Sleep in fishes

Stéphan G. Reebs
Université de Moncton, Canada
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Do fishes sleep? This is not an easy question. It depends on what you mean by “sleep”. Most sleep researchers, being focused on mammals, recognise sleep when they see distinctive patterns of electrical activity of the brain. Fish, however, lack the complex brain structures from where these patterns originate. Another criterion to define sleep, used mainly in the field or in situations where electroencephalographs are not available, is prolonged eye closure. But fish do not have eyelids!

Fortunately, other criteria exist that can be expanded throughout a vast array of animal classes, including fish.[1] These are (1) a state of prolonged inactivity, (2) a typical resting posture, usually in a typical shelter, (3) 24-h rhythmicity, and (4) high arousal thresholds. Thus, most people would agree that an animal is, for all practical purposes, asleep when it remains almost completely immobile (criterion # 1), in almost always the same posture and same location (# 2), at the same time every day (# 3), and in a state of decreased sensitivity to disturbances (# 4). Another criterion is the presence of a "rebound" after sleep deprivation: if an animal is experimentally prevented from engaging in the behaviour that looks like sleep, that behaviour should become more frequent after the animal is left alone in the following days. This phenomenon goes by the technical name "homeostatic regulation of sleep".

A few scientists have applied these criteria to fishes and taken the question to the laboratory. Colin Shapiro reported that his Mozambique tilapias, *Oreochromis mossambicus*, used to rest on the bottom of their tank at night, with a lower respiratory rate and no detectable eye movement, and that they did not respond as readily as during the day to stimuli such as an electrical current or the delivery of food.[2] Similarly, at the Academy of Sciences of the USSR in Leningrad, I.G. Karmanova and his team witnessed brown bullheads *Ameiurus nebulosus* in a typical sleep posture, with the tail lying flat on the ground, the other fins stretched out, and the body inclined to one side at an angle of 10-30^o to the vertical. Cardiac and respiratory rhythms were much slower than normal and the fish were less sensitive to sound and tactile stimulation. The researchers touched the bullheads with glass rods and the catfish did not move.[3] This certainly fulfils the criterion of reduced sensitivity.[4] In fact, when it comes to lack of sensitivity during sleep, there might be even better examples: several researchers have said that the Spanish hogfish *Bodianus rufus*, the bluehead *Thalassoma bifasciatum*, the wrasse *Irideo bivittata* (which is probably the slippery dick *Halichoeres bivittatus*), the cunner *Tautogolabrus adspersus*, and even requiem sharks could be picked up by hand at night and even sometimes lifted all the way up to the surface without evoking a response.[5]

At night, zebrafish *Dania rerio* appear to "float" in the water column, either horizontally or with the head slightly up. Their frequency of mouth and gill movement is reduced by almost half and they are twice as hard to arouse as during the day. If they are deprived of this sleep-like behaviour, the sleep bouts thereafter are longer and the arousal threshold is higher than usual, suggesting a rebound effect.[6]

In studies of this kind, one has to be mindful of the lighting that is used during the nocturnal observation. There is a phenomenon called “light shock” which happens in some fishes – not all!– when they are exposed to a sudden bright light at night. In response to the light, these fishes sink to the bottom and remain motionless for several minutes.[7] This may give the illusion of sleep when in fact it is only a short-lived reaction to a temporally abnormal stimulus. For experiments on sleep, it is preferable to use very dim illumination constantly throughout the night.

Another solution is to resort to near-infrared technology.[8] I have obtained infrared goggles from an Army Surplus store and used them in conjunction with a powerful flashlight fitted with an infrared filter (Kodak # 87B) to unobtrusively observe captive fishes in complete darkness. I concentrated on members of the family Cichlidae, as they are known to be blind to infrared light. What I found was that these fish were indeed quiescent at night. Adult oscars were sluggish and unresponsive, resting on the bottom with their eyes turned downwards. Severum cichlids *Heros severus* were also quiescent, either near the bottom or higher up in the water column. Rainbow cichlids *Herotilapia multispinosa* and convict cichlids *Archocentrus nigrofasciatus* were often immobile as well, with their pelvic fins lowered all the way down, but occasionally they set off on slow promenades with their pelvic fins brushing against the gravel bottom.[9]

Yet another solution to the problem of artificial light at night is to switch criteria and to concentrate on the use of typical resting places (most sleeping fishes will not leave their shelter just because they are suddenly lit by a bright light – if anything, they will dig in). Based on this criterion alone, many fishes do seem to sleep.[10] Divers in the field have often seen fishes “settling down for the night” in holes and crevices, underneath ledges, amidst vegetation or corals, inside sponges, or buried in sand. Such shelters were found to harbour fish throughout the night. Some extra protection can be afforded by special secretions, such as the mucous envelope that is produced by several species of wrasse and parrotfish, either around the fish themselves or at the opening of their shelter. Spotted moray eels prey more heavily on sleeping parrotfish that do not secrete mucous envelopes as compared to those that do. Presumably the mucous cocoon masks the odour of the fish and makes it less detectable.[11] Mucous envelopes also protect sleeping parrotfish against attack by ectoparasites.[12]

Another sleep criterion is the existence of a period of inactivity that alternates with a period of activity on a 24-h basis. Here, direct observation is tough: either you stay up at all hours of the day and night, many days in a row, just to watch fishes sleep, or, if you filmed the fish’s behaviour, you spend hours upon hours analyzing videotapes.[13] Who really wants to do that? Instead, researchers resort to automated activity-recording systems. The most common of these systems involves infrared light beams criss-crossing the aquarium. When a fish swims into the path of a beam, it cuts the electrical circuit linked by that beam, and such interruptions can be recorded by computer, day and night continuously. Another method consists of setting up an ultrasonic wave throughout the aquarium. Large movements on the part of a fish stir the water and alter the wave. Given that the wave received at one end of the aquarium can be electronically compared to the one generated at the other end, and that any difference can be made to create a voltage pulse recorded automatically on computer, the large movements of the fish can be continuously monitored. There is also a third method, reserved for those who study electric fishes, and it is simply to record the occurrence of electrical discharges in the aquarium. This is based on the fact that some electric fishes discharge at low rates when they are inactive, and high rates otherwise.[14]

Other methods can be used in the field. Researchers can set traps and nets, and check them every few hours or so, day and night. Sleeping fishes are not supposed to swim into traps, but they often do so when they are active, and therefore a 24-h pattern of captures can be interpreted as a 24-h pattern of activity. One can also use fishing implements that catch both active and inactive individuals (a seine net, for example), and then dissect a subsample of these fish to look at their stomach contents, the idea being that sleeping fishes do not feed and their stomach should be empty. A 24-h pattern of stomach fullness can therefore be interpreted as a 24-h pattern of activity.

Now, for the sleep researcher, all of these lab and field methods share one disadvantage: they record only one criterion of sleep – behavioural quiescence. But for yielding continuous information, they are fairly reliable, and accordingly they have been used quite extensively. The scientific literature is replete with studies of 24-h activity patterns.[15] As expected, most fishes are found to be either diurnal or nocturnal, although inactivity during the rest period is seldom absolute. In diurnal fishes for example, we can still find a few captures, a few food items in the stomach, or a few beam interruptions at night. Obviously, we are not talking about sound sleep for every member of the population here. And to complicate things further, a fair number of species seem to be crepuscular, specialised primarily for the twilight conditions of dawn and dusk. Such crepuscular species are often predatory, taking advantage of the increased traffic that occurs at dusk when diurnal fishes hurry to their resting places while nocturnal fishes emerge out of theirs, or vice-versa at dawn.

Indeed, it would be a mistake to believe that all fishes can sleep, or that sleep in fishes is as absolute as it is in mammals. So now we come to the matter of exceptions, which are numerous (they may not deserve to be called exceptions) and can be summarised as follows: (1) some fishes apparently never sleep, (2) some fishes may not sleep in early life, although they do so as adults, (3) some fishes do not sleep during migration, (4) some fishes do not sleep during the spawning season, (5) some fishes do not sleep while caring for their young, and (6) some fishes are capable of switching from night-rest to day-rest. Let us review the evidence for these statements.[16]

Complete lack of sleep

The observation that a fish never seems to sleep often tends to be dismissed as an artefact of captive conditions and the stress such conditions impose. Either that or it is not reported in the literature because sleep researchers are in the business of studying concrete aspects of sleep and not the lack of it. Yet, the number of fish species that never sleep may be greater than we think. There are, in fact, a few mentions of non-sleeping species here and there in the scientific literature. For example, Bori Olla and Anne Studholme have reported that bluefish *Pomatomus saltatrix* and Atlantic mackerel *Scomber scombrus* keep on swimming day and night in large seawater aquaria, and although these fish swim more slowly at night, they remain responsive to disturbances or the introduction of food 24 hours a day.[17] Could it be that some pelagic (open water) species need to swim all the time, either to breathe ("ram ventilation" of their gills) or to keep afloat, or to prevent being swept away by the current, and this is incompatible with sleep? Possibly. Certainly this argument has been put forward not only for mackerels but also for tunas, bonitos, and some sharks. [18]

Some species do not need to swim all the time but they remain constantly alert nonetheless. For example many coral reef species are nocturnal and feed only at night; during the day they form schools that are stationary but still responsive to predators. Another case is that of the nocturnal California horn shark, *Heterodontus franscisci*. At night it swims around and feeds, but during the day it hides in caves. Despite being inactive in such a shelter, it still responds very quickly when disturbed by divers.[19] (Astute readers will notice that these sharks fulfil at least two criteria of sleep – use of a typical shelter on a 24-h basis – but not another – decreased sensitivity to disturbances. Truly, it is not easy to define sleep in fishes.)

Lack of sleep that may not be a true lack of sleep

Speaking of pelagic species that swim all the time, or coral reef fishes that form more or less stationary schools during their daily period of inactivity: J. Lee Kavanau argues that such cases are the exceptions that confirm one possible function for sleep.[20] One popular hypothesis for why animal need to sleep is that the brain requires some time every day to consolidate into memory the things it has learned during the animal's normal period of activity. But the brain might not be able to do this while still assailed by new stimuli and new information to process. Therefore the role of sleep would be to periodically shut down sensory input to allow the brain to form memories. In some cases, sensory input could be shut down without true sleep. Pelagic species swim in an environment that is rather boring (kilometers upon kilometers of open water with not much happening in it). In such species, the sensory input is so low that memory formation could take place even if the fish keeps on moving (a repetitive activity) and does not fall asleep in the traditional sense of the word.

In the case of fish being inactive in large schools, the total number of eyes capable of detecting an approaching danger is so great that at any time a good proportion of the individuals forming the school could allow their minds to "drift" (a kind of daydreaming) and form memories while stopping to pay attention to environmental stimuli. This could be done in short bouts and inattention would not be so deep that the fish could not detect any alarm raised by the attentive shoalmates when a predator shows up.

In these cases, the fish could be said to be "partially asleep", in a way.

Lack of sleep during the juvenile stage

Studying the sleeping habits of a fish throughout its whole life has not been done very often – boredom takes hold of you after a while! One rare example is a study by Colin Shapiro and his colleagues on the Mozambique tilapia. After a few long days and sleepless nights spent in constant observation, these researchers came to the conclusion that juvenile tilapia do not show any sign of sleep, at any time. In fact it took these young fish 22 weeks to develop the adult sleep patterns.[21] As of yet nobody knows if such lack of sleep in the early stages of life is common place among fishes (it is worth mentioning here that the sleep behaviour of zebrafish described earlier in this article was observed in both adults and larvae) and no adaptive explanation for this delayed development has been put forward.

Lack of sleep during migration

Many birds do not sleep during migration, and the same may be true of fishes. Olla and Studholme have looked at the activity patterns of a demersal (bottom-dwelling) wrasse, the tautog *Tautoga onitis*. In summer, in the lab, these fish were active only by day. However, when photoperiod and temperature were adjusted to simulate fall conditions, a time when adults normally migrate offshore to overwinter, Olla and Studholme’s fish became active day and night, if not more so at night. Such continuous activity did not leave much room for sleep. Interestingly, this increase in nocturnal activity was observed in adults only, not in juveniles. This is consistent with the fact that juveniles do not migrate in the fall, preferring instead to stay inshore to overwinter.[22]

As an additional example, there is the case of lake chubs *Couesius plumbeus* living in streams. These fish are caught in minnow traps only at dawn, dusk, or during the day in summer, an observation that classifies them as diurnal/crepuscular. However, at the time of in-stream (spring) or out-stream (fall) migrations, counting fences set up across the waterway intercept these fish mostly at night.[23] Fishes moving within streams must go over many shallow areas where they are probably more visible and more susceptible to predation by kingfishers, and it may therefore be safer to migrate at night, even if it means going without sleep.

Lack of sleep during the spawning season

It seems that mating in fishes cannot be restricted to just one half of the day. 24-h patterns of activity often break down during the spawning season in fishes. Spawners become active day and night. Examples include the tautog mentioned above, as well as yellow perch, minnows, various centrarchids, bullheads, river lampreys, and others.[24] I have observed diurnal convict cichlids showing signs of being ready to spawn at the end of the day, and turning off the lights for the night did not frustrate them. They kept on digging pits and shoving gravel away in complete darkness (even the pilot lights of the heaters had been disabled – my infrared goggles came in handy here). In complete darkness the fish nudged and skimmed the spawning substrate in apparent cleaning movements, and they even laid eggs! The broods of such night-spawners tended to be more scattered on the substrate than those of day-spawners, but they did not comprise more unfertilised eggs.

Lack of sleep during the parental phase

Human parents of newborn babies know how hard it is to have to wake up at all hours of the night. They would envy fishes, who seem to be able to forego sleep and stay active 24 h a day when they have to care for their eggs. Some fish species stay with their brood of eggs and fan them, a behaviour that provides a steady supply of oxygenated water to the eggs. Because eggs consume oxygen 24 hours a day, we would expect parents to fan all the time, and that is indeed what they do. Using my infrared equipment once again, I have witnessed convict cichlid females fanning their eggs day and night.[25] In fact, they fanned three times as much at night as during the day – maybe they got interrupted by visual stimuli during the day, or maybe nocturnal fanning is a hard-wired adaptation to lower oxygen availability caused by the absence of oxygen-producing photosynthesis by aquatic plants at night. With a different piece of equipment (a light-magnifying starlight scope), I have also documented high levels of nocturnal fanning by threespine sticklebacks in the wild.[26] And there have been other reports of continuous (day and night) parental care in various damselfishes,[27] in smallmouth and largemouth bass,[28] and in the brown bullhead.[29]

Day/night sleep switches

A notable difference between fish sleep and human sleep is the fact that for many fishes, sleep (or inactivity) does not seem to be tied to a particular phase of the 24-h day. There are a number of documented switches from nocturnalism to diurnalism, or vice-versa, in fishes.[30] Sometimes, part of a fish population is diurnal and part is nocturnal. Even the same individual can be diurnal for a length of time, and then become nocturnal at some point.

Some of these switches can occur according to the seasons, particularly up north. In the 1960s and 70s, Karl Müller and Lars-Ove Eriksson, from the University of Umea in Sweden, worked at a field station located at 66° N – above the Arctic Circle – and found that captive burbot, sculpins and brown bullheads, although nocturnal in summer, became diurnal under the short photoperiod of the Arctic winter. This switch happened only at high latitudes. When tested at field stations below 60° N, the fish remained nocturnal throughout the year. Diurnal species, for their part, did not switch (the researchers looked at European minnows, yellow perch, and various diurnal salmonids).[31] Interestingly, some Arctic voles have also been reported to switch from nocturnalism to diurnalism in winter.[32] The adaptive significance of this phenomenon, however, remains unknown.

In salmonids, temperature may affect the phasing of activity. Neil Fraser and a number of Scottish and Norwegian co-workers have manipulated the activity phase of juvenile Atlantic salmon simply by chilling the water. They started by using infrared light to spy on the behaviour of captive juveniles (parr) at night. These fish could either stay underneath a shelter or come out and look for food. After artificially lowering the water temperature from 18 °C to 2 °C in summer, Fraser and his team saw that the salmon left their shelter less and less often during the day, but still very readily at night. Essentially the fish became proportionally more nocturnal as water temperature decreased. This jibes well with a number of field observations to the effect that young salmon in the wild are less often seen during the day as temperatures plummet in the fall, or that they remain exclusively nocturnal all year long in cold streams. The scientists surmised that cold salmon react less quickly to predators because of their lower metabolism, and so when the mercury takes a dive they tend to become proportionally more nocturnal to avoid the diurnal warm-blooded birds that prey upon them. When it is warmer and they feel better at eluding predators, the salmon become more diurnal to take advantage of the better lighting conditions to catch food.[33]

This interplay between food availability and predation risk can be used to tentatively explain other types of day/night switches. For example, white suckers *Catostomus commersonii* are known to be diurnal when living in a shoal but nocturnal when living alone.[34] They, as well as many other freshwater fishes, also tend to be diurnal as juveniles but nocturnal as adults.[35] What could explain these differences? Well, perhaps smaller (that is, less visible) and shoaling fish are less vulnerable to predatory birds such as kingfishers and can therefore afford to look for food during the day. Or maybe the smaller food items on which juveniles feed are more available during the day. Such hypotheses still remain to be tested.

There is no doubt that the temporal availability of food can affect activity patterns. Richard Spieler and his collaborators have spent a fair amount of time studying fish rhythms in the back rooms of the Milwaukee Public Museum. In one experiment, Spieler and Teresa Noeske fed some goldfish only at night, others only during the day, and yet others only at dawn or dusk. Then, after a few weeks, the food was withheld for 10 days. During that period of fasting, each fish turned out to be active only around the hour at which they used to be fed, be it during the day, the night, or at twilight.[36] This could not be a direct response to food because food was not delivered any more. Instead it seems that the fish had learned to adopt a daily phasing of activity that maximised their foraging success. Diurnal, nocturnal, crepuscular, they did not care, as long as they could get food. (A similar manipulation of activity phasing has been attempted with a nocturnal mammal, the weasel. Food was made much easier to obtain during the day, but the weasel remained stubbornly nocturnal, showing less plasticity than fishes.[37])

In humans, sleep is preferably done at night because our senses (vision, especially) are adapted to day-living. But many fish species seem to get by in complete darkness just as well as in broad daylight. For these animals, being strictly diurnal or nocturnal is not an obligation. Accordingly, they can easily switch between being diurnal and being noctunal. Food and predators are probably the main determinants of their preferred phase of activity, and therefore their phase of sleep (if they sleep at all).

Last word

So, what is the answer to the question “do fishes sleep”? As unsatisfactory as it is, the answer seems to be: it depends! It depends on which and how many criteria you are willing to use to define sleep. And it depends on the species, the age of the fish, its reproductive status, the time of year, the water temperature, the presence of predators, the availability of food, and who knows what other factors that still remain to be investigated. The last word is probably that, although signs of sleep are present in fishes, we should not equate it with the kind of sleep that we, humans, are used to experience.

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[1] For an enlightening dissertation on the ecological function of sleep and the application of behavioural criteria to the definition of sleep, see: Meddis, R., 1975, On the function of sleep, Animal Behaviour 23, 676-691; also: Meddis, R., 1977, The Sleep Instinct, Routledge and Kegan Paul, London. In these works, Ray Meddis championed the view that sleep serves as a great immobiliser, forcing animals to stay quiet, avoid detection by predators, and save energy during the ecologically unprofitable part of the 24-h cycle.

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[3] Titkov, E.S., 1976, Characteristics of the daily periodicity of wakefulness and rest in the brown bullhead (*Ictalurus nebulosus*), Journal of Evolutionary Biochemistry and Physiology 12, 305-309; Karmanova, I.G., Belich, A.I., and Lazarev, S.G., 1981, An electrophysiological study of wakefulness and sleeplike states in fish and amphibians, pp. 181-202 in: Brain Mechanisms of Behaviour in Lower Vertebrates (P.R. Laming, ed.), Cambridge University Press, Cambridge.

[4] For other examples, see: Ryder, R.A.,1977, Effects of ambient light variations on behavior of yearling, subadult and adult walleyes (*Stizostedion vitreum vitreum*), Journal of the Fisheries Research Board of Canada 34, 1481–1491; Siegmund, R., 1969, Lokomotorische Aktivität und Ruheverhalten bei einheimischen Süsswasserfischen (Pisces, Percidae, Cyprinidae), Biologisches Zentralblatt 88: 295-312; Peyrethon, J., and Dusan-Peyrethon, D. ,1967, Étude polygraphique du cycle veille-sommeil d'un téléostéen (*Tinca tinca*), Compte-rendus de la Société de Biologie 161, 2533-2537; Weber, E., 1961, Uber Ruhelagen von Fischen, Zeitschrift für Tierpsychologie 18, 517–533.

[5] Tauber, E.S., Weitzman, E.D., and Korey, S.R., 1969, Eye movements during behavioral inactivity in certain Bermuda reef fish, Communications in Behavioral Biology A 3, 131-135; Tauber, E.S., 1974, The phylogeny of sleep, pages 133-172 in: Advances in sleep research, vol. 1 (E.D. Weitzman, ed.), Spectrum Publications, New York; Clark, E., 1973, “Sleeping” sharks in Mexico, Underwater Naturalist 8, 4-7; Dew, C.B., 1976, A contribution to the life history of the cunner, *Tautogolabrus adspersus*, in Fishers Island Sound, Connecticut, Chesapeake Science 17, 101-103.

[6] Zhdanova, I.V., Wang, S.Y., Leclair, O.U., and Danilova, N.P., 2001, Melatonin promotes sleep-like state in zebrafish, Brain Research 903, 263-268; Yokogawa, T., Marin, W., Faraco, J., Pézeron, G., Appelbaum, L., Zhang, J., Rosa, F., Mourrain, P., and Mignot, E., 2007, Characterization of sleep in zebrafish and insomnia in hypocretin receptor mutants, PloS Biology 5: 2379-2397; Zhdanova, I.V., 2006, Sleep in zebrafish, Zebrafish 3: 215-226.

[7] As far as I know, light shock was first reported and studied in bluegill sunfish: Davis, R.E., 1962, Daily rhythm in the reaction of fish to light, Science 137, 430-432. Light shock (or maybe it was sleep?) has also been seen in the field by SCUBA divers: Hobson, E.S., 1965, Diurnal-nocturnal activity of some inshore fishes in the Gulf of California, Copeia 1965, 291-302. However, not all species react to light in this way; some fishes quickly dart away when illuminated at night: Emery, A.R., 1973, Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes, Journal of the Fisheries Research Board of Canada 30, 761-774.

[8] Near-infrared refers to the wavelength that is just beyond visible red. Near-infrared technology requires a source of infrared light to illuminate the subject. A flashlight fitted with an infrared filter does the job nicely. Far-infrared, for its part, would refer to the wavelengths that correspond to heat emission. Here a light source would not be necessary because the subject itself is generating the heat. Far-infrared technology can be used for night-viewing of birds and mammals but obviously not for fishes, which are ectotherms (cold-blooded) and do not give off much heat. Unfortunately, even near-infrared technology is not without drawbacks for observing fishes. The main problem is that water absorbs infrared light very readily. This means that subjects can only be illuminated through a relatively thin layer of water. Using more powerful lights does not necessarily solve the problem, as visible red light may then bleed through the filter, or the heat produced by the light may burn off the filter if it is made of gelatin, as is the Kodak filter I used and mentioned in the text.

[9] For other examples on the use infrared or other special technologies for night observation of fishes, see: Reebs, S.G., Whoriskey, F.G. and FitzGerald, G.J., 1984, Diel patterns of fanning activity, egg

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respiration, and the nocturnal behavior of male threespined sticklebacks, *Gasterosteus aculeatus* L. (f. *trachurus*), Canadian Journal of Zoology 62, 329–334; Hinch, S.G. and Collins, N.C., 1991, Importance of diurnal and nocturnal nest defense in the energy budget of male smallmouth bass: insights from direct video observations, Transactions of the American Fisheries Society 120, 657–663; Collins, N.C. and Hinch, S.G., 1993, Diel and seasonal variation in foraging activities of pumpkinseeds in an Ontario pond, Transactions of the American Fisheries Society 122, 357–365; Popiel, S.A., Pérez–Fuentetaja, A., McQueen, D.J. and Collins, N.C., 1996, Determinants of nesting success in the pumpkinseed (*Lepomis gibbosus*): a comparison of two populations under different risks from predation, Copeia 1996, 649–656; Mussen, T.D. and Peeke, H.V.S., 2001, Nocturnal feeding in the marine threespine stickleback (*Gasterosteus aculeatus* L.): modulation by chemical stimulation, Behaviour 138, 857-871.

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[13] A few people have done it; see: Tobler, I. and Borbély, A.A. (1985) Effect of rest deprivation on motor activity of fish, Journal of Comparative Physiology A 157, 817–822; Massicotte, B. and Dodson, J.J., 1991, Endogenous activity rhythms in tomcod (*Microgadus tomcod*) post-yolk-sac larvae, Canadian Journal of Zoology. 69, 1010-1016; Zhdanova, I.V., Wang, S.Y., Leclair, O.U. and Danilova, N.P., 2001, Melatonin promotes sleep-like state in zebrafish, Brain Research 903, 263-268.

[14] Schwassmann, H.O., 1971, Biological rhythms, pp. 371-428 in: Fish Physiology Vol. 6 (W.S. Hoar and D.J. Randall, eds.), Academic Press, New York.

[15] For a review, see: Reebs, S.G., 2002, Plasticity of diel and circadian activity rhythms in fishes, Reviews in Fish Biology and Fisheries 12, 349-371;Zhdanova, I.V., and Reebs, S.G., 2006, Circadian rhythms, pages 197-238 in: Behaviour and Physiology of Fish (K.A. Sloman, R.W. Wilson, and S. Balshine, eds.), Elsevier, San Diego.

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