CHAPTER 1

Fish Reproduction

- *Salinity*
  - *Exposure and Temperature*
- *Lifetime Spawning Strategies*
- *Sites*
  - Migrations
  - Habitats
- *Behavior*
- *Secondary Sexual Characters*

Each fish species has evolved in response to a unique set of selective pressures, hence species often differ in their life-history strategies; each life-history strategy is a set of developmental adaptations that allows a species to achieve evolutionary success. Each life-history stage (i.e., egg, larval, juvenile, adult) has a number of possible alternative states, but the life history of a given species consists of only one of these states for each life-history period.

Since each fish species evolves under a unique set of ecological conditions, it has a unique reproductive strategy with special adaptations including anatomical adaptations, developmental adaptations, behavioral adaptations, physiological adaptations, and energetic adaptations.

The reproductive process allows species to perpetuate themselves. Almost all fishes reproduce sexually, thus permitting mixing of the genes of the two sexes. The reproductive processes of fishes form the basis for early life-history studies. The great variety of these processes among fishes make their study worthwhile, but also determine how early life-history studies of various fishes can be conducted. For example, fishes reproduce in fresh and marine waters, have external and internal fertilization, have short annual reproductive periods, or produce gametes at regular intervals throughout the year. This chapter summarizes the reproductive patterns of fishes, with an emphasis on how these patterns affect early life-history studies. A more exhaustive account (and extensive reference lists) of modes of reproduction is found in Breder and Rosen (1966) and of developmental biology in Kuntz (2004). There is also a very useful chapter on reproductive ecology by DeMartini and Sikkel (2006).

WHAT ARE FISHES?

The answer to this question is not as simple as it may first appear. This book deals with bony, ray-finned vertebrates, that is, actinopterygians. This includes nearly 24,000 extant species, but excludes such “fishes” as sharks and rays (chondrichthyans) and lungfishes (dipnoians). Sharks and rays have internal fertilization and produce small numbers of large, yolky eggs. Some retain the developing embryos in the parent and give birth to miniature copies of the adults. Others lay the eggs in elaborate egg cases where embryonic development occurs. In either case, this reproductive pattern is quite different from that seen in most bony fishes where larger numbers of small eggs (often ≤ 1 mm) are produced. Even in bony fishes that brood their young (e.g., live-bearers [poeciliids], surfperches [embiotocids]), small eggs with relatively little yolk are produced. Maximum egg sizes in bony fishes are up to 10 mm in salmons and 15 mm in sea catfishes (ariids). Besides the skeletal features that distinguish bony fishes, they generally share the same basic early life-history pattern of producing small unfertilized eggs that undergo indirect larval development before becoming juveniles. Exceptions to this pattern have arisen in several lineages within the bony fishes.

SEXUALITY

The following is a synopsis of sexuality in fishes. A much more detailed account can be found in Breder and Rosen (1966) and DeMartini and Sikkel (2006).

Range of Sexuality

Fishes have a large range of sexuality (they stand out amongst vertebrates), and because of this there have been a number of studies into the questions of sex determination and sex differentiation—are they due to environment or heredity? Fishes may exhibit hermaphroditism, unisexuality (parthenogenesis), bisexuality (gonochorism), or a combination of sexualities.

Hermaphroditism

Hermaphroditism may be genetically programmed or a function of the social surrounding and is particularly prevalent in tropical reef regions.

In **synchronous** or **simultaneous hermaphroditism,** the left gonad is the ovary and the right one is the testis or vice versa, or there may be an ovotestis. Although self-fertilization exists, it is rare because recessive traits become present such as albinism, a physoclistous swim bladder, and others. Synchronous hermaphroditism is usually found in species where potential mates are sparsely dispersed because if the energy costs are the same for a synchronous hermaphrodite as for a male or female, it is clearly advantageous. It is common among bathypelagic and mesopelagic species living in the darkness of the ocean depths in low-population densities. In general, these species are continuously reproductively mature so that a chance encounter is always fruitful, but encounters may only occur once or twice in a lifetime. However, some seabasses (serranids) are also synchronous hermaphrodites, which is perplexing because they are not dispersed in low numbers.

In **asynchronous, consecutive, successive,** or **sequential hermaphrodites,** the fish start functionally as one sex and then switch to another; this strategy is confined to lower percoid groups such as parrotfishes (scarids), wrasses (labrids), and seabasses. A more detailed discussion of this strategy can be found in Warner (1975).

In **protandric hermaphrodites,** the fish are first males, then females; this is more common in porgies (sparids), flatheads (platycephalids), hagfishes (myxinids), and lightfishes (gonostomatids). The theory behind this reproductive method is that it has evolved under conditions where there is a strong female fecundity exponential increase because of volume change and asymmetry of age-specific fecundities between the two sexes. Protandry occurs when there is no advantage to males accruing larger size and, presumably, the gain is considerably greater than the cost of the change.

In **protogyny,** the fish are first female, then male, and there is asymmetrical reproductive success due to greater success by larger males in monopolizing several females. Possibly predation avoidance is also a factor, where males display and females choose, with the male acquiring the female according to their size. It is also an advantageous strategy when a male guards a harem of females since it becomes an advantage to switch from a female to a male because there is greater reproductive success when males are larger.

Unisexuality or Parthenogenesis

Rarer than hermaphroditism, but it is found in some live-bearers (only females). Development of young is without fertilization and females produce only female offspring. There are two ways this is done. In **gynogenesis,** the sperm of a closely related species is used to trigger development of the egg nucleus but does not fuse with it; and in **hybridogenesis,** fusion occurs but only the haploid female genome is transmitted to the developing ovum.

Bisexuality

Also called **gonochorism,** it is by far the most common mode of reproduction practiced by the majority of fishes and is what this book will focus on.

REPRODUCTIVE PATTERNS (FIGURE 1.1, TABLE 1.1)

Live-Bearing

Several groups of fishes have developed a live-bearing (i.e., giving birth to free-living larvae or juveniles, rather than laying eggs) life-history pattern. A prerequisite to this pattern is mating, copulation, and internal fertilization. Viviparous fishes have internal fertilization and are characterized by the embryo developing in close contact with the nourishing maternal tissue—no egg membrane covers the embryo. There are very few truly viviparous species. One of the best known examples is the surfperches (embiotocids) of the coastal waters of the Northeast Pacific, which produce well-developed

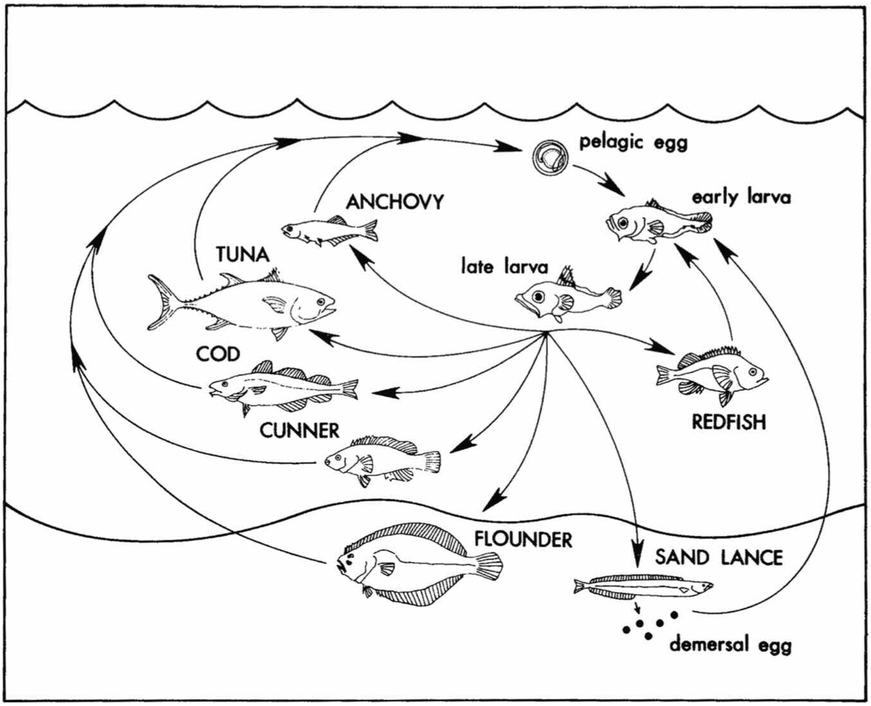

Figure 1.1. Diagram representing some of the variety of reproductive patterns of marine fishes. Objects are not to scale. Most fishes regardless of adult size or habitat spawn pelagic eggs that develop into pelagic larvae (e.g., flounders [pleuronectids], cunner [*Tautogolabrus adsperus*], cod [*Gadus morhua*], tuna [*Thunnus* spp.], anchovy [engraulids]). Other species (e.g., sand lance [*Ammodytes* spp.]) spawn demersal eggs that hatch into pelagic larvae. A few species (e.g., redfish [*Sebastes* spp.]) have internal fertilization and incubation followed by a pelagic larval stage.

young with the males of some species capable of breeding when born. In such fishes parental care of the eggs is maximum since the eggs are within the mother throughout development. Fecundity is low, usually < 100, and nourishment is primarily from the parent, not the egg (eggs small, embryo large), with the weight of the embryo increasing from fertilization to birth. In surfperches, embryos have large medial fins for absorbing nutrients. Once the young are released as juveniles, parental care normally ends. The series of events involving reproduction in viviparous fishes can be somewhat involved. For example, striped seaperch (*Embiotoca lateralis*) in Puget Sound breeds from June to August; after mating, the sperm is stored in a compartment of the ovary until September, when the sperms penetrate the ovary, fertilizing the eggs and causing gestation to start. Ten to 40 young are born, about 50 mm in length, tail first, usually in July of the following year.

TABLE 1.1. Reproductive Patterns of Teleosts

Timing of spawning	*Semelparous*	*Iteroparous*					
		Isochronal	*Heterochronal*	*Indeterminate*			
	(Spawn once, near end of life)	(Spawn one batch of eggs per year)	(Spawn several batches during a spawning season)	(Spawn several times during a protracted spawning season)			
Fertilization	*External*				*Internal*		
Embryonic nutrition	*Oviparous*					*Lecithotrophic*	*Viviparous (matrotrophic)*
	NO PARENTAL CARE POST-FERTILIZATION						
Release eggs (Spawn)							
Individual pelagic eggs	*Anguilla*	—	*Theragra*	*Engraulis*	—	—	—
Individual demersal eggs	—	*Lepidopsetta, Gadus macrocephalus*	—	—	—	—	—
Pelagic eggs in gelatinous masses	—	*Scorpaena, Sebastolobus, Lophius*	—	—	—	*Helicolenus percoides*	—
Demersal eggs in masses	*Onchorhynchus*	—	—	—	Some cottoids	—	—

	PARENTAL CARE POST-FERTILIZATION						
Release eggs (Spawn)							
Demersal eggs in masses, guard nests	—	*Ophiodon*, *Scorpaenichthys*, Centrarchids	—	Pomacentrids	—	—	—
Release larvae	—	—	—	—	—	Hemiramphids	*Sebastes*
Release juveniles	—	—	—	—	—	*Poecilia reticulatus*	*Zoarces viviparous*, Embiotocids, Some poeciliids

NOTES: "Isochronal spawn" = total spawn, "Heterochronal spawn" = serial spawn; semelparous, isochronal, and heterochronal are forms of determinate spawning in which all oocytes for a spawning season are matured simultaneously in the ovary.

Since **viviparity** has developed independently several times in fishes, the means of transferring nutrition from the female to the young is quite variable (Wourms 1981). In the case of rockfishes (*Sebastes* spp.), fertilized, relatively undeveloped late yolk sac larvae are produced. The yolk may be supplemented by maternal nourishment as the eggs and larvae develop in the female (Boehlert and Yoklavich 1984). Fecundity of rockfishes does not seem to be reduced significantly in conjunction with the apparent added protection afforded by foregoing the free-living egg stage. Such fishes in the past have been termed "ovoviviparous," and characterized by having internal fertilization. The mother may or may not nourish the embryo, but at any rate the embryo and the maternal tissue are separated by the egg membrane—that is, no "placenta-like" structure is present. Typically, the eggs hatch internally and are released as early larvae. Again, the parental care of eggs is maximum since the eggs are retained internally, but fecundity may be much higher (e.g., in the case of rockfishes tens of thousands of young may be produced per year). As a general example of the type of annual reproductive cycle in rockfishes, we can use golden redfish (*Sebastes norvegicus*), which is an extremely important commercial species in the Atlantic and which has been studied in some detail (Magnuson 1955 in Hempel 1979). Golden redfish mate in the winter when the male is ripe but the female eggs are not yet ripe, so the female stores the sperm until early spring at which time fertilization occurs. Within a single female it has been found that the embryos are all the same size, indicating a single fertilization event. The eggs hatch internally, and then are extruded (born) as early larvae in late spring, which is 2–3 months after fertilization and 6–7 months after mating. At the time of extrusion it is thought that the oxygen requirements of the larvae exceed that provided by the mother, although in the rockfishes it has been demonstrated that in at least some species a special vascular system to the ovary ensures a particularly good gas exchange (Moser 1967).

Egg Laying

Actually, internal fertilization is very rare among teleosts. Eggs of the vast majority of teleosts, especially marine fishes, are released before fertilization—these are the **oviparous** fishes (literally, "egg-laying" fishes). Males and females swim close together so that the eggs are shed into a cloud of spermatozoa. Because mating and courtship occur in many oviparous species, one important aspect is that the activity of sperm depends on small concentrations of Ca or Mg ions, which allows sperm to remain active in salt water for up to an hour or so as opposed to a minute or so in fresh water. The eggs are then fertilized and develop in the environment outside the female. An egg membrane is present, and the embryonic stage is nourished entirely by the yolk. In a few cases (e.g., sea horses and pipefishes [syngnathids]), after being released, the eggs are carried in a pouch in the adult (males in sea horses), or in the mouth of one of the parents (e.g., some catfishes [siluriforms] and cichlids [Cichlidae]). The eggs of most fishes develop either in nests constructed by the adults, or they develop in the environment at large. Fecundity of marine oviparous fishes can be extremely high (> 300 million in the ocean sunfish [*Mola mola*] and commonly 1 million or more). Among the oviparous fishes, there are so-called **demersal spawners** and **pelagic spawners**—actually, the eggs they extrude are either demersal (on the bottom) or pelagic (above the bottom, and often at or near the surface), whereas the juveniles and adults of the species may be either demersal or pelagic in both cases (Table 1.2).

Demersal Eggs. Demersal egg spawners produce eggs that are heavier than the surrounding water and which develop on the bottom. These eggs are either attached to the substrate or float loosely on the bottom and are generally adhesive. Eggs of almost all freshwater fishes are attached to the substratum or are loosely in contact with the bottom, that is, are demersal. This is a reflection of the fact that protein is the main constituent of fish eggs, and protein has a higher specific gravity than fresh water, and demersal eggs have a low water content. Hempel (1979) points out that among the marine groups which spawn demersal eggs are the smelts (osmerids), herring (*Clupea* spp.), greenlings (hexagrammids), and sculpins (cottids). It's interesting that on the Arctic and Antarctic Shelves, fish eggs are mainly demersal with large yolk reserves and long incubation periods (e.g., Greenland cod [*Gadus ogac*] and Arctic flounder [*Liopsetta glacialis*]), whereas most other cods (gadids) and

TABLE 1.2. Summary of Differences Between Demersal and Pelagic Eggs

Characteristic	*Demersal*	*Pelagic*
Usual Size	> 1 mm	≤ 1 mm
Specific Gravity	greater	less
Envelope	thicker	thinner
Color	opaque, colored	transparent
Amt. of Yolk	large	small
Period of Dev. (Temperate)	longer (up to 2 mos)	short (~ 1 wk)
Parental Care	common	none
Fecundity	low	great (> 1 million)
Larvae	swim/feed @ once	float/yolk sac
Dispersal	probably low	probably high

right-eyed flounders (pleuronectids) have pelagic eggs. It's possible that spawning demersal eggs may protect the eggs against the risk of freezing and/or also against the low salinity of the surface water (where osmoregulation is difficult) during the melting of the ice.

In demersal spawning fishes there is a more or less continuous line of increasing parental care from deposition of eggs on selected substrate to complete protection of egg masses (Hempel 1979; Gross and Shine 1981). Examples include the eggs of Pacific herring (*Clupea pallasi*), which are plastered on seaweed and no parental care is involved. The male Atlantic spiny lumpsucker (*Eumicrotremus spinosus*) protects the egg mass against a variety of predators and blows water on the egg mass almost continuously for several weeks to increase oxygenation and remove debris. Male lingcod (*Ophiodon elongatus*) protect "nests" of eggs, attacking intruders (including human divers) and picking off snails and other egg-preying invertebrates and small fishes (e.g., sculpins)—normally the only items you find in the stomach of a male lingcod guarding a nest. Some gobies (gobiids) lay their eggs in the shell of a bivalve. Other stages of care include protection by the parent body. Some gunnels (*Pholis* spp.) roll their egg mass into a ball and then one parent coils around the eggs. A well-known example of advanced care is the male sea horses and pipefishes carrying their eggs in the brood pouch. And of course, there is the extreme example of mouth brooding in some freshwater and marine catfishes (siluriforms). Fecundity is generally related to the amount of parental care involved—that is, *the more parental care involved, the lower the fecundity.*

Mating associations in both demersal and pelagic spawners are not related to the type of egg produced, but rather to whether they are schoolers or nonschoolers. Schooling species in which the sexes are notably alike often form large mating associations. Breder and Rosen (1966) say that contrary to general belief, there does not seem to be any evidence of "mass spawning" in the sense of random scattering of the sexual products in a milling school of males and females, although clearly the possibility exists that several males may fertilize the eggs of several females successively.

Bottom-dwelling territorial fishes in which the sexes are notably dimorphic may generally be expected to form breeding pairs and to have demersal eggs. Most of these dimorphic mating pairs with demersal eggs are in fresh water (where nearly all eggs are demersal because of their specific gravity). The fishes in salt water with demersal eggs are found in the nearshore zone and are common from the Arctic (Greenland cod and Arctic flounder) and the Antarctic Shelves (cod icefishes [nototheniids]), and, are also common in the temperate nearshore region, which is unpredictable and changeable. It can be hypothesized that having demersal eggs reduces the risk of getting eggs cast ashore or damaged by abrasion. Fishes with demersal eggs are found not only among families appearing early in the fossil record (i.e., herrings [clupeids], smelts) but also among more recent groups (combtooth blennies [blenniids], sculpins, greenlings, etc.).

Common expressions of parental care are nest building, nest cleaning (removal of dead eggs and decaying matter from the nest), and fanning (behavior for aeration), and guarding (predator removal, e.g., lingcod). In a wide variety of fishes the eggs are laid in nests constructed by the parents. In most cases the male builds the nest and attracts the female to lay her eggs there, where he fertilizes them. In many fishes the eggs are guarded from predators, aerated, and cleaned during development by one or both parents. Care often extends for some time after the eggs hatch. Examples of fishes exhibiting the guarding behavior mode include most sunfishes (centrarchids) and sculpins. However, some fishes that build nests for the eggs or hide them take no further care of them. For example, Pacific salmon (*Oncorhynchus* spp.) lay their eggs in depressions (called redds) they dig in the gravel of the streambed, but the adults die shortly thereafter.

Pelagic Eggs. For the majority of marine fishes that are pelagic spawners, there is little to say about modes of reproduction. As previously mentioned, the male and female swim close together and the eggs and sperm are broadcast into the water. No parental care is involved with the eggs and the spent (spawned-out) adults may resume their prespawning activities. This is the most common spawning mode in the marine environment regardless of whether the habitat is demersal or pelagic, whether it is a coastal or oceanic distribution, whether tropical or boreal ranges, and whatever the systematic affinities are. Out of about 12,000 marine teleosts, about 9,000 (75%) produce pelagic (buoyant) eggs and the eggs are spawned, fertilized, and float individually (although a few species have floating egg masses), usually near the surface. The large number of eggs produced and their rapid dispersal makes it impossible for the adults to show any form of parental care. Sexual dimorphism and dichromism are reduced or absent in pelagic spawners.

A few pelagic spawners lay pelagic eggs in gelatinous masses. Goosefishes (*Lophius* spp.) and thornyheads (*Sebastolobus* spp.) are among these. Thousands to millions of eggs are produced by each female in these cases, and the egg masses can be quite large (several liters). However, the large majority of marine fishes lay pelagic eggs that float individually in the water. The eggs are spawned, fertilized, and develop in the water column as part of the plankton. Rather than caring for the eggs, cannibalism by the adults can be a significant source of mortality in some fishes with planktonic eggs.

GONADAL DEVELOPMENT

Gonads

Female fish have paired ovaries that produce eggs, and male fish have paired testes that produce sperm, which along with seminal fluid is termed *milt.* Although this is the general rule, there are many exceptions. Some fish change sex during their lifetime, some from male to female (protogynous hermaphrodites) and some from female to male (protandrous hermaphrodites), whereas some even produce both sperm and eggs simultaneously (synchronous hermaphrodites). Most fishes are capable of spawning several times during their life (semelparous); however, a few (e.g., Pacific salmon, freshwater eels [anguillids]) spawn once and die (iteroparous).

Oogenesis (Figure 1.2) and Spermatogenesis

Oogenesis is the process that results in the formation of a haploid cell and a mature egg capable of supporting a developing embryo (Foucher and Beamish 1977). The basic stages are the duplication phase, primary growth phase, follicle development, yolk vesicle formation, vitellogenesis and envelope formation, maturation, ovulation, and the spawning-fertilization and egg activation stage.

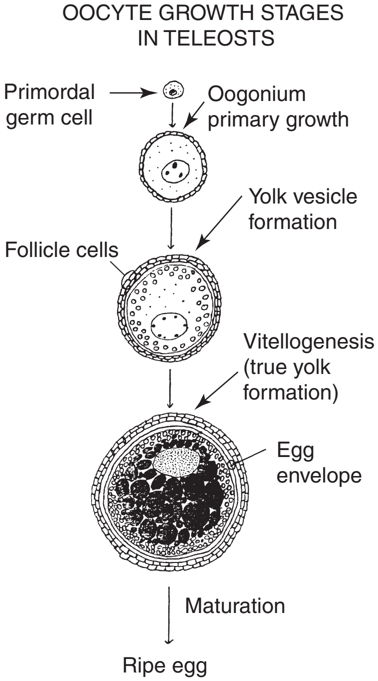

Figure 1.2. Oogenesis in teleosts (adapted from Carla Stehr, personal communication).

Duplication Phase. The ovary and oogonia develop from primordial germ cells, which are endodermal in origin. The reserve oogonia undergo repeated mitotic divisions (remaining diploid), and are no longer oogonia after mitosis stops—this is the starting point for oocytes.

Primary Growth Phase. The growth of the primary oocytes which occurs when they are still diploid cells, and ends with a meiotic division forming a secondary oocyte and a polar body each of which are haploid.

Maturation Phase. The secondary oocyte undergoes a second meiotic division resulting in a mature ovum and another polar body, whereas the first polar body may divide into two polar bodies (i.e., results in three polar bodies and one ovum); the polar bodies are eventually resorbed. Follicle development, yolk vesicle formation, vitellogenesis, and envelope formation are occurring during the maturation phase.

Follicle Development. This refers to the structure formed surrounding the developing oocytes, which is formed by two layers of cells that are the outside theca cells and the inside follicle cells (also called the glandular granulosa).

Yolk Vesicle Formation. The formation of yolk vesicles—a misnomer because they are not true yolk, but instead, they contain polysaccharides; they are also known as cortical alveoli. Generally, cortical alveoli are found around the periphery of the oocyte.

Vitellogenesis. This is stimulated by pituitary gonadotropin (Figure 1.3) and is a true yolk formation where the yolk forms and pushes the cortical alveoli to the margins. Microvilli extend from follicle cell (or oocyte) cytoplasm through pore canals providing passageways to transport yolk material and nutrients across membranes to oocytes. Proteins produced in the liver are carried by blood vessels to the follicles, which transfer them to the oocyte cytoplasm where they are assembled into yolk.

Envelope Formation. This occurs during yolk vesicle formation and vitellogenesis. The egg envelope may also be called the chorion, zona pellucida, zona radiata, or vitelline membrane. We prefer the term "envelope" over the more commonly used mammal term "chorion," because "chorion" suggests a cellular layer on the outside, which is not the case in fish eggs. However, chorion is most commonly used in fish literature. The envelope may be composed of as many as three layers, namely: (1) The primary layer, which is produced by the egg, is the innermost layer and is the true "envelope" layer. The primary layer is usually the only envelope present in pelagic eggs for buoyancy reasons, and to allow for the remnants of the pore canals to be seen externally on the egg; (2) the secondary layer, which is produced by the follicle cells (maternal tissue) after rupture, and which usually is found in demersal eggs (if this layer

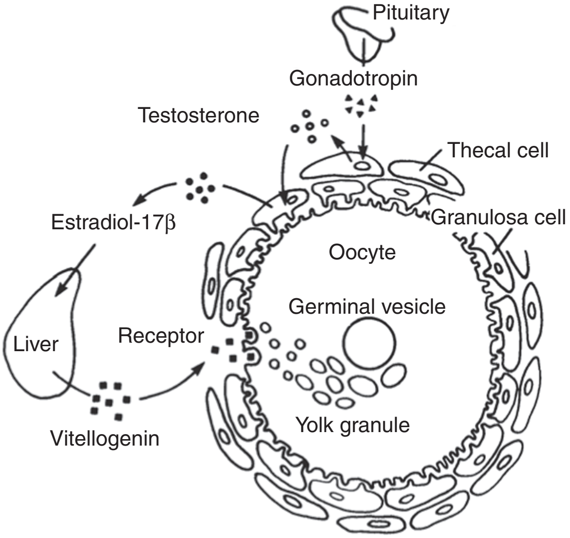

Figure 1.3. Hormonal regulation of vitellogenesis in fishes (from Nagahama et al. 1995).

is present, the remnant pore canals cannot be seen externally); and (3) the tertiary layer, which is produced by the ovary after the egg has ovulated—not common, but present in sharks and rays (elasmobranchs).

Maturation. This is stimulated by steroids, which are produced by follicle cells. At this point the oocyte undergoes the final meiotic division, the oocyte begins to hydrate by taking up ovarian fluid, the egg increases 3–4 times its size, the microvilli withdraw from pore canals which shut off as the egg imbibes body fluid, the yolk coalesces, and the envelope stretches.

Ovulation. This occurs when the follicle cells burst as oocytes hydrate. Not all eggs are ovulated, but there are usually varying amounts of atresia thought to occur due to such things as stress, nutritional factors, and gonadotropin; atretic eggs are reabsorbed.

GROSS MATURATION STAGES

Introduction

A record of the state of maturity of fish is often required to determine the proportion of the stock that is reproductively mature, the size or age at first maturity, the current reproductive status, and the nature of the reproductive cycle for a particular population or species. Some of the general ways of determining the reproductive state are by staging of ovaries using gross anatomical criteria, calculation of Gonadal-Somatic Index (GSI) or Egg Mass Ratio (EMR), by classifying ovaries histologically, and by use of mean egg diameters.

Gross Anatomical Examination

Gross examination can be done because although maturation of the gonads occurs at a cellular level, the maturation state or the spawning state of the gonads can be determined upon gross visual examination of the gonads in the field. This is a particularly useful technique when you are on a trawler or at the fish market and it is not feasible to examine gonads in detail. For this purpose a field key is often handy as an aid in judging the general appearance and size of the gonads. An important aspect of such a classification is that it be standardized. Fortunately, in fishes with one short, clear-cut spawning season per year, there are a number of stages visible by macroscopic inspection. In general, the immature stage (or resting stage) usually covers the major part of the year and is characterized by a very thin ovary similar to that in a juvenile (immature) fish, although the wall of the ovary is usually thicker in repeat spawners than in recruit spawners advancing toward maturity. After the immature stage, there are a number of preparatory phases to spawning which are actually continuous with the immature stage but which investigators have attempted to define for classification purposes. In general terms, there is the "developing" stage during which sperm and eggs are developing, then the "mature" stage characterized by large testes and large ovaries with eggs filled with yellow yolk, which usually are visible through the body wall. Ovulation takes place, the eggs become transparent from the intake of body fluid, and the female is ready to spawn—this is the spawning (or "ripe") stage. (A live fish is referred to as "ripe and running" if pressure on the abdomen results in eggs or sperm being released.) After spawning, the ovary is soft and bloody with some unshed eggs and the fish is referred to as spent (or "spawned out")—the unshed eggs will be resorbed during the recovery phase. In summary, the simplest classification scheme includes the following stages: **Immature, Developing, Mature, Spawning, Spent,** and **Recovery.** Do not dismiss the usefulness of the gross anatomy observations—they are especially valuable when combined with one of the other ways of examining maturity stages (similar to the usefulness of gross pathology observations to histopathology).

Example of Maturity Classification

A more detailed classification system is used by NOAA-Fisheries for walleye pollock (*Theragra chalcogramma*) (Table 1.3).

TABLE 1.3. Maturity Stages (by Code Number) for Walleye Pollock (Sarah Hinckley, personal communication)

Males		
1	Immature	Testes thread-like and contained within a transparent membrane.
2	Developing	Testes uniformly ribbon-like. Surface of testes appears smooth and uniformly textured.
3	Mature	Testes large and highly convoluted; sperm cannot be extruded. Body wall incision causes gonads to be expelled from opening.
4	Spawning	Testes milk freely or extrude sperm when compressed.
5	Spent	Testes large, but flaccid, watery, and bloodshot.
Females		
1	Immature	Ovaries small, tapered, and transparent. Will not spawn this year. Sex may be difficult to determine.
2	Developing	Early: Ovaries tapered, forming two distinct, transparent lobes with well-developed blood vessels. No or few individual ova present. Late: Developing lobes fill up to half of the body cavity, with distinctly visible opaque, orange eggs.
3	Mature	Ovaries fill more than half of the body cavity and contain distinctly visible eggs. Eggs are not extruded when ovaries are compressed. Most eggs are opaque, but scattered clear (hydrated) eggs may be present. Eggs cannot be easily separated from each other.
4	Spawning	Ovaries large, filling the body cavity. Most eggs are transparent (hydrated) though some opaque eggs may remain. Eggs are extruded from the body under slight pressure or are loose in the ovary and easily separated from each other.
5	Spent	Ovaries are large, but flaccid, watery, and generally reddish. Scattered unspawned eggs can be seen. Ovaries that are “Recovering” will appear red and contain scattered eggs, but will not be as large or quite as flaccid as very recently spawned ovaries, and should be classified as “Early Developing.”

NOTE: For both males and females, codes 2 through 5 refer to adult fish.

Egg Mass Ratio (EMR) and Gonadal-Somatic Index (GSI)

The EMR and GSI measure reproductive strain on fishes by measuring general body weight ratios. When males and females are compared, females invest more energy in gonads than males although in pelagic spawners it may be more similar since males need to produce a lot of sperm to ensure fertilization; however, the investment of females is still many times greater than males. These indexes are calculated as follows:

$$\text{EMR} = \frac{\text{Total wt. of all eggs in one season (dry wt. in g or cal)}}{\text{Body wt. (including ovary)}}$$

$$\text{GSI} = \frac{\text{Gonad wt. (g or cal)}}{\text{Body wt. (including gonad)}}$$

FECUNDITY

Fecundity, the number of eggs ripened by female fish during a spawning season, or event, varies from a few dozen in some continuously reproducing livebearing fishes to millions in some species that spawn pelagic eggs on an annual basis. In general, fecundity varies among species inversely with the amount of "care" given to the individual progeny: viviparous fishes have lower fecundity than ovoviviparous fishes, which in turn have lower fecundity than oviparous fishes, and nest builders have lower fecundity than pelagic spawners. Within species fecundity is positively related to size; generally it is close to a function of the cube of fish length. Although fish eggs range from about 0.5 to 20 mm in diameter, the size of the adult limits the fecundity in smaller species. In most species with high fecundity, several batches of eggs are usually produced at intervals of a few days to weeks during the spawning season.

General Uses

Some general reasons for determining fecundity is that it is useful for making total population estimates, it is useful in studies of population dynamics or productivity, and it is useful for characterizing specific populations, subpopulations, and/or stocks of fishes.

Definitions

"Absolute fecundity" is the number of ripe eggs produced by a female in one spawning season or year (this is the usual meaning when the general term "fecundity" is used, although on occasion it might also mean the number of eggs produced in a lifetime). "Relative fecundity" is the number of eggs produced in a season per unit somatic weight of the fish (i.e., eggs/gram), and is useful if it is shown that the fecundity of a fish is proportional to its weight, which is not uncommon. "Population fecundity" is the number of eggs spawned by the population in one season, is the sum of the fecundities of all females, and is usually expressed as the product of the expected fecundity of an average female × the number of breeding females in the population (an example of why classifying maturity stages may be useful).

Absolute fecundity varies with age, length, weight, and type of fish (species and population). For example, sharks and rays have few eggs whereas ocean sunfish have up to 300 million. The highest fecundity is in pelagic spawners, 100,000 to millions (e.g., Atlantic and Pacific cod [*Gadus* spp.] with several million). Intermediate fecundities are found in demersal spawners (1,000 to 10,000, although there are exceptions like the lingcod with 500,000). The lowest fecundity is in live-bearing fishes with few to 100 or so (usually less), although there are quite a few exceptions including rockfishes which often extrude > 100,000 larvae, but which developmentally are closer to the larval stage of pelagic spawners than of other live-bearers, or even of demersal egg spawners. Fecundity is also affected by the nutritional status of the female, and in the population there may also be compensatory mechanisms regulating fecundity.

Many investigators have made scatter plots of fecundity versus length and have come up with the general relationship where the increase in fecundity with length can be described by the power relationship $F = aL^b$, where F = fecundity, a = constant, L = length, and b = nearly 3. A logarithmic transformation gives the straight-line regression of log (or natural log, ln) fecundity on log length, which helps take care of the problem of the larger fish having greater variation in fecundity than the smaller, that is,

$\log F = \log a + b \log L$. (Equation is of the simple $y = a + bx$ form, i.e., if $\log F = y$, and $\log a = a$, and $b = b$, and $\log L = x$, then $y = a + bx$.)

When $b \cong 3$, it means F is about proportional to the fish weight because of the surface area-to-volume ratio and allometric growth; that is, as the fish grows in length, the volume (weight or fecundity) gets larger to the cube. However, for Atlantic herring (*Clupea harengus*) stocks, in some situations, values between 3 and 7 have been found, indicating fecundity was increasing faster than body weight (Hempel 1979). For many stocks, in terms of egg production of a population, this implies that if F increases with a power of L higher than 3, a stock of large (and old) fish will produce far more eggs than a spawning stock of the same total weight but consisting of mainly small fish (Figure 1.4). This is an obviously important concept to consider when managing a fishery, but is also an important concept to consider in reproductive ecology and recruitment ecology studies. As fish mature, they have a much higher fecundity because less energy is devoted to growth so more can be given to reproduction.

Variations in Fecundity

Relationships between fecundity and age and weight are not as apparent as with length because there is too much variation in age and weight. This is also a problem with using GSIs to compare fecundities of different fishes from different years, from different localities, and when fish are of different sizes.

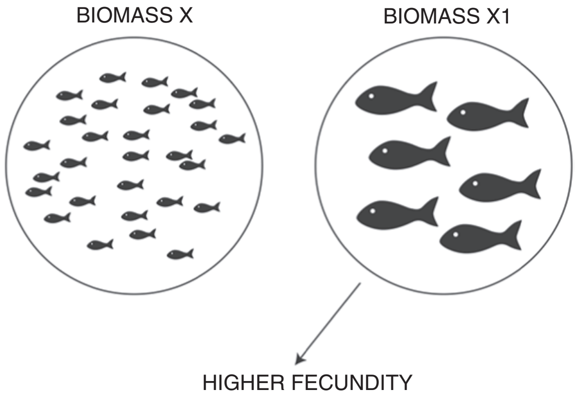

Figure 1.4. Concept of two spawning stocks of the same species and same total weight (biomass), but with one stock (X) composed of mainly small fish and the other stock (X1) of fewer but larger (and older) fish producing far more eggs.

In general, within a population, the size of ripe eggs is not very variable, regardless of the fish size or age. However, there is a relationship between egg size and environmental conditions. For example, there is some evidence that shows a negative correlation between the condition of the mother and egg size—that is, well-fed fish produce more but smaller eggs. Comparisons between species and populations also show that the size of the egg (and of the newly hatched larvae) is negatively correlated with fecundity. Larger eggs have more yolk, which is an extended protection strategy so that when the egg hatches the larva has more yolk although it is now independent of the mother.

One way to think of this is that the production of large eggs with considerable yolk supply and large initial size of the larvae is a kind of extended maternal care for the individual offspring, whereas a high number of small eggs can be considered as a protective measure to ensure survival of the species against high egg and larval mortality, particularly by predation. This argument has been used in the interpretation of fecundity differences between various herring populations in the North Sea, which spawn at different seasons with the result that larvae face different conditions (Hempel 1979). Thus, herring spawning in winter produce large eggs in low numbers, whereas summer spawners produce much smaller eggs in high quantity. The newly hatched larvae of the winter herring meet fewer predators but also less of the very small food organisms that are present for the summer spawners. The general validity of this hypothesis needs much more testing.

These concepts (and other relationships thought to be true) were presented in the 1975 thought-provoking paper by Johnson and Barnett. In their study, "midwater fishes" are real midwater, not herring, but viperfishes (chauliodontids), which live at depths of hundreds of meters. Table 1.4

TABLE 1.4. Larval Survival and Natural Selection (based on Johnson and Barnett 1975)

Productivity Regime	*Average Egg Size*	*Average Fecundity*	*Average Larval Size*	*Number of Meristics*
Less productive—low food densities (danger of larval starvation)	Larger	Lower	Larger	Higher
More productive—high predator densities (danger of predation on larvae)	Smaller	Higher	Smaller	Lower

summarizes the authors' findings (how natural selection favors larval survival, based on similar reasoning as in the winter-summer spawning herring concept given previously).

There was definitely a negative correlation found between three measures of productivity and meristic values (anal fin rays, vertebrae, longitudinal photophores). Measures of productivity were phosphate-phosphorus concentrations, net primary production, and zooplankton standing stocks. Meristics were found not to correlate with temperature, salinity, oxygen, or any other physical or chemical factor known to possibly affect meristic variation in fishes.

What these authors are hypothesizing is that the inverse relationship between meristic values and measures of food availability reflects adaptations to low food densities (for larvae) in areas of low productivity and higher predator densities in areas of higher productivity. Their reasoning is that in areas of low food densities, natural selection has favored mechanisms tending to offset the danger of larval starvation (i.e., larger egg size, lower fecundity, larger larval size).

The advantages of being a larger larva in areas of low food density include (1) a longer period of survivorship solely on yolk reserves, (2) increased mobility, (3) wider search volume, and (4) increased diversity of potential prey organisms. Presumably, in areas of high productivity, the danger of starvation is less, but the danger of predation (more potential fish egg and larvae predators) is greater. Here, selection favors smaller average egg size, higher fecundity, and smaller average larval size, the theory being that the increased number of eggs and larvae overwhelms or saturates the predators so that at least some eggs and larvae survive.

Finally, these authors hypothesize that the inverse correlation between productivity and number of meristics is explained by the findings of others that large egg size may result in a longer embryonic and larval duration during which the meristic values are being determined and which will result in higher meristic values.

The caveat is that unfortunately almost no actual data exist for midwater fishes to test their hypothesis—e.g., nothing is known for midwater fishes about age and size at first spawning, number of spawnings per female, fecundity, seasonality of reproduction, course of larval development, or factors actually determining survivorship of larvae. The advantage of using midwater fishes was that reliable productivity measurements were available for the oceanic regimes they are found in, which is not the case with most other groups of fishes, especially nearshore fishes, upon which most experimental meristics and developmental work has been done.

Methods of Estimating Fecundity

Mean Ova Diameter Determination. For many fishes, as part of a fecundity determination, it is important to first do an ova diameter analysis by measuring a representative sample of eggs in the ovary when they are close to being spawned. Plotting of mean ova diameters, for many temperate water fishes, indicates the eggs to be spawned in the present year, and those to be spawned in future years. Laboratory Exercise 1 indicates the general technique followed in doing ova diameter measurements.

Histological Examination. The best method for determining if multiple spawnings are occurring is a histological examination. This must be done if the fish species is a multiple spawner; for example, the northern anchovy (*Engraulis mordax*). The frequency of multiple spawning can be determined by using postovulatory follicles (cannot tell grossly, and often not clear by measuring ova diameter). Ovaries can also be distinguished between immature and postovulatory ovaries by using histology—that is, atresia can easily be seen. For more about this method, see Laboratory Exercise 2.

Fecundity Estimation Techniques. Fecundity is generally estimated by using a volumetric technique, a wet or dry weight technique, or use of a device that is able to actually count individual eggs. The volumetric and weight techniques rely on simple proportionality to estimate the total fecundity from a known number of eggs in a known volume or weight of a subsample, and a known value for the total volume or weight of the sample, and then calculate the total number of eggs in the ovary. The real trick is to make sure that the subsample is truly representative of the whole ovary. Laboratory Exercise 3 demonstrates the fecundity determination technique for the volumetric and wet weight methods.

SPAWNING

Introduction and Terminology

Spawning refers to the release of unfertilized planktonic eggs by female fish, which is the reproductive pattern for most marine fishes. The eggs are fertilized shortly after release by males. Some fishes also deposit unfertilized eggs in nests where they are fertilized and develop. Fishes with internal fertilization release free-swimming larvae, or juveniles. The ripening of eggs and spawning are controlled by hormones, nutrition of the female, and external (ecological) factors (Hempel 1979). Usually maturation and spawning are controlled by a combination of endogenous and exogenous controls and are not governed by any specific factor.

TERMINOLOGY USED IN DISCUSSING SPAWNING

Mating pairing (one-on-one) for the purpose of fertilizing eggs; copulatory organ present.

Spawning release of unfertilized eggs into the environment or release of larvae into the environment; mating and spawning need not occur simultaneously (e.g., surfperches). Spawning can occur without true mating (e.g., herring, which are broadcast spawners).

Fertilization fusion of eggs and sperm (creating diploids from haploids); mating and fertilization need not occur simultaneously (e.g., surfperches and rockfishes).

Incubation time time from egg fertilization to hatching.

Gestation applies only to live-bearing fishes; it is the time young stay within the female.

Hatching when the larva frees itself from the egg.

Breed to produce offspring by hatching (or gestation).

Brood guard and groom eggs until they hatch.

Factors Triggering Maturation and Spawning

There are three primary factors that influence the events leading up to spawning: nutritional state of the female, physiological factors (hormones), and ecological factors.

Nutrition of the Female. The feeding condition of the mother can have an important effect on the final maturation of the eggs. Two examples from Hempel (1979) show that in some of the Atlantic herring populations spawning may occur only every other year if environmental conditions, particularly those affecting food supply, are poor. Also, it has been found in the laboratory that in Atlantic sole (*Solea solea*) no spawning occurred when the flatfish were fed a diet (mussels only) deficient in certain amino acids; however, when the flatfish were force-fed the missing amino acids they spawned, indicating the ovary had been unable to obtain the needed amino acids from maternal tissue when the nutrition of the female had been inadequate (Hempel 1979).

Physiological Factors. Hormones govern migration and timing of reproduction, morphological changes, mobilization of energy reserves, and elicit intricate courtship behavior. The pituitary is the major endocrine gland that produces gonadotropin, which controls gametogenesis, the production of gametes, namely sperm (spermatogenesis) and eggs (oogenesis), by the gonads. The pituitary also controls the production of steroids (steroidogenesis) by the gonads; once the gonads are stimulated by the pituitary they begin producing steroids, which in turn control yolk formation (vitellogenesis) and spawning. The control of spawning by the pituitary is often used in fish farming such as in the production of caviar from sturgeon (*Acipenser* spp.) where spawning is induced by injecting pituitary extract at a late stage of gonadal development, usually in combination with changes in temperature and light periodicity.

Ecological Factors. Often ecological factors are associated with timing so that food availability is optimal for the larvae. Some ecological factors important to spawning are temperature, photoperiod, tides, latitude, water depth, substrate type, salinity, and exposure.

TEMPERATURE. An important factor in determining geographical distributions of fishes. Although little is known about the mechanism by which temperature controls maturation and spawning in fishes, for many marine and freshwater fishes the temperature range in which spawning occurs is rather narrow, so that in higher latitudes the minimum and maximum temperature requirement for spawning is often the limiting factor for geographical distribution and for the successful introduction of a species into a new habitat. For example, Pacific halibut (*Hippoglossus stenolepis*) are found spawning primarily in areas with a 3–8°C temperature on the bottom and therefore do not spawn in Puget Sound, although the adults are caught in the northern areas of Puget Sound. In fact, even in highly migratory tuna, spawning is restricted to water of specific temperature ranges.

PHOTOPERIOD AND PERIODICITY. The daylength (photoperiod), in some cases at least, is thought to influence the thyroid gland and through this the fishes' migratory activity, which is related to gondal development (maturation). In the northern anchovy, by combining the effects of temperature and daylength, continued production of eggs under laboratory conditions was brought about by keeping the fish under constant temperature conditions of 15°C and a light periodicity of less than 5 hours of light per day (Lasker personal communication). In high latitudes, spawning is usually associated with a definite photoperiod (and temperature), which dictates seasonal pulses of primary production in temperate regions to assure survival of larvae. In low latitudes, where there is little variation in daylength, temperature, and food production, other factors may be important such as timing with the monsoons, competition for spawning sites, living space, or food selection.

Reproductive periodicity among fishes varies from having a short annual reproductive period to being almost continuous. There is a tendency for the length of the reproductive period to shorten with increasing latitude. Thus tropical fishes spawn nearly continuously, whereas subarctic fishes spawn predictably during the same few weeks each year. Presumably times of spawning have evolved so larval development will coincide with an abundant food supply. Within spawning seasons, fish may spawn on a daily or monthly tidal cycle or on a diel cycle, or in association with some other environmental cue, such as a change in daylength, temperature, or runoff. A notable instance of spawning periodicity associated with the tidal cycle is the California grunion (*Leuresthes tenuis*), which spawns intertidally at the peak of the spring high tides (Walker 1952). Within species, spawning times may vary with latitude: Generally, in species that spawn as daylength increases, spawning occurs earlier in the year in lower latitudes than at higher latitudes. In species that spawn as daylength decreases, spawning takes place earlier in the year at higher latitudes than at lower latitudes.

TIDES (MOON CYCLES). The dependence of spawning on moon cycles in California grunion spawning on California beaches is an extreme example of external factors controlling reproduction in fishes. Grunion are adapted to spawning on the beach every two weeks in the spring during a new or full moon. Spawning is just after the highest high tide (Figure 1.5); therefore, eggs deposited in the sand are not disturbed by the surf for 10 days to a month later. Eggs will hatch when placed in agitated water (which simulates surf conditions). In Puget Sound, surf smelt (*Hypomesus pretiosus*) spawn year-round, except in March. Surf smelt deposit eggs at high tide in sand and gravel (but not necessarily at the highest tide). On the open ocean shores, spawning occurs at midtidal heights (for different subpopulations) (Dan Pentilla personal communication).

LATITUDE AND LOCALITY (Table 1.5). Pacific herring show a definite relationship between latitude and spawning time. Spawning is early in San Francisco (December, January); later in Washington State (February, March, April, May); and still later in Alaska (April, May, June). These fishes are perhaps of different, distinct subpopulations.

In temperate waters a biomodal distribution of eggs is usually seen, which indicates discontinuous spawners (Figure 1.6). The smaller-sized mode represents resting eggs for a future spawning, and the larger mode represents maturing eggs (oocytes), which will presumably be spawned within the year. Temperate water fishes are also usually deterministic, which means all eggs to be spawned are determined at the start of the year.

A polymodal distribution of eggs is typical of tropical areas and some temperate water fishes, which signifies continuous or serial spawners, and indicates several spawnings. A well-known temperate example would be Pacific sardine (*Sardinops sagax*), which spend 7 months spawning and 2 months developing/maturing (Clark 1934). Batch spawning has been

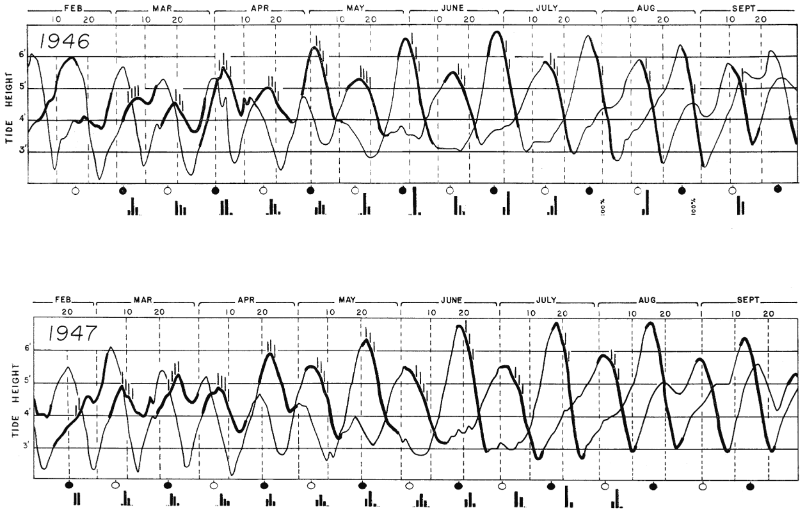

Figure 1.5. California grunion (*Leuresthes tenuis*) runs observed at La Jolla, California, in 1946 and 1947, plotted in relation to variations in observed high-tide heights at La Jolla. Only the heights of high tides have been plotted. The high tides about 24 hours apart have been connected by smooth lines. The two tides of each day yield the two series of curves. Tides occurring during darkness are indicated by the heavier lines. The occurrence of grunion runs is indicated by the short, vertical lines above the tide curves. The moon phases are indicated at the bottom of each graph. A solid circle indicates new moon and a hollow circle indicates full moon. The histograms at the bottom portray the percentage intensity of runs in each series. Seasonal variation in strength of runs is not indicated. All data are based on observations made at Scripps Beach, La Jolla. Data for time and height of tides are from records of the tide-recording machine maintained for the Coast and Geodetic Survey on Scripps Pier (from Walker 1952).

described for northern anchovies (Laroche and Richardson 1983). Tropical spawners are usually nondeterministic, which means the eggs to be spawned are not determined at the start of the year but are produced throughout the year; however, nondeterministic can also represent the spawning potential for successive years, an example being the Atlantic cod (*Gadus morhua*), which will have several years' spawn in the ovary.

In general, older fish usually spawn first and younger fish later, which means that a prolonged spawning period for a population may not be true for individual fish. Once a set of eggs is mature and hydrated, the female may release them all at once or in several batches. An example of releasing several batches is plaice (*Pleuronectes platessa*), where a single

TABLE 1.5. Summary of Spawning Variation with Latitude

	Temperate Latitudes	*Tropical Latitudes*
Timing	Early winter, spring	Late (spring, summer, or continuous)
Duration	Short (3–4 months)	Long (5–6 months or more)
Frequency (per year)	Once (refers to entire group of eggs to be spawned, not how spawned)	Several times

female two weeks after releasing one batch of eggs releases more eggs, and then three weeks later she releases the remaining eggs. Another example is the Pacific herring, which spawn once a year and females lay about 100 eggs per spawning act, which they repeat several hundred times over a few days (Hourston and Haegele 1980). In the lab, walleye pollock spawned an average of nine times in an average period of 27 days (Sakurai 1983).

It also needs mentioning that a long duration of the spawning season of a population cannot necessarily be taken as an indication of prolonged spawning of the individual fish. The prolonged period may be due to differences in spawning time between age groups since older fish tend to spawn earlier in the season. Furthermore, the coexistence of different spawning subpopulations must be taken into account, since winter and summer spawners may be distinct stocks, although shifts from one seasonal spawning pattern to the other may occur. An example of how unpredictable this can be is that certain Atlantic herring of low fecundity have been found to always spawn in the winter, regardless of whether they originated from winter or summer spawning (Hempel 1979).

WATER DEPTH. Pacific herring spawn along beaches, marine grasses, and algae. Atlantic herring do not spawn along shore but in deeper water up to 200 m (the clearest difference between the Pacific and Atlantic herring,

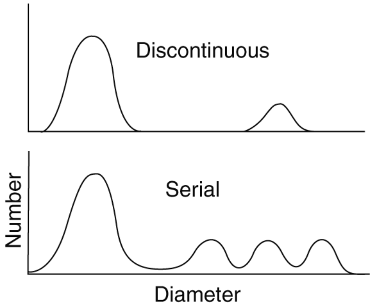

Figure 1.6. Differences in size distribution of oocytes of discontinuous and serial spawners (from Hempel 1979).

which are usually designated distinct species on the basis of genetic analysis). Of course fishes often spawn at one depth but live at different depths during other times of the year. For example, petrale sole (*Eopsetta jordani*), in which spawning occurs in a specific offshore area 300–400 m deep, were found by fishermen and eventually had to be protected with regulations to prevent overfishing (A.C. Delacy personal communication).

SPAWNING SUBSTRATE TYPE. Pacific herring spawn on vegetation whereas Atlantic herring spawn on solid substrate (e.g., gravel). Lingcod spawn on rocks, pilings, and cracks in solid substrate; this species protects the egg mass. Some species such as buffalo sculpin (*Enophrys bison*) and plainfin midshipman (*Porichthys notatus*) spawn intertidally and will stay with the egg mass even when they are exposed at a low tide.

SALINITY. Also a factor affecting spawning. There are varying salinities in many areas of estuaries. Some species will shift spawning sites because of salinity changes. Various degrees of mixing, precipitation, and freshwater runoff may alter spawning habits.

EXPOSURE AND TEMPERATURE. A clear example of shifting spawning sites in response to temperature and exposure is the black prickleback (*Xiphister atropurpureus*), where spawning is shifted from winter in protected areas to spring in exposed areas (Marliave 1975). The complex effects of lower or higher wave action and lower or higher temperatures on courtship, gonadal development, and spawning behavior that result in the spawning site shift.

Lifetime Spawning Strategies

TERMINOLOGY

Semelparous: spawn only once in a lifetime (e.g., many anadromous fishes, the common example is the Pacific salmon).
Iteroparous: spawn many times in a lifetime (e.g., most marine fishes).

Within the same species of fishes one can find two different strategies presumably due to ecological differences, the classic example being American shad (*Alosa sapidissima*), which is entirely semelparous in Florida, whereas those north in the New Brunswick area are ~ 50 to 75% iteroparous, and intermediate populations have intermediate values (T. Quinn personal communication). The explanation is that northern rivers are a more harsh and variable environment for eggs and larvae so iteroparity is a better strategy for this species.

Sites

Many fishes use only a portion of their overall range for reproduction. Many species return to natal areas to reproduce, the Pacific salmon being the best known and most extreme example of this pattern. Adult salmon spend from one to several years in the open Pacific Ocean, and return to their natal streams, which may be hundreds of kilometers from the ocean, to spawn. Even fishes that spend their entire life in the ocean, or a freshwater stream or lake, often select a particular part of their habitat for reproduction.

Migrations. Spawning migrations may require fish to move hundreds of kilometers, or from one depth range to another. The anadromous pattern of salmon and striped bass (*Morone saxatilis*), where the fish move from the marine environment to the estuarine or freshwater environment for spawning, is contrasted to the catadromous pattern of American and European freshwater eels (Anguillidae), which descend rivers and migrate to the Sargasso Sea in the North Atlantic for spawning. Aside from these extremes, most fish move from feeding areas to congregate in spawning areas. Presumably these areas have been selected through evolution to provide a suitable environment for survival of the eggs and larvae.

Habitats. The habitats utilized by fishes for reproduction and development are quite varied. The essentials of the habitat for eggs and larvae are that it remains oxygenated and within temperature and water quality requirements suitable for development. Ecological considerations include protection from predators and microbes, and production of adequate food for the larvae. Most marine fishes produce planktonic eggs and larvae that drift in the upper 200 m of the ocean, although some regularly occur much deeper. Many fishes that occupy much greater depths as adults undergo early development in the epipelagic zone. Various species of fishes build nests or deposit eggs in a wide variety of places. Many fishes dig a nest in the bottom where they deposit and sometimes guard their eggs. Species may have very specific substrate requirements for nest building. Many freshwater and some marine fishes deposit adhesive eggs on the surface of the bottom (gravel or rocks) or plants. The depth chosen for deposition of demersal eggs may be very specific, especially in fishes that spawn intertidally where there is danger of dessication, or exposure to temperature and salinity extremes. Some deposit their eggs in other animals such as clams or crabs in a parasitic relationship.

Behavior

Reproductive behavior of fishes generally involves some sort of courtship, which may aid in species and spawning-readiness recognition. Pairing of individuals probably occurs even when fish appear to spawn in large schools. Communication among potential mates may include visual, olfactory, and auditory cues. As courtship proceeds, the mates eventually swim together with their genital openings touching. Male and female gametes are then released simultaneously. In the case of nesting fishes, the female often deposits a number of eggs, which the male then swims over as he releases sperm (milt). In fishes with internal fertilization the male possesses an intromittent organ to deposit sperm into the female, either directly into the ovary, or into a sperm storage area.

Secondary Sexual Characters

The sexes of species that produce pelagic eggs are generally indistinguishable except for their gonads, and the larger size attained by the females. However, as parental care increases, so do differences between the sexes. Sexual dimorphism includes the intromittent organs of males in species with internal fertilization, and morphological adaptations for nest building and guarding. Sexual dichromatism occurs in some species, apparently as an aid in mate recognition. The ultimate in sexual dimorphism is found in some anglerfishes (ceratioids) in which the males are parasitic on the females.