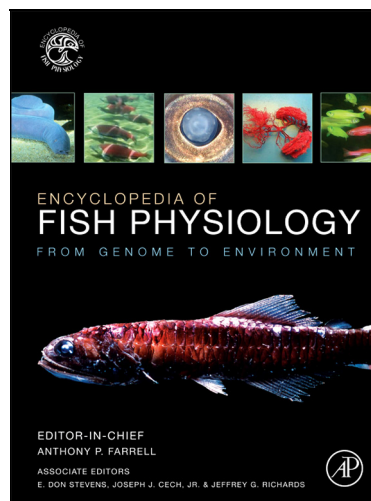


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Circadian Rhythms in Fish

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Glossary

Circadian Internally generated with a periodicity of about 24 h. From the Latin *circa* (about) and *dies* (day).

Circadian clock Cellular mechanism or multicellular structure that spontaneously expresses a rhythm with a periodicity of about 24 h. Also called circadian oscillator or, in the case of a master clock that drives others, circadian pacemaker.

Circatidal Internally generated with a periodicity of about one cycle of the tide, that is, about 12.4 h.

Daily With a periodicity of exactly 24 h. Synonymous with 'diel' or 'nycthemeral'. Used for environmental cycles. Should also be used for physiological and behavioral rhythms whose endogenous nature is not certain and whose observed periodicity is 24 h.

Entrainment Forced synchronization of an endogenous rhythm to the periodicity of an external factor, called a zeitgeber. Opposite of freerun.

Freerun State of an endogenous rhythm that follows its own natural periodicity, called the 'freerunning period'. Usually expressed under constant conditions. Opposite of entrainment.

Hourglass A mechanism that triggers an output after a certain amount of time has elapsed from a resetting event (which can be the output itself). It is a conceptual alternative to circadian clocks in some phenomena, although there is little evidence for it.

Masking Effect of an external factor on a circadian variable, resulting in the variable expressing a different state than that prescribed by the internal clock. For example, light can mask the wake–sleep cycle by rendering an animal active at a time when it would normally be asleep.

Phase A particular reference point or segment during an oscillation.

Phase shift A resetting of the internal clock or its zeitgeber. In a phase advance, the rhythm is temporarily shortened and its expression occurs earlier than expected. In a phase delay, the rhythm is temporarily lengthened and its expression occurs later than expected. Advance values (usually in hours) are assigned a positive sign and delay values are assigned a negative sign.

Subjective day or night Under constant light or constant darkness, the time segment during which the internal clock would expect to see day or night.

Transients Cycles that are temporarily shortened or lengthened during a phase shift. They reflect a gradual readjustment of the clock to a new steady state.

Zeitgeber An environmental factor that varies cyclically (e.g., light intensity) and that synchronizes (entrains) an endogenous clock to its own periodicity.

Introduction

The rotation of the Earth on its axis imposes a daily cycle of light and darkness on almost all organisms. Depending on the habitat, temperature and humidity can also vary on a 24-h basis. Such environmental cycles have led to the evolution of internal clocks in almost all living things. These clocks are cellular or multicellular structures that

generate an output with a periodicity of about 24 h. The daily approximation defines the clock and its output rhythm as being circadian (from the Latin *circa* (about) and *dies* (day)). Other biological clocks exist with different periodicities, such as the duration of the tide cycle (12.4 h, circatidal clock) or the year (circannual clock), but the circadian variety is by far the most common and the most studied.

Circadian clocks have adaptive value for animals. With them, animals can keep track of time and anticipate significant events, such as dawn, dusk, and food arrival. Physiological systems can thus be revved up in advance of activity and food intake. Circadian clocks can also be involved in daylength measurement and thus in photoperiodic responses. Finally, circadian clocks can synchronize sleep with that portion of the day to which the animal's sensory abilities are less well adapted. If slumber were only a blind response to darkness, for example, any animal venturing into a permanently dark place would be transformed into a sleeping beauty, a serene but not very profitable state of affairs.

The basic procedure to demonstrate the existence of a circadian clock is to continuously measure a physiological or behavioral variable under constant laboratory conditions (constant light (LL) or darkness, stable temperature and oxygen content, and food available *ad libitum* or given at random intervals), and observe cycles that persist for at least a few days. The rhythm always exhibits a periodicity (called the 'freerunning period') slightly different from 24 h. This deviation from 24 h is a fundamental feature of circadian rhythms. It illustrates the fact that biological clocks (like most manufactured watches) need not keep exact time. Some clock drift is allowed as long as there is a mechanism that resets the clock every day to the environmental cycle being tracked. This synchronization of the biological clock by an external cycle is called 'entrainment'.

The deviation from 24 h is also providential, for it proves the endogenous nature of the rhythm. If the freerunning period was exactly 24 h, it could be argued that the animals were responding directly to an environmental cycle which the laboratory conditions failed to control (e.g., noise in the building, or some hard-to-detect geophysical phenomenon). However, no such environmental cycles could explain circadian rhythms of, say, 23 h. Moreover, there is often considerable variation between individuals in the exact value of their freerunning periods, another indication that the rhythms are generated internally and not driven by an exogenous factor.

Circadian physiology has been extensively studied in mammals, most notably in humans, rats, mice, and hamsters. Comparatively little work has been done with fishes. This is due, in part, to the fact that we are yet to find a fish species that is easy to keep, obtainable in great numbers, and that gives precise rhythms which last for a long time in constant conditions. As compared to laboratory rodents (the workhorses of circadian rhythms research), whose clocks remain self-sustained for months, fishes in constant conditions exhibit circadian rhythms that usually damp out within several days, or several weeks at most. We do not know the reason why these endogenous cycles seem to persist longer in mammals than they do in fishes.

Expressions of Circadian Rhythmicity

As is the case for other animal groups, locomotion is the most commonly measured circadian variable in fishes, probably because it is relatively easy to automate the continuous recording of swimming movements. Usually, an infrared light beam is set up across the aquarium and beam interruptions are recorded by computer. Other less-common methods include automated video-image analysis and recorded disruptions of a standing ultrasound wave. Freerunning rhythms of locomotion have been observed in more than 40 different fish species, including hagfish, lamprey, sharks, cyprinids, ictalurids, gymnotids, salmonids, and labrids. Freerunning periods generally vary between 20 and 29 h. The activity rhythms are often represented in the form of an actogram, as in [Figure 1](#).

Another variable that can freerun is 'demand feeding'. Fishes can be taught to push an object in order to obtain

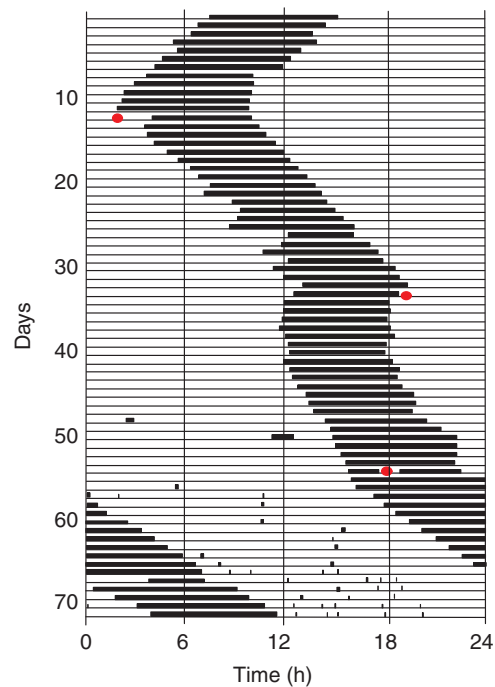


Figure 1 Actogram of the freerunning activity rhythm of an inshore hagfish in constant darkness. Lines represent successive days, with the thick parts showing the times when the fish was active. The fish was active for about 7.5 h each day. On the first day, the fish was active from 7.22 a.m. to 3.05 p.m.; these times gradually changed so that on day 10 the fish was active from 2.14 a.m. to 9.46 a.m. Thus, the biological clock in this fish, using activity onsets as reference points, had a freerunning period of 23.43 h during the first 10 days. The three circles represent 15-min pulses of light shown to the fish to phase-shift its rhythm. Adapted from [figure 3 in Ooka-Souda S and Kabasawa H \(1995\) Circadian rhythms in locomotor activity of the hagfish, *Eptatretus burgeri* V. The effect of light pulses on the freerunning rhythm. *Zoological Science* 12: 337–342.](#)

food. The hits are recorded by a computer. Freerunning rhythms of demand feeding with periodicities of 20–30 h have been obtained from the European sea bass (*Dicentrarchus labrax*), the rainbow trout (*Oncorhynchus mykiss*), the wels catfish (*Silurus glanis*), and the goldfish (*Carassius auratus*).

Freerunning rhythms have also been reported for the electric discharges of gymnotid fishes, air gulping of the river loach *Indoreonectes evezardi*, body color change in mummichogs (*Fundulus heteroclitus*), as well as oxygen consumption, retinal cell proliferation, and hormone levels in several species.

The freerunning rhythms of fishes are usually noisy (there is a fair amount of activity during the supposed rest phase, or inactivity during the supposed activity phase). Moreover, as already mentioned, seldom are the rhythms self-sustained for more than several weeks. The most precise and long-lasting fish rhythms to date have come from the electric discharges of *Gymnorhamphichthys hypostomus*, and the locomotor activity of the inshore hagfish (*Eptatretus burgeri*), the white sucker (*Catostomus commersoni*), the lake chub (*Couesius plumbeus*), the burbot (*Lota lota*), and various wrasses, with the inshore hagfish leading the pack with maximum reported durations of 75 days (Figure 1). It is noteworthy that *G. hypostomus*, the inshore hagfish, the burbot, and the wrasses prefer to sleep hidden, either buried in sand or underneath rocks. The search for a model subject in fish circadian research might benefit from a focus on species that sleep deeply and out of sight.

The value of the freerunning period (symbolized by τ , the Greek letter tau) is calculated by fitting a regression line through predefined reference points (e.g., daily activity onset), or, more commonly in the case of the noisy rhythms of fishes, with the help of a special technique called 'periodogram analysis'. This mathematical tool assesses the most likely period of a rhythm and assigns a statistical probability value to it.

The freerunning period of fishes can be influenced by the seasonal timing of the animals' capture. Lake chubs express longer freerunning periods of activity immediately after a winter capture than after a summer capture. Burbot and longnose dace (*Rhinichthys cataractae*) also show a summer–winter difference, but reversed: their freerunning period is longer after a summer capture. The causes of such seasonal variation and interspecific differences remain unknown.

Freerunning periods can also vary depending on whether the fish are single or in shoals. In both the white sucker and the mummichog, groups of 25 fish have yielded longer freerunning periods than fish kept separately. The reasons for this are not understood.

Finally, freerunning periods depend on whether the rhythm is measured in LL or in constant darkness (DD). Early work on the circadian physiology of animals led to the formulation of what is known as Aschoff's rule:

increased light intensity lengthens the period in nocturnal animals but shortens it in diurnal ones. It is difficult to say whether fishes follow this rule; first because many species are hard to categorize as diurnal or nocturnal (see below), and second because fish rhythms are not always expressed in LL. However, a few studies have managed to document some influence of light intensity on the freerunning period of fishes. Zebrafish (*Danio rerio*) and mummichogs are diurnal in the laboratory and show longer freerunning periods in DD than in LL, as predicted by Aschoff's rule. Conversely, goldfish go against Aschoff's rule: they are mostly diurnal, and their period is longer in LL than in DD. In the nocturnal gymnotids, the period is lengthened as light intensity is increased from 0 to 100 lux, congruent with Aschoff's rule. However, in the nocturnal Amur catfish (*Silurus asotus*), the period decreases as light intensity increases from 0 to 10 lux. It has been suggested that Aschoff's rule should be altered to state that the periods are lengthened with increasing light intensity in animals whose freerunning period in DD is less than 24 h, with the opposite being true for animals with a freerunning period in DD over 24 h. The validity of this new formulation remains to be established for fishes. Whatever the most correct formulation turns out to be, the physiology behind these effects of light intensity on freerunning periodicity is still unknown.

Some fishes have failed to show freerunning rhythms in the laboratory, be it under LL or under DD. Most interesting among them are cave populations. The Mexican tetra (*Astyanax mexicanus*) includes both a blind cave form and a sighted surface form; the cave form is arrhythmic in the laboratory, while the sighted one freeruns in both LL and DD. Lack of rhythmicity in cave dwellers is a likely case of regressive evolution in an environment devoid of daily cycles. However, not all cavernicolous fishes are arrhythmic. There is need for further research to determine how widespread the loss of internal clocks is in cavefishes.

Another expression of circadian rhythmicity, besides freeruns, is the anticipation of daily recurring events. When fishes are fed at the same time every day, they commonly become more active and pay more visits to the feeding site a few hours before mealtime. This so-called food-anticipatory activity is not an expression of hunger because activity dips down to its normal level past the usual mealtime even when food is withheld. Even though the fish are still hungry, their internal time sense tells them that foraging past the regular mealtime would be unprofitable. This time sense could be based on an hour-glass mechanism reset by dawn or dusk rather than on a circadian clock; however, this hypothesis has been refuted by a few observations of freeruns of food-anticipatory activity when scheduled feeding was interrupted and constant conditions were put in place, and also by cases of anticipation that began before dawn or dusk when the

food arrived soon after dawn or dusk (an hourglass set by a light signal would trigger anticipation after the light signal, and not before).

More than one feeding time can be anticipated. Shoals of golden shiners (*Notemigonus crysoleucas*) and individual rainbow trout are capable of anticipating two daily feeding times, even when one is at night and the other during the day. In the same vein, golden shiners and inangas (*Galaxias maculatus*, ex-*Galaxias attenuatus*) can anticipate the arrival of food in one part of their aquarium in the morning and in another part in the afternoon, a phenomenon called 'time–place learning', which is commonly thought to be based on a circadian mechanism. Golden shiners can also learn to feed in one-half of their aquarium in the morning, the other half at midday, and back to the first half in the afternoon.

Fish can anticipate events unrelated to food, such as dawn and dusk. Activity often increases or decreases a few hours before dawn or dusk even in the absence of changes in sunlight intensity. For example, nocturnal American eels (*Anguilla rostrata*) in the wild have been seen moving up toward the entrance of their dark cave shelter several hours before dusk. In addition, parental convict cichlids (*Argocentrus nigrofasciatus*) can retrieve their young a few minutes before nighttime, even in a laboratory setting where no light attenuation announces the end of the day.

A somewhat indirect way to demonstrate the existence of a circadian clock is to phase-shift the light–dark cycle, advancing or delaying it by a few hours, and to observe transient cycles of activity in the next few days. Rather than start right away at the new time of lights-on or lights-off (depending on whether the fish is diurnal or nocturnal) following the phase shift, activity onset occurs at first at the old time of lights-on or lights-off and slowly drifts across clock times from day to day until it is resynchronized with the new phase of the light–dark cycle. This reflects the gradual readjustment of the clock. As a rule, fishes seldom provide such evidence, as they usually resynchronize very quickly to phase shifts of the light–dark cycle. They show no, or at most one, transient cycle. However, two cases of prolonged transients have been documented: in one, golden shiners exhibited 2–3 days of transients after a 6-h shift; in the other, inshore hagfish showed 7–13 days of transients after a 12-h shift (Figure 2). It is unclear whether cases with no or very few transients reflect an easily shifted clock or a masking effect of light and darkness on activity levels.

Circadian clocks are also likely to be involved in sun-compass orientation, the ability to use time of day and the position of the sun to find cardinal points. At least a dozen fish species are known to orient by sun compass. For example, when bluegill sunfish (*Lepomis macrochirus*) are displaced from shore to open waters, they swim in a fairly consistent direction (the one that would take them to shore) on sunny days, but they set off in random directions on

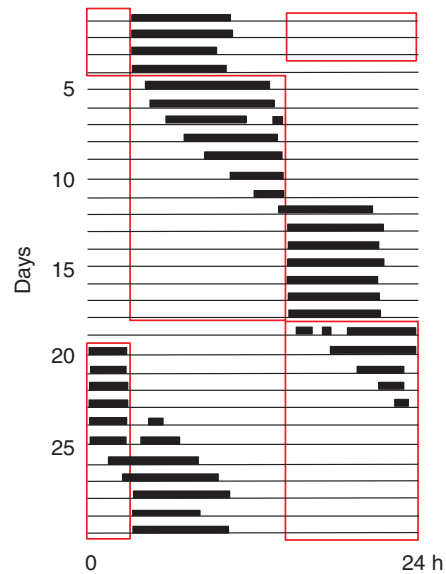


Figure 2 Transient cycles in the activity rhythm of an inshore hagfish following 12-h phase shifts of the light–dark cycle. Boxes show light times. Adapted from figure 6 in Ooka-Souda S, Kabasawa H, and Kinoshita S (1985) Circadian rhythms in locomotor activity in the hagfish *Eptatretus burgeri*, and the effect of reversal of light–dark cycle. *Zoological Science* 2: 749–754.

overcast days; moreover, their orientation is shifted by 90° when sunrise is artificially made to appear 6 h ahead of time (6 h is a quarter of the full day, just as 90° is a quarter of a full circle).

Entrainment of the Circadian Clock

As a rule, circadian clocks do not freerun in nature. (There are a few exceptions, such as beavers in their winter lodge.) Instead, they are synchronized by daily environmental cycles. The entraining cycle is called a 'zeitgeber', a German word that translates literally as time giver. By far the most important zeitgeber in nature is the light–dark cycle.

Two models explain how an exogenous cycle could entrain an endogenous one. The first one is parametric entrainment. This is the notion that an environmental factor can speed up or slow down the internal clock in a manner proportional to the intensity of the factor, so as to synchronize the clock to 24 h. The second one is nonparametric entrainment. According to this model, the clock is synchronized by daily jumps, or phase shifts, caused by the environmental factor being perceived by the animal at specific times. For example, to be entrained to a period of 24 h, a 26-h freerunning rhythm would need to jump backward (to be phase advanced, in the jargon of the trade) by 2 h every day. In a 26-h rhythm, the end of the subjective night (the end of the activity phase in a nocturnal animal, or the end of the sleep phase in a

diurnal one) soon runs into dawn. If light at the end of the subjective night causes a 2-h phase advance in the clock, then the rhythm would become synchronized to 24 h.

Almost all research to date supports the theory of nonparametric entrainment. One key evidence is the phase-response curve, a graph depicting phase-shift size as a function of the circadian time at which a stimulus is given to the animal. Nonparametric entrainment theory predicts that pulses of light shown at the end of the subjective night should yield phase advances that become larger as the light pulse is administered earlier into the subjective night. The theory also predicts phase delays at the beginning of the subjective night, delays that become larger as the light pulse is given later into the subjective night. Somewhere around the middle of the subjective night, phase delays should quickly give way to phase advances.

Phase-response curves, with the correct shape, have been obtained in almost all organisms tested to date with light. Unfortunately, very few of these organisms have been fishes. This is because the study of phase shifts requires long-lasting rhythms with precise reference points (e.g., activity onsets), and fishes seldom show such rhythms. However, at least three phase-response curves have been obtained with fishes, all with roughly the expected shape. The first two came from the locomotor rhythms of the inshore hagfish and the canary wrasse (*Halichoeres chrysus*), two species that bury themselves in sand to sleep and that show exceptionally clean separation between their activity and rest phases. The third phase-response curve came from the rhythm of melatonin release from the pineal organ of the ayu (*Plecoglossus altivelis*) in flow-through culture.

Besides light, two other possible zeitgebers in fishes are time-restricted food availability and temperature cycles. Food delivery at the same time every day can entrain rhythms of activity in otherwise constant conditions, as has been shown in mummichog, goldfish, wels catfish, European seabass, and oriental weatherfish (*Misgurnus anguillicaudatus*). Entrainment of locomotor activity to cycles of 12 h of 20°C and 12 h of 26°C has also been reported for zebrafish. The mechanism of entrainment in these cases has not been identified. In the case of entrainment by food, the possibility exists that the circadian clocks being entrained are anatomically distinct from the ones normally entrained by light. This has led to the notion of separate light-entrained oscillators (LEOs) and food-entrained oscillators (FEOs). There is some evidence for the existence of FEOs in fishes, but work remains to be done to distinguish them from LEOs that could have a memory of mealtime being stamped onto a particular phase of their oscillation.

In mammals, there are known examples of entrainment by daily social interactions, induced physical exercise, and sleep interruptions. These factors appear not to have been tested in fishes. Another potential zeitgeber

apparently untested in fishes, despite its presence in many freshwater habitats, is a daily cycle of oxygen concentration in water.

Diurnality and Nocturnality

The circadian clock of mammals and birds is responsible for maintaining the integrity of the sleep–wake cycle and its synchronization to the light–dark cycle. Conceivably, the same could be said of fishes. However, many fishes (mostly freshwater ones) do not sleep very deeply and do not appear too restricted by light or darkness in the timing of their activity. For example, goldfish can be nocturnal, diurnal, or constantly active, even in the same laboratory. There have even been reports of individual goldfish starting a study as diurnal and then switching to a nocturnal mode, or vice versa. Lake chub tend to be diurnal in the laboratory, but they have been seen feeding at night in the wild, and during their spawning season they migrate only at night. The spawning season itself tends to disrupt daily activity cycles in many species. Sticklebacks and cichlids are normally diurnal but during their parental phase they fan their eggs day and night. Some species switch from a nocturnal or crepuscular pattern of activity to a diurnal one when daylight is dimmed (e.g., in turbid waters). Many more species change the timing of their activity phase between summer and winter. Salmonids also can be nocturnal, diurnal, or aphasic; however, they consistently suppress daytime activity either in winter or simply when water turns colder. In captivity, European seabass and white suckers are mostly diurnal when kept in groups, but nocturnal when housed individually. Many cyprinids can be either diurnal or nocturnal, depending on when food is made available. Interestingly, all these flexible species (with the exception of the lake chub) exhibit circadian rhythms of activity that are neither particularly clear-cut nor long-lasting in the laboratory.

However, there are examples of fish species that do sleep soundly, marine ones in particular. Such species tend to keep to the same time of day for their activity phase, and those that have been tested for circadian rhythmicity have yielded rhythms that are better than most. It is interesting to note that the two species, which had activity rhythms strong enough to yield phase-response curves (see above), were both sound sleepers and marine as well. At this stage, the relationship between habitat, sleep soundness, and the self-sustainability of circadian rhythms remains tentative, but it may become better studied in the future. A worthy goal would be to identify the mechanism by which the circadian clock determines the exact phasing of activity relative to the light–dark cycle, something that remains a mystery at present in fishes as well as in other animals.

Location of the Circadian Clock

Circadian clocks can be located anywhere in the body of an animal, and there may be many present. In mammals, one clock drives the others. This so-called pacemaker, or master clock, is located in the suprachiasmatic nucleus (SCN) of the hypothalamus. It receives input from the retina allowing entrainment to the light–dark cycle. In birds, both the hypothalamus and the pineal gland can act as circadian pacemakers, independently or in tandem depending on the species. Light can reach these structures directly through the thin skull or via messages from the eyes.

In fishes, no master clock has been identified yet; no structure analogous to the mammalian SCN has been documented in them. Nevertheless, the pineal is present, it is directly photosensitive, and it contains an intrinsic circadian clock. The fish pineal exhibits a circadian rhythm of melatonin production, even when isolated in culture. This rhythm can be entrained by light–dark cycles and phase-shifted by light pulses, both *in vivo* and *in vitro*. Melatonin is produced only during the subjective night, and, being a hormone, it could act as a body-wide signal to synchronize other, more peripheral clocks. Thus, the fish pineal has all the necessary characteristics of a master circadian clock.

However, pinealectomy usually does not eliminate circadian rhythms of activity. The ablation often alters freerunning periods (Figure 3), and has been reported to split rhythms in white suckers (Figure 4), but the rhythms usually persist. Moreover, in some species, such as salmonids, the pineal is photosensitive but does not express any freerunning rhythms of melatonin production; melatonin is just secreted whenever there is darkness. Thus, for most fish species, the pineal cannot be the master clock in and of itself, although it may be an important cog in the circadian machinery.

The fish retina is capable of several circadian phenomena. Rod and cone migrations anticipate daily changes in lighting and they freerun in DD. Dopamine release also follows a circadian pattern in constant conditions, even in isolated retina, with production being high during the subjective day. However, ophthalmectomy does not abolish freerunning rhythms of activity, nor does it prevent entrainment of these rhythms to light.

Clock genes are transcribed on a circadian basis under constant conditions in isolated heart and kidney tissue from zebrafish. Moreover, these tissues are responsive to light. Hearts and kidneys must therefore have circadian clocks. We must seriously envision the possibility of a complex network of central (brain) and peripheral clocks in fishes, either linked or responding independently to the same zeitgebers to maintain

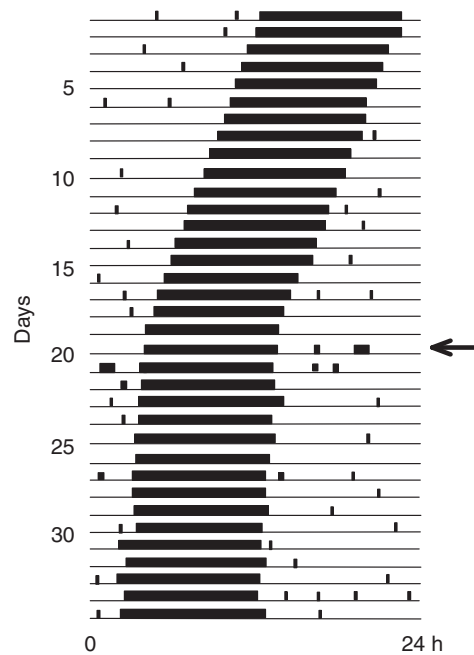


Figure 3 Freerunning activity rhythm of a burbot in constant darkness. The arrow on the right indicates the day when the fish was pinealectomized. The endogenous rhythm persisted after the pinealectomy, but the periodicity increased slightly from 23.61 to 23.89 h. Adapted from figure 1A in Kavaliers M (1980) Circadian locomotor activity rhythms of the burbot, *Lota lota*: Seasonal differences in period length and the effect of pinealectomy. *Journal of Comparative Physiology A* 136: 215–218.

physiological integrity within the whole body, rather than a single pacemaker driving all other clocks as in mammals.

Clock Genes

The molecular basis of circadian rhythmicity has been described in fruit flies and mice. Four main genes are involved. The *Clock* and *Bmal* genes encode proteins that are transcription factors. These activate the expression of the genes *Period* (*Per*) and *Cryptochrome* (*Cry*). The PER and CRY proteins, in turn, repress the transcription of their own genes by the CLOCK and BMAL proteins. This system is a feedback loop in which the expression of the genes is suppressed by their protein products with a periodicity of about 24 h.

Homologs of these genes have been found in zebrafish. All have multiple copies in the genome. Three *Clock* genes (*zfClock1*, 2, and 3), three *Bmal* genes (*Bmal1*, 2, and 3), three *Per* genes (*Per1*, 2, and 3), and six *Cry* genes (*zCry1a*, 1b, 2a, 2b, 3, and 4) have been identified in zebrafish. All of the *Clock* and *Bmal* genes are expressed rhythmically in various tissues in DD. The first four *Cry* genes are also expressed rhythmically in the retina, pineal organ, and other parts of the brain.

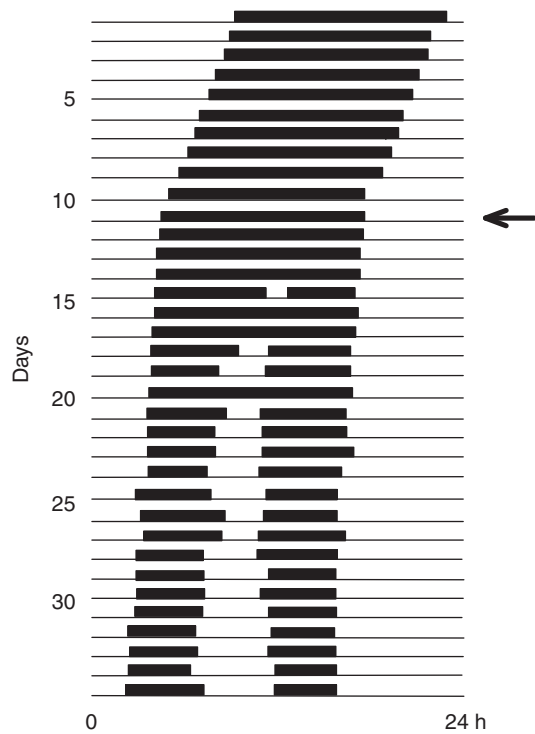


Figure 4 Freerunning activity rhythm of a white sucker in constant light. The arrow on the right indicates the day when the fish was pinealectomized. The rhythm persisted but split after the pinealectomy. Adapted from figure 2 in Kavaliers M (1980) Circadian organization in white suckers *Catostomus commersoni*: The role of the pineal organ. *Comparative Biochemistry and Physiology* 68A: 127–129.

Circatidal Rhythms

Tides along coasts and tidal currents offshore represent another type of environmental cycle that can impact the life of fishes. Many species use intertidal zones as feeding and spawning grounds. These fishes should benefit from being able to anticipate the flooding and ebbing tides. They should therefore have a circatidal clock, one that runs with a periodicity of about 12.4 h, which is the duration of the tidal cycle in most locations (sometimes, geographical features can greatly dampen one of the tides, resulting in a 24.8-h cycle). Indeed, some intertidal species do exhibit self-sustained rhythms of activity with a period of about 12.4 h under constant laboratory conditions. Such species include the rock goby (*Gobius paganellus*), the shanny (*Lipophrys pholis*), the Montagu's blenny (*Coryphoblennius galerita*), the Molly miller (*Scartella cristata*, ex-*Bleinnius cristatus*), and the mudskippers *Scartelaos histopborus* and *Periophthalmus modestus*.

Unfortunately, circatidal rhythms in fishes under constant conditions are even noisier and shorter-lived than circadian rhythms. In this regard, fishes are bested by invertebrates. Various species of intertidal crabs and mollusks have proved to be better subjects of study.

Despite this, some entrainment and phase-shift studies have been conducted with fishes and they suggest that cyclic changes in hydrostatic pressure and periodic wave action are the most likely zeitgebers of fish circatidal rhythms in nature. However, nothing is known of the anatomical location of the circatidal clock, nor of its molecular mechanism.

Other Rhythms

Lunar rhythms have a periodicity of 29.53 days, as exemplified by the recurrence of the full moon every month. Semilunar rhythms have a periodicity of 14.76 days, such as the recurrence of spring tides (tides of maximum amplitude) on the days of new moon and full moon. Many fishes exhibit lunar or semilunar rhythms, but we do not know if these rhythms are the product of an endogenous clock or simply a direct response to external stimuli, such as tide amplitude, moonlight intensity, and gravitational pull by the moon. The problem is threefold: first, it is essentially impossible to place the animal in truly constant conditions (the gravitational pull of the moon is always present); second, it is difficult to reproduce the complex variables of a lunar or semilunar environment in the laboratory; and, third, these rhythms are slow and require a relatively long time to express many cycles. With the possible exception of ovarian activity in mummichogs, freerunning lunar or semilunar rhythms have not been convincingly demonstrated in fishes (or in other animals, for that matter).

Many intertidal species spawn only during the high tides that surround the days of new moon and full moon. Examples include the California grunion (*Leuresthes tenuis*), the Gulf grunion (*Leuresthes sardina*), the Atlantic silverside (*Menidia menidia*), the mummichog, the inanga, the surf smelt (*Hypomesus pretiosus*), and the four-eye (*Anableps microlepis*). The eggs are deposited high on the shore on spring tides, and, during the following 2 weeks, they remain in wet sand, uncovered by water and thus unexposed to marine predators. They hatch only during the next series of spring tides, which will take the larvae away. Semilunar patterns of spawning have also been observed in some blennies and damselfishes that live near but not on the intertidal zone, and, in such cases, the rhythm might help synchronize the mating activity of the population and facilitate dispersal of the larvae by tidal currents. Semilunar rhythms also exist in a few freshwater species, especially in the growth rate and food intake of various salmonids.

Examples of lunar rhythms include the seaward migration of adult eels (more fish move during the waning moon), the downstream migration of juvenile Atlantic salmon (*Salmo salar*, more movement around the time of

new moon), and commercial catches of various clupeids (more captures around the full moon).

A final type of clock is circannual; it runs with a periodicity of about 1 year. Many examples are known from birds and mammals. Under conditions of constant temperature and stable photoperiod in the laboratory, starlings keep on molting, ground squirrels still fatten up and hibernate, and deer continue to grow and shed their antlers at a periodicity that is often short of the full year. In fishes, however, no endogenous circannual rhythms have been found. Annual cycles obviously exist in wild fish, in growth for example, but they may not be endogenous.

See also: Behavioral Responses to the Environment: Sleep in Fish. Sensory Systems, Perception, and Learning: Spatial Orientation: How do Fish Find their Way Around?.

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