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## SLEEP, INACTIVITY AND CIRCADIAN RHYTHMS IN FISH

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### INTRODUCTION

Sleep is a behaviour pattern that can be observed in most animals, yet its adaptive significance is still a matter of debate. One view, developed and championed by Meddis (1975, 1977), is that sleep acts as an immobiliser. By forcing an animal to find a safe shelter and remain immobile in it during an ecologically unprofitable part of the solar day, sleep renders the animal less vulnerable to predators. Moreover, by making it less sensitive to external stimuli, sleep allows the animal to conserve energy.

To fulfill this function, sleep must be limited to that part of the solar day to which the animal is ill-adapted. One way to achieve this aim might be to put sleep under the direct control of light. Diurnal animals could fall asleep whenever darkness comes, whereas nocturnal animals could do the same whenever light appears. However, it is possible to imagine a number of situations in which such a strategy would not be adaptive. For example, diurnal animals venturing into places where darkness always prevails (a tree hole, a burrow, the underside of a submerged log) would soon be transformed into sleeping beauties, a tranquil but not very profitable state of affairs. Similarly, nocturnal animals falling asleep in well-lit places would be very vulnerable to predators.

A better alternative is to put sleep under the control of a circadian clock that "tells" the animal when it is appropriate to sleep and when it is not. We can therefore surmise that one of the adaptive functions of circadian clocks is to maintain the temporal integrity of sleep. When the circadian clock of rats is removed (by lesions of the suprachiasmatic nuclei, or SCN), the rats continue to sleep for the same number of hours per solar day, but sleep now occurs in short episodes and is distributed equally between day and night (Ibuka and Kawamura, 1975). It would be interesting to release SCN-lesioned mammals in their natural

habitat and study their rate of survival. Presumably, they would not do as well as sham-lesioned individuals.

How do the above considerations apply to the fish world? First, can fish sleep? If not, do they at least show prolonged inactivity that functionally resembles sleep? Is sleep or prolonged inactivity under the control of circadian clocks or under the direct control of light? And are there exceptions to the patterns we observe? The present chapter provides a literature survey that addresses these questions.

## SLEEP IN FISH

Whether or not fish can sleep depends on the criteria we use to define sleep. In birds and mammals, characteristic patterns in electroencephalograms (EEGs) constitute the criterion of choice. However, EEGs are normally recorded in the cortex, and fish lack this brain structure. Moreover, EEG techniques are difficult to apply in an aquatic environment. Another popular criterion, prolonged eye closure, cannot be used in fish because fish do not have eyelids. Fortunately however, other behavioural criteria allow us to recognize sleep, especially when we consider them together. They are (1) prolonged quiescence in a typical rest posture, (2) the use of shelter, and (3) high arousal thresholds. Thus most people would agree that a fish is for all practical purposes asleep when it remains almost completely immobile, always in the same posture and protected location, and in a state of decreased sensitivity to disturbances. Certainly this corresponds well to Meddis' (1975, 1977) ecological view of sleep function.

A few laboratory studies have looked at fish sleep with the above criteria in mind. Shapiro and Hepburn (1976) have reported that Mozambique mouthbrooders, *Tilapia mossambica*, sink to the bottom of their tank at night (a very dim light was present to allow observations). The fish showed a lower respiratory rate and no detectable eye movement, and they did not respond as readily as during the day to electrical discharges and to the delivery of food (light intensity has a confounding influence on detection of food, but the authors controlled for this by delivering food at the end of a 2h dark pulse given in the middle of the day). Ontogenetically, it took about 22 weeks for this sleep pattern to develop, although the time was shortened when adults were placed together with the young fish (Shapiro *et al.*, 1981).

Titkov (1976), Karmanova *et al.* (1981), and Karmanova and Belich (1983) have used contact and noncontact polygraphic recordings to study sleep in brown bullheads, *Ictalurus nebulosus*. These nocturnal catfish spent the day in a shelter with the tail fin lying flat on the ground, other fins stretched out, and the body inclined at an angle of 10-30° to the vertical. The cardiac rhythm was much slower. The respiratory rhythm was slower, shallower, and became asymmetric. The fish did not respond to the approach of a foreign object, even when the object touched them. They did not react to sound. Similar characteristics were observed during "nocturnal rest" but they were not as pronounced as during the day. Karmanova and his colleagues have extended their observations to seven other fish species from the Black Sea and have found that while some exhibited patterns similar to those of the catfish (e.g. grey mullet, *Mugil sp.*, and ribbon-tail, *Dasyatis pastinaca*), others showed no sign suggestive of sleep (e.g. *Sciaenops ocellatus*; Karmanova *et al.*, 1981).

The tench, *Tinca tinca*, is another nocturnal fish whose sleep behaviour has been recorded with polygraphic techniques (Peyrethron and Dusan-Peyrethron, 1967). During the day, the fish lay at the bottom of their tanks for periods of 15-20 minutes without moving and

with respiratory rates reduced to 65% of the normal (nocturnal) value. The fish did not react to the approach of an object until the object touched them. Activity occurred during only 20% of the daytime, as compared to 60% at night. However, if lights were left on at night (the authors do not mention if this was done for several consecutive nights), then nocturnal activity decreased to 26%.

Tauber and Weitzman (1969) have described how the wrasse *Iridea bivittata*, once it has partially buried itself in sand at night, can be touched and lifted by hand without evoking a response. Higher arousal thresholds in diurnal fish at night have also been observed in the field by SCUBA and snorkel divers; unfortunately, artificial lights were used in all cases, raising the possibility that light itself caused the observed behaviour. During numerous dives in the southern Gulf of California, Hobson (1965) observed that "some fishes, both diurnal and nocturnal, were immobilized when held in the flashlight's beam at night. At such times they could be approached and occasionally gently handled without showing alarm." The fact that both nocturnal and diurnal species showed the same lack of response to light at night suggests that a direct effect of light, rather than sleep controlled by a circadian clock, was involved. Following dives in Ontario lakes, Emery (1973a) wrote that "fish were found to be more easily approached at night than in the daytime. Many species could actually be touched at night, whereas this was never possible in the daytime". Here too, however, nocturnal species (e.g. catostomids, cottids) could be approached as easily as diurnal ones (e.g. gasterosteiids, cyprinids, percids).

Immobility following a sudden exposure to light has been studied in the bluegill sunfish, *Lepomis macrochirus*, by Davis (1962) who referred to this behaviour as a "light shock". Davis reported that the intensity of the reaction varied according to the time of night. This variation may suggest circadian influence on this particular behaviour but it does not enlighten us about the relation between circadian clocks and sleep. It is also worth noting that some species do not show the light shock reaction, as they quickly dart away when illuminated at night (Emery, 1973a).

Direct observations in the field are useful to document the use of sheltered resting places by diurnal species at night (or by nocturnal species during the day). Such places include holes and crevices (Hobson, 1965; Emery, 1973b; Ebeling and Bray, 1976; Luckhurst and Luckhurst, 1978; Taborsky and Limberger, 1980; Helfman, 1981; Kohda, 1988), overhanging ledges (Hobson, 1965), vegetation (Emery, 1973a; Helfman, 1981), corals (Dubin and Baker, 1982), sponges (Emery, 1973b; Luckhurst and Luckhurst, 1978), or sand in which the fish can bury themselves (Tauber and Weitzman, 1969; Bray and Ebeling, 1975; Ebeling and Bray, 1976; Hobson 1986). Individuals may return to the same sleeping site on many consecutive nights (Ehrlich *et al.*, 1977; Dubin and Baker, 1982). Some species, most notably scarids and labrids, secrete a mucous envelope around themselves or at the opening of the crevice in which they have found shelter (Winn, 1955; Hobson, 1965; Tauber and Weitzman, 1969; Ogden and Buckman, 1973).

Many species, however, remain exposed during their inactive period (Emery, 1973a; Helfman, 1981; Hobson *et al.*, 1981). According to Hobson *et al.* (1981), size may play a role in this dichotomy, with smaller species being most often found in shelters (see also Helfman, 1981). Even within some species (eg. acanthurids, chaetodontids), smaller individuals seek shelter while the larger ones remain exposed (Hobson, 1972, 1974). Presumably, larger individuals are less vulnerable to predators and can forego the use of shelters. It would be useful to experimentally test for correlations between body size, predation rate, and use of shelter. It would also be interesting to try to find correlations

between any of these variables and the depth of sleep (or the degree of insensitivity to disturbances).

To my knowledge, no measurement of sleep-like behaviour has been attempted under prolonged and constant light conditions, especially constant darkness (see Shapiro and Hepburn, 1976, for observations throughout 96 h of constant light, during which sleep was abolished). Therefore we do not know whether such behavior is regulated by circadian clocks, by light, by some homeostatic mechanism, or by a combination of these. A role for homeostatic mechanisms has been claimed on the basis of "rest deprivation" experiments: Tobler and Borbély (1985) observed diurnal convict cichlids, *Cichlasoma nigrofasciatum*, during and after a "night" when the lights were left on (light was the rest-depriving treatment). They reported high activity during the "night" (although not as high as during the day) and lower activity than normal during the following day. They interpreted this low activity as a recovery period, suggesting homeostasis of sleep similar to that documented in mammals. However, several aspects of the results can also be explained in terms of direct light effects (or even after-effects) and circadian influence. More work is necessary to tease apart these possible, nonmutually exclusive modes of control.

### PERIODIC INACTIVITY IN FISH

Higher arousal thresholds and the use of typical resting places are fairly convincing criteria for the definition of sleep, but unfortunately their confirmation often requires direct observation or extensive experimentation. This may explain why sleeplike phenomena have not been studied continuously for many consecutive days under constant conditions. Locomotor activity, on the other hand, can easily be monitored for long periods of time via remote recording systems. This makes activity the parameter of choice for studies of biological rhythms. The researcher who is also interested in sleep might argue that inactivity by itself is a poor criterion to define sleep, but if we agree that complete inactivity fulfills the same ecological functions as sleep, i.e. keeping the animal out of harm's way and saving energy, then it becomes worthwhile to investigate whether inactivity is organized in time according to circadian principles.

A few caveats are worth bearing in mind, however. The less complete the inactivity, the less convincing the argument that inactivity is functionally similar to sleep. It is therefore worthwhile to point out that many studies of the chronobiology of fish still detect some activity during the "inactive", or rho, phase: a few interruptions of infrared light beams are still counted, a few fish are still captured on film or in fishing gear, a few movements are still recorded by ultrasound telemetry. Admittedly, in experiments where groups of fish are tested, these little signs of activity may be the result of a few individuals only, "jokers" that tend to mask the fact that most individuals are indeed completely inactive. On the other hand, it may also be that sleep and/or inactivity in fish is simply not as profound as what we, humans, are used to experiencing.

Another caveat is that remote recording systems are often selective. Infrared beams monitor only one small part of the aquarium; fishing gear has a finite catchment area. Therefore, variations in results may reflect a qualitative rather than a quantitative change in activity levels; the fish may simply be active in an area not monitored by the recording system. It can be argued in this regard that oxygen consumption represents a better measure of activity levels. Oxygen consumption can reveal circadian rhythms under constant conditions, although special respirometers are required and a fine control must be exerted over temperature, a potential confounding variable (Forstner, 1983; Ross and McKinney,

1988). Heart rate can also be correlated with activity, but stress, temperature and timing meals can add variability to the data (Priede, 1978).

These points notwithstanding, one can find in the literature many actograms that reveal periods of prolonged daily inactivity alternating with periods of steady activity, there forming activity rhythms; these rhythms freerun under constant conditions, suggest circadian control. Lake chub, *Coxesius plumbelus*, show solid activity during the day and almost continuous inactivity at night, as recorded by ultrasound systems (Kavaliers, 1979). In constant darkness (DD), the two phases remain distinct and the whole rhythm freeruns for 1520 days. The same can be said of sexually immature burbots, *Lota lota* except that they are nocturnal and their freerun in DD is maintained for up to 40 days (Kavaliers, 1980a). The bagfish, *Epiplatys burgeri*, also shows strong activity at night but none during the day, as recorded by infrared photocells; in DD the two phases remain distinct and freerun for several weeks (Ooka-Souda et al., 1985; Kabasawa and Ooka-Souda, 1985). The same can be said of the electric fish *Gymnorhamphichthys hypostomus* if we equate inactivity with low-frequency electric discharges, a fact that seems to be supported by direct observation (Schwassmann, 1971).

Groups of diurnal mummichogs, *Fundulus heteroclitus*, also show solid activity-inactivity cycles freerunning in either DD or constant light (LL); in general, the rhythms are stronger in DD and in larger groups (Kavaliers, 1980b). The grouping of white sucker *Catostomus commersoni*, also leads to clearer demarcation between active and inactive phases, and to more durable freerunning rhythms in DD (Kavaliers, 1980c).

Nelson and Johnson (1970) have studied two nocturnal bottom-dwelling sharks, the swell shark, *Cephaloscyllium ventriosum*, and the horn shark, *Heterodontus francisci*, both field and laboratory. Swell sharks in the wild showed signs of sleep, "lying motionless in rocky crevices and caves" and being "very lethargic by day ... usually responding (to escape or by swelling) only when roughly handled". In the laboratory, the sole swell shark tested exhibited freerunning activity-inactivity rhythms (measured by electromechanic sensors) in both DD and LL. In contrast, horn sharks were arrhythmic in the lab under DD and LL, and in the field this species showed fewer signs of sleep, being "relatively alert and responding quickly (by rapidly swimming away) when prodded...". They still retreated to caves and crevices during the day, however. In addition to showing the great interspecific variability that seems to exist in fish, Nelson and Johnson's (1970) study is a fine example of the potential rewards of the comparative approach in the study of sleep and circadian rhythms. Their study suggests that there might be a link between soundness of sleep and strength of circadian organization.

Besides strong freerunning rhythms, another sign of circadian control over activity-inactivity cycles is activity anticipating the arrival of dawn or dusk (depending on whether the fish is diurnal or nocturnal) or inactivity anticipating the arrival of dusk or dawn. Example of this can be found in Andreasson (1973), Reynolds and Casterlin (1976), Shapiro and Hepburn (1976), Eriksson (1978a,b) and Westin and Aneer (1987).

### EXCEPTIONS TO CIRCADIAN ACTIVITY-INACTIVITY PATTERNS

Endogenous control of sleep and inactivity may be advantageous in some situations, but there might also be circumstances where being a slave to sleep and to circadian clocks would not be favorable. Consider the challenge faced by parental species having to care for their young. Many fish species care for their eggs by fanning them. Fanning provides the egg

with a more or less continuous flow of water which prevents oxygen depletion in the boundary layer around the eggs. Because eggs consume oxygen 24 hours a day, it must be advantageous, maybe even necessary, for the parent to keep on fanning day and night. But outside of the reproductive season the parent fish may exhibit strict diurnalism or nocturnalism. Can the need for continuous parental care overcome the dictates of the internal clock?

The answer seems to be yes. Males of the damselfish *Abudefduf saxatilis* fan day and night; interestingly enough for this normally diurnal species, fanning levels at night are about four times higher than during the daytime (Albrecht, 1969). Reebbs *et al.* (1984) observed three-spine sticklebacks, *Gasterosteus aculeatus*, also fanning day and night; the percentage of time spent fanning at night was slightly, but not significantly, higher than during the day. The convict cichlid and the rainbow cichlid, *Herotilapia multispinosa*, have also been observed fanning day and night, with nocturnal levels about three times as high as diurnal values (Reebbs and Colgan, 1991). In the case of the convict cichlid, nocturnal care extends beyond the egg stage to the wiggler and fry stage (personal observation; see also Mckaye and Hallacher, 1973, for an anecdotal report of nocturnal retrieving by Midas cichlids, *C. citrinellum*, caring for fry). Several other cichlid species, i.e. *C. severum* and *C. spellerum*, also show nocturnal fanning (personal observation). Besides fanning, continuous nest guarding and defense have also been reported (brown bullhead, various centrarchids, Helfman, 1981), as well as spawning during the normally inactive period (bluntnose minnow, *Pimephales notatus*, Westman, 1938; yellow perch, *Perca flavescens*, Helfman, 1981; *Lesueurigobius friesii*, Nash, 1982).

These observations seem to indicate that circadian organization disappears during the parental phase. This, however, would be too hasty a conclusion, because a rhythm of high versus low fanning levels is still present. To test whether the rhythm is caused by light directly or by a circadian clock still at work, Reebbs and Colgan (1991) exposed parental convict cichlids to dark pulses in the middle of the day, and to constant darkness and constant light. They found that fanning levels were raised at the end of dark pulses, but not as high as the levels normally observed at night. In constant conditions, the fish still showed a rhythm of fanning activity, with higher levels at the time of subjective night. Reebbs and Colgan (1991) concluded that the fanning rhythm under light-dark conditions is the result of an endogenous rhythm whose amplitude is modulated by light. Interestingly enough, a similar conclusion was reached by Levinson and Burnside (1981) about the rhythm of retinal cone elongation in Midas cichlids.

Life-threatening situations might also modify circadian activity-inactivity cycles, although this possibility has seldom been tested under controlled conditions. Many species show typical daily patterns of habitat use, alternating between one place during the day and another at night. Sometimes, this pattern can be reversed or eliminated altogether when predators are introduced either artificially (Schlosser, 1988) or naturally (Bowen and Allanson, 1982). Similarly, when shelters are removed, fish that are normally strictly nocturnal can become active day and night (Harden Jones, 1956; Woodhead, 1965).

#### AVENUES FOR FUTURE RESEARCH

There is room for much more research in the areas of fish sleep and circadian rhythms. I have already mentioned the paucity of observations of sleep-like behaviour under constant conditions. Admittedly, LL often abolishes sleep (Shapiro and Hepburn, 1976; Tobler and

Borbély, 1985) and DD poses problems for direct observation. In the case of DD however, better use could be made of infrared equipment, such as infrared videos (Bruski and Dunham, 1987), infrared scopes (Reebbs and Colgan, 1991), or infrared-sensitive cameras. Other recording methods are also effective in complete darkness: ultrasound systems (Kavaliers, 1978, 1980a,b,c), noncontact recordings of heart rate (Belich, 1984) or opercular rate (Spoor *et al.*, 1971), and contact recordings of brain activity (Peyrethron and Dusan-Peyrethron, 1967) and heart rate (Priede, 1978). Freerunning rhythms of sleep-like behaviour provide evidence of circadian control, thereby reinforcing the idea that circadian clocks are adaptive because they maintain the temporal integrity of sleep.

Going one step further, experimenters could submit these freerunning rhythms to various treatments by light, temperature, food (see Weber and Spieler, 1987) and other factors, looking for patterns of entrainment, phase-shifts (phase-response curves), changes in phase relationship between rhythm and zeitgeber (see Eriksson, 1978b), and transient cycles.

Sleep could be studied not only in circadian species but also in circatidal ones. If sleep has adaptive functions during ecologically unprofitable parts of the day, then species living in the intertidal zone should sleep between tides. Circatidal activity-inactivity rhythms have been documented (e.g. Gibson, 1971) but sleep has never been measured in relation to these rhythms.

Finally, fish offer wide scope for comparative studies, owing to the diversity of habitats and ecological niches they occupy, not to mention the apparent ease with which one can find exceptions to any patterns of wake-rest organization in this class. Inspiration could be derived from comparative studies in mammals, where factors such as metabolic rate, risk of predation, and foraging needs have been correlated with sleep duration (see Elgar *et al.*, 1988; Berger, 1990; and references therein). Studies of this kind were possible because of an extensive database (69 species in the case of Elgar *et al.*, 1988). It may not be necessary to match this in fish, but certainly comparisons based on the judicious choice of a few key species and parameters might go a long way towards explaining the wide range of activity-inactivity patterns exhibited by fish.

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