systems and factors affecting reproduction are discussed.

**Keywords**

Reproduction · Mating · Physiology · Spawning · Fish

## 1.1 Introduction

Reproduction is a process by which organisms replicate themselves wherein genetic material is passed from one generation to the next. There are wide variety of organisms and animals on earth and each group of organism has a unique mode of reproduction. The reproduction mode ranges from simple division to sexual method.

J. Betsy
Department of Aquaculture, Fisheries College and Research Institute, Tamil Nadu
Dr. J. Jayalalithaa Fisheries University, Tuticorin, India

S. Kumar (✉)
Directorate of Sustainable Aquaculture, Tamil Nadu Dr. J. Jayalalithaa Fisheries University, Thanjavur, India



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Single-celled organisms such as bacteria and protozoans exhibit wide range of reproductive methods. In some unicellular algae, the youngones can be produced by multiple fission, while in case of yeasts, the organism itself turns into a gamete and fuses its nucleus with the opposite sex through a process called conjugation. Ciliate protozoans reproduce by binary fission.

Reproductive modes differ among multicellular organisms also. Most of the plants follow asexual or vegetative method of reproduction by giving off asexual spores or by budding off and giving a new individual or by spreading rhizoid or giving off new sprouts from rhizome or producing new plant from shoot. Similarly, lower animals like sponges produce gemmules, which later become sponges; coelenterates can reproduce by budding; worms can divide into two and each half can then regenerate. However, higher animals can reproduce only by sexual method, which produce gametes which are haploid in nature and after fertilization becomes a diploid, uninucleate zygote. The gametes may be equal in size as in isogamy, or one may be slightly larger than the other as in anisogamy, but the majority of forms exhibit oogamy wherein there is a large egg and a minute sperm.

## 1.2 Reproduction in Fishes

As in higher animals, reproduction in fishes takes place by sexual method. Sex differentiation in fishes is determined by interactions between genes and the environment. According to Patzner (2008), about 88% of fishes are gonochoristic, the case where fishes may be either male or female. However, about 2% of teleost species representing approximately 30 families exhibits functional hermaphroditism. Avise and Mank (2009) have stated that hermaphroditism in fishes can be synchronus or asynchronus. In synchronus hermaphroditism, male and female gonads mature at the same time as it can be seen in *Serranus scriba*. Asynchronus hermaphroditism includes protandrous, in which fishes function as males first and then becomes females as in *Lates calcarifer* and *Sparus auratus*; and protogynous in which fishes function as females first and then become males as in *Epinephelus* sp. Fishes belonging to the four families of the order Perciformes such as Serranidae, Sparidae, Centracanthidae and Labridae; four families of the order Myctophiformes; few species of the order Cyprinodontiformes, stomiatioids of Salmoniformes and few species of order Synbranchiformes and Scorpaeniformes exhibit hermaphroditism (Atz 1964). The reproduction processes and their behaviours in fishes are given in Table 1.1.

## 1.3 Spawning Dynamics

Fishes exhibit two major temporal patterns of reproductive activity such as semelparity and iteroparity (Roff 1992, 2002; Stearns 1992; Wootton 1998). In semelparity, fishes breed once and then die because in these organisms, the physiological changes associated with reproduction result in consequences that inevitably

**Table 1.1** Reproduction in fishes

| | |
|---|---|
| A. Non-guarders | |
| *(a) Open substrate spawners* | |
| Pelagic spawners (Pelagophils) | *Lates niloticus* |
| Rock and gravel spawners with pelagic larvae (Lithopelagophils) | *Prochilodus sp.* |
| Rock and gravel spawners with benthic larvae (Lithophils) | *Labeo sp.* |
| Nonobligatory plant spawners (Phytolithophils) | *Rutilus rutilus* |
| Obligatory plant spawners (Phytophils) | *Puntius gonionotus* |
| Sand spawners (Psammophils) | *Gobio gobio* |
| Terrestrial spawners (Aerophils) | *Brycon petrosus* |
| *(b) Brood hiders* | |
| Beach spawners (Aeropsammophils) | *Leuresthes tenuis*, puffer fish, stickleback |
| Annual fishes (Xerophils) | *Nothobranchias sp.* |
| Rock and gravel spawners (Lithophils) | Salmonid sp. |
| Cave spawners (Speleophils) | *Julidochromis* sp. |
| Spawning in live invertebrates (Ostracophils) | *Rhodeus sericeus* |
| *B.* Guarders | |
| *(a) Substrate choosers* | |
| Pelagic spawners | *Channa sp.* |
| Above water spawners (Aerophils) | *Copeina arnoldi* |
| Plant spawners | *Polypterus sp.* |
| Rock spawners | *Loricaria parva* |
| *(b) Nest spawners* | |
| Bubble nest builders (Aphrophils) | Gouramis |
| Hole nester | *Cottus aleoticus* |
| Miscellaneous nest builders (Polyphils) | *Notopterus chitala* |
| Rock and gravel nesters | *Ambloplites rupestris* |
| Anemone nesters | *Amphiprion sp.* |
| Plant material nesters—glue making | *Gasterosteus aculeatus* |
| Plant material nesters—non glue making | *Micropterus salmoides* |
| C. Bearers | |
| *(a) External bearers* | |
| Transfer brooders | *Oryzias latipes* |
| Skin brooders | *Bunocephalus sp.* |
| Forehead brooders | *Kurtius gullivers* |
| Gill chamber brooders | *Typhlichthys subterraneus* |
| Pouch brooders | *Syngnathus sp.* |
| Mouth brooders | *Oreochromis sp.* |
| Intestinal brooders | *Tachysurus barbus* |
| *(b) Internal bearers* | |
| Facultative internal bearers | *Rivulus marmoratus* |
| Obligate lecithotrophic live bearers | *Poecilia reticulata* |
| Viviparous trophoderms | *Anableps dowii* |

end in death. Iteroparous fishes survive after reproduction to breed again where reproduction takes place at yearly intervals. Similarly, within a breeding season, two temporal patterns of spawning occur in female fishes namely total and batch spawners (Wootton 1998; Patzner 2008). In total spawners, the female releases all her eggs in single spawning, whereas in batch spawners, the female releases her eggs in batches at intervals during the breeding season.

## 1.4 Mating Systems

Shuster and Wade (2003) defined mating system as the species-specific pattern of male–female associations. Mating systems imply the number of mates individuals acquire with a description of how those mates are acquired, the characteristics of pair bonds and patterns of parental care by each sex and resolves the sexual conflicts since both the sexes have different roles in reproduction, the optimal behaviors and traits for each are likely to be different (Berglund 1997).

In promiscuity, both the sexes have multiple partners during the breeding system with little or no mating choice (*Clupea harengus*). A form of promiscuity, where a male will spawn with several females and a female with several males with mate choice is polygynandry (*Rhodeus amarus*). In polygamy, an individual of one sex has multiple partners during the breeding system, but individuals of the opposite sex have only one partner. Polygamous mating system is further divided into polygyny and polyandry. In polygynous, male has multiple female partners during the breeding season and it is the common form and can be seen in many cichlids like *Oreochromis niloticus*. Polyandry mating system is one in which a female has multiple male partners during the breeding season. However, it is an uncommon form of polygamy and has only been reported in anemone fish (*Amphiprio ninae*). In contradictory to all these, in monogamy, a single male and female form a mating pair and show some degree of bonding with the mate (*Cichlasoma*).

## 1.5 Fertilization in Fishes

Fertilization is union of a spermatozoa nucleus, of paternal origin, with an egg nucleus, of maternal origin, to form the primary nucleus of an embryo which results in fusion of the hereditary material of two different gametes, each of which carries half the number of chromosomes typical of the species. Gilkey (1981) defined fertilization as a process which encompasses all the events between release of gametes and fusion of male and female pronuclei.

In fishes, generally, females have separated ovaries. However, in some fishes, the right and left ovaries are fused and resemble as single organ. The ovary connects to the body wall by a short oviduct and opens posteriorly to the anus. Ovulated eggs are spawned with the ovarian fluid out of the genital pore. Males with internal fertilization have gonopodium which is a modified anal fin to introduce spermatozoa into the female genital tract. However, such a copulation organ is not found in fishes with external fertilization (Iwamatsu 2000).

At the time of breeding, fishes exhibit secondary sexual characteristics with which a male and female can be identified. Permanent dimorphism can be noticed in *Betta splendens,* whereas temporary dimorphism can be seen in many fish species (e.g., *Gasterosteus aculeatus*) only during breeding season.

### 1.5.1 External Fertilization

Most of the fishes are external spawners. In this mode of fertilization, female releases the egg either in the water or on any substrate over which males release their sperm. Water serves as activating medium and induces motility in spermatozoa. Thus, spermatozoa find their way to the eggs and fertilize them by entering through their micropyle. In this type of fertilization, female fertility can be limited by sperm availability.

### 1.5.2 Internal Fertilization

In this mode of fertilization, gametes fuse inside the female reproductive tract. In order to transfer sperm from males to females, males have a specialized copulatory structure like gonopodium (*Poecilia reticulata*). It has been reported that in teleosts, male intromittent organs are found in a number of families (Wootton and Smith 2015).

In species with internal fertilization, spermatozoa are often organized into bundles termed as spermatophores but in others, they are arranged into unencapsulated sperm bundles termed as spermatozeugmata, e.g., in viviparous kelp blennies (Clinidae) (Fishelson et al. 2006) and *P. reticulata* (Magurran 2005). As in the case of external fertilization, mucins also occur in the ejaculates of internal fertilizers, whose function is to increase fertilization efficiency by extending the period over which motile spermatozoa are released (Ginzburg 1968).

As in *P. reticulata,* some internal fertilizers can store sperm (Magurran 2005), which helps females to produce broods in the absence of males for up to 8 months. However, the capacity to store sperm appears to vary among populations. Stored spermatozoa are used to fertilize eggs even if the female mates with additional males, but the fertilization success of stored spermatozoa is typically lower than that from recently deposited sperm (Wootton and Smith 2015).

### 1.5.3 Quasi-Internal Fertilization

Fertilization which is basically external, but takes place in a site so restricted that it is analogous to internal fertilization is called quasi-internal fertilization. In mouth-brooding cichlids, buccal fertilization takes place where females deposit eggs on a substrate and collect them immediately into her mouth. In many species, males possess coloured spots on their anal or pelvic fins, termed egg spots, which resemble the female's egg in size and colour (Fryer and Iles 1972). Female cichlids respond to egg spots by nipping at the male's fins, and the male releases sperm into her buccal cavity where the eggs are fertilized.

Bronze corydoras catfish (*Corydoras aeneus*, Callichthyidae) have a specialized mating system, sperm drinking. In this type of fertilization, female collects sperm in her mouth from the male's genital opening. The live spermatozoa pass rapidly through the length of her digestive tract and are discharged to her eggs, which she releases into a pouch created by her paired pelvic fins (Kohda et al. 1995). The rapid passage of spermatozoa through the female's digestive tract is possible because this fish exhibits intestinal breathing, whereby air is gulped at the surface and passes through the stomach to the intestine where it is absorbed. This adaptation appears to facilitate the rapid passage of water and spermatozoa through the intestine and to the eggs (Kohda et al. 1995).

In the bitterling fishes (Cyprinidae), fertilization occurs in the gill chambers of living freshwater mussels. Female bitterling deposits their eggs into the gill chamber of a mussel with an unusually long ovipositor and males fertilise the eggs by releasing sperm into the inhalant siphon of the mussel, so that water filtered by the mussel carries the sperm to the eggs (Smith et al. 2004).

## 1.6 Factors Affecting Reproduction

Reproduction in fishes is affected by internal and external factors. According to Lowerre-Barbieri et al. (2011), environmental factors that show seasonal changes have two possible roles in determining the temporal pattern of reproduction viz., ultimate factors and proximate factors.

### 1.6.1 Ultimate Factors

The timing of reproduction maximises the individual fitness of the reproducing fishes either by the effect of timing on the survival of the progeny as in most teleosts (Wingfield 2008; Lowerre-Barbieri et al. 2011) or by the effect of timing on the future reproductive success of the reproducing adult as in the case of iteroparous species. Lowerre-Barbieri et al. (2011) stated that ultimate factors act as selective agents operating on heritable changes between generations. The important ultimate factors for the progeny are usually assumed to be availability of suitable food, no risk of predation and avoidance of adverse physical conditions.

### 1.6.2 Proximate Factors

Factors that affect the physiological processes in order to regulate reproduction are called as proximate factors which include photoperiod, temperature, the lunar and tidal cycles, the chemical composition of water and the flow rate of water. These factors act during the ontogeny of individuals and must be detectable by the sensory systems of the individual fish so that the information can be passed to the central nervous system (CNS). Proximate factors can affect the timing of reproduction by their effects on the initiation of gametogenesis, the stimulation of vitellogenesis and the induction of the final maturation, ovulation and oviposition (Wang et al. 2010). In addition to predictive, proximate cues that initiate gametogenesis, and any local or synchronising cues that are required for ovulation and spawning, there may also be terminating cues, which bring spawning to a close. In some species, the end of spawning may occur even in constant environmental conditions because of an endogenous process (Wootton and Smith 2015).

#### 1.6.2.1 Lunar Related Reproductive Cycles

Lunar cycle influences the seasonal variation in spawning activity. The spawning of estuarine and shallow water marine species is closely related to the lunar cycle (Taylor 1984; Takemura et al. 2010) because of the close association between the lunar cycle and the tidal cycle. Lunar cycles influence spawning in few freshwater species also.

#### 1.6.2.2 Photoperiod

Light appears to be an important factor in controlling the reproduction of fishes. The photoperiod is the most reliable of geophysical cues, and temperate and higher latitudes frequently act as a predictive cue for teleost species, sometimes in association with water temperature. Harrington (1956, 1957) suggested that long photoperiods initiate the gonadal activity and the fishes can spawn in advance of the natural time. However, the influence of light in activating the productive cycle varies from species to species.

Hazard and Eddy (1951) reported that functional maturity can be advanced in *Salvelinus fontinalis* first by exposing them to an increasing photoperiod and later to a decreasing photoperiod. An accelerated light regime can enhance the time of functional maturity in trout (Henderson 1963).

Early maturation under short photoperiod and delayed maturation under long photoperiod were observed in salmonids by Shiraishi and Fukuda (1966). When exposed to longer photoperiods, *Cirrhina reba* attained early maturity (Verghese 1967). According to Sanwal and Khanna (1972), both very long and very short photoperiods are unfavourable for maturation of ovaries in early stages in *Channa gachus*, and there is a delay in the appearance of yolk. But during vitellogenesis, a short photoperiod accelerates the formation of mature oocytes.

#### 1.6.2.3 Temperature

Temperature has direct effects on metabolic rates and can modulate the rate at which all physiological process can occur, including reproduction (Wang et al. 2010). Temperature is known to influence the maturation of gonads in fishes. There is an optimum temperature for breeding of fishes, above and below which they may not reproduce (Hoar and Robertson 1959; Ahsan 1966).

Ahsan (1966) showed that warm temperature stimulates maturation of gonads and spermiation in lake chub. During induced breeding of Indian carps, spawning occurs at a temperature ranging from 24 to 34 °C with an optimum water temperature of about 27 °C (Chaudhuri 1968). Similarly, spawning in *Cirrhinus reba* was observed by increasing water temperature from 25 to 29 °C at the time of injection, and then allowing the water to cool (Bhowmick 1969). Thus, temperature appears to be a triggering factor for spawning in carps.

Hontela and Stacey (1990) reported that decreasing photoperiod and high water temperatures cause gonadal regression in rose bitterling (*Rhodeus ocellatus*, Cyprinidae). Such gonadal regression is frequently followed by a refractory period (Baggerman 1990) during which period, even the usual initiating proximate cues have no effect on gonadal recrudescence. Only at the end to the refractory period proximate cues initiate gonadal recrudescence. This refractory period provides a basic pattern of timing on the reproductive cycle, and probably prevents recrudescence at times unfavourable for reproduction (Wootton and Smith 2015).

#### 1.6.2.4 Habitat and Repressive Factors

The nature of the habitat, like the presence of stones, plants, suitable substratum to lay eggs, also serves as an important stimulus for the fish to breed. Swingle (1956) reported that the excretory matter of fish released into the water constitutes the 'repressive factor', a hormone-like substance which inhibits reproduction in fishes. Similar observation was made by Tang et al. (1963) who observed that *Cyprinus carpio*, *Carassius auratus* and *Tilipia mossambica* do not spawn when overcrowded but spawn when transferred to fresh water and spawning takes place when the repressive factor is sufficiently diluted by the flood water in bunds or ponds. They also stated that ammonia itself may not be the repressive factor, but many other excretory substances may bring about inhibition of spawning in carps.

#### 1.6.2.5 Petrichor

Factor which stimulates the fish to spawn when rain water comes into contact with dry soil is known as "Petrichor" (Lake 1967). This can be obtained by steam distillation of silicate minerals and rocks available in the breeding habitat of the fish. Fishes possess a remarkable olfactory sense, and the odour of petrichor works as a stimulant for spawning. Nikolsky (1962) reported that ripe male secrete a steroid hormone called "copulin" which induces females to spawn followed by mating. Petrichor and copulin stimulate gonad-stimulating hormones after which neurosecretory material (GnRH) is transported from the hypothalamus to the hypophysis through the nerve fibres of the hypothalamico-hypophyseal axis and hypothalamus exercises primary control over the secretion of hormones from the pituitary gland.

#### 1.6.2.6 Food

Availability of required quantity of food at appropriate times during the reproductive cycle is a major factor affecting reproduction. It was reported that high food levels support the growth of fishes, leading to larger body size (Wootton 1998). High level of food intake leads to high fecundity in female fishes. Some fishes stop feeding during spawning season and for reproduction it utilises reserves built during active feeding. Houston et al. (2006) and Stephens et al. (2009) described about capital breeders and income breeders. In capital breeders, prior to breeding fishes consume more feed than its regular feeding level in order to compensate starvation during reproduction. In case of income breeders, energy for reproduction is met from regular feeding.

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