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Timing reproduction in teleost fish: cues and mechanisms

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Fish comprise half of extant vertebrate species and use a rich variety of reproductive strategies that have yielded insights into the basic mechanisms that evolved for sex. To maximize the chances of fertilization and survival of offspring, fish species time reproduction to occur at optimal times. For years, ethologists have performed painstaking experiments to identify sensory inputs and behavioral outputs of the brain during mating. Here we review known mechanisms that generate sexual behavior, focusing on the factors that govern the timing of these displays. The development of new technologies, including high-throughput sequencing and genome engineering, has the potential to provide novel insights into how the vertebrate brain consummates mating at the appropriate time.

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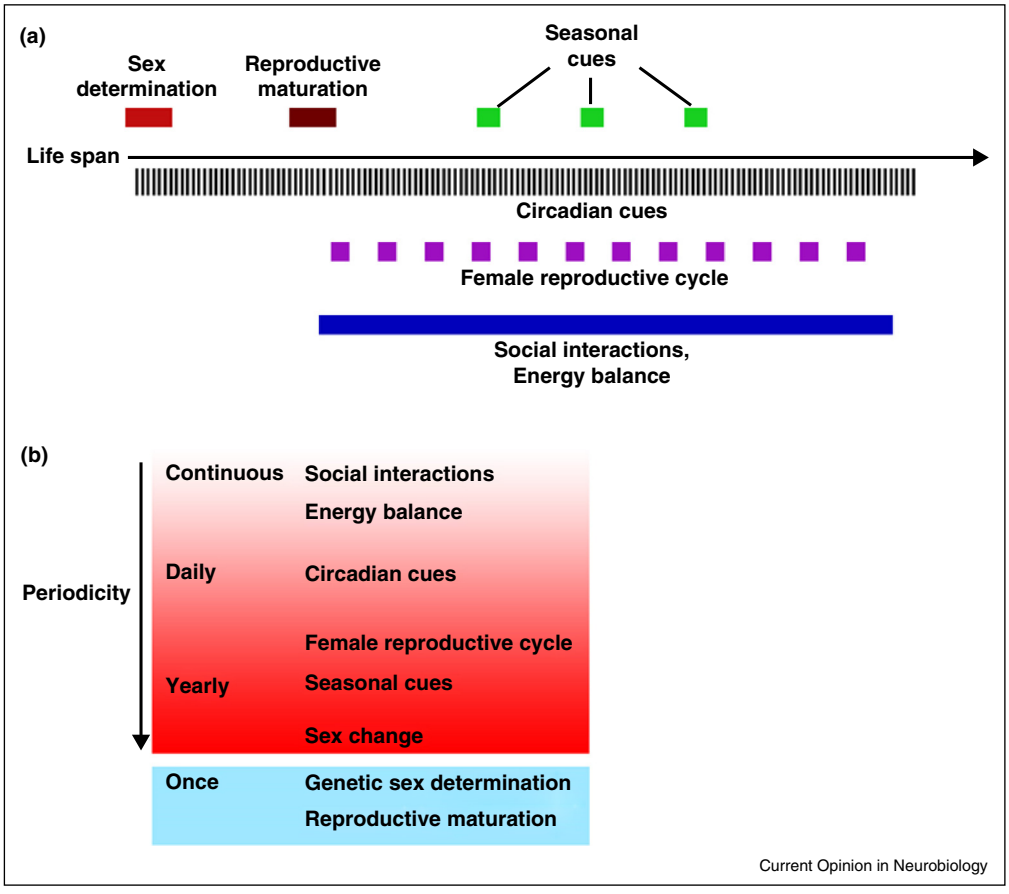
All animals face the critical challenge of deciding when to mate, to maximize their lifetime reproductive success. The factors that regulate the timing of mating can be divided into two groups, which we will call 'chronological' and 'continuous' (Figure 1). Chronological factors promote reproduction in specific, restricted time windows, while continuous factors may affect reproduction at any time. Among chronological factors are processes such as sexual differentiation and puberty, as well as environmental influences like seasonal and circadian cues. Continuous challenges that animals face include finding food, avoiding danger, and struggling for social dominance. Negative outcomes of these challenges may result in hunger, stress, or social subordination, which can prevent reproduction. In this review, we highlight some of the factors that induce reproductive behavior in the fish, and what is known about the physiological mechanisms responsible.

Chronological factors that control reproduction

Sex determination in fish occurs early in embryogenesis, and may be initiated by either chromosomes or environmental influences [1]. Unlike most mammals, which carry a single gene, *Sry*, that determines sex, fish species may utilize multiple different genes. In some species, a single gene appears sufficient to specify sex [2], while other species carry multiple alleles that interact to determine sex [3]. Despite the wide range of signals that may initiate male or female differentiation, these pathways ultimately converge on a core network of genes that is conserved across vertebrates, and some of the sex-determining genes are themselves known components of the core in other animals [2]. As a result of sex determination, the gonads differentiate into testes or ovaries, and the hormones they produce (i.e. androgens, estrogens, and progestins) shape the neural circuits that control sexual behavior in parallel with effects throughout the body. These effects may in fact be more extensive than those in mammals, since treating some species of fish with gonadal hormones results in a fully sex-reversed — and fertile — adult [4]. Many of these effects are likely mediated through sex steroid receptors that are ligand-activated transcription factors. The neural changes effected by these hormones are not well understood in fish, but may include changes in cell number, connectivity, gene expression, and neural activity patterns. Unlike mammals, fish sex is not always fixed for life. Some species of fish also change sex, a process regulated by the social environment discussed in more detail below.

Factors that influence fish reproduction act on many timescales, from daily to once in a lifetime (Figure 1). Although the sex of most fish species is set early in development, there is a period of sexual quiescence as juveniles grow. Like puberty in mammals, fish begin to exhibit sexual behavior when they have reached a size sufficient to fend off rivals and attract a mate, and/or care for young. Timing of sexual maturity can be advanced or delayed by factors including energy balance and the composition of the social environment. One of the most dramatic examples of the timing of reproduction occurs in salmon (*Salmo salmo*). These fish hatch in rivers, then move to the ocean for years while they grow to reproductive maturity. Salmon spawn once in their lives, and will navigate vast distances to return to their spawning site.

Figure 1



Control of reproduction acts at multiple timescales. **(a)** During the lifespan of a typical fish, sex is determined early in life, and after reproductive maturation, cues with a variety of timescales may affect reproduction. For a given species, one or more of these factors may regulate the onset of sexual behavior. **(b)** Categorization of classes of regulators of reproduction by the periodicity at which they act.

There is good evidence that an inherited magnetic map guides their return from the ocean to their natal stream [5]. Upon finding a stream that matches the olfactory signature of their natal stream, salmon initiate a search for a spawning site [6,7]. Once they release their gametes, the majority of salmon die.

In contrast to the life history of salmon, other fishes exhibit asynchronous egg development, in which only a portion of eggs are laid at a given time and others remain in an immature state. This strategy occurs in fish such as medaka (*Oryzias latipes*), which can lay eggs daily. In medaka, a long light:dark ratio and warm temperatures initiate reproduction [8,9]. The light phase is also important for fish including medaka and zebrafish to determine the timing of spawning within the reproductive season [10]. In these species, ovulation occurs in the dark phase, and spawning occurs shortly after light onset (i.e. dawn). In geographical regions where environmental conditions remain relatively constant, such as tropical zones, mating may occur year-round, depending on food availability. Females of these species also tend to exhibit asynchronous egg production, but spawning in these species is still regulated by environmental cues such as solar or lunar cycles [11]. In the California grunion (*Leuresthes tenuis*), spawning occurs at high tide, which is tied to the lunar cycle [12]. Eggs are buried and fertilized in the sand and at the next high tide young are washed out to sea. The tides, controlled by the moon, also open up new territories that species such as the grass pufferfish (*Takifugu niphobles*) use for spawning twice per month [13]. During mass spawnings of this species, hundreds of fish crowd the shorelines.

Continuing factors

Fish sense and interpret specific environmental cues to reproduce at a time that has been selected to maximize the survival of offspring. Correspondingly, in some species, social interactions reinforce hierarchical status that can be a crucial factor in reproduction. In an African