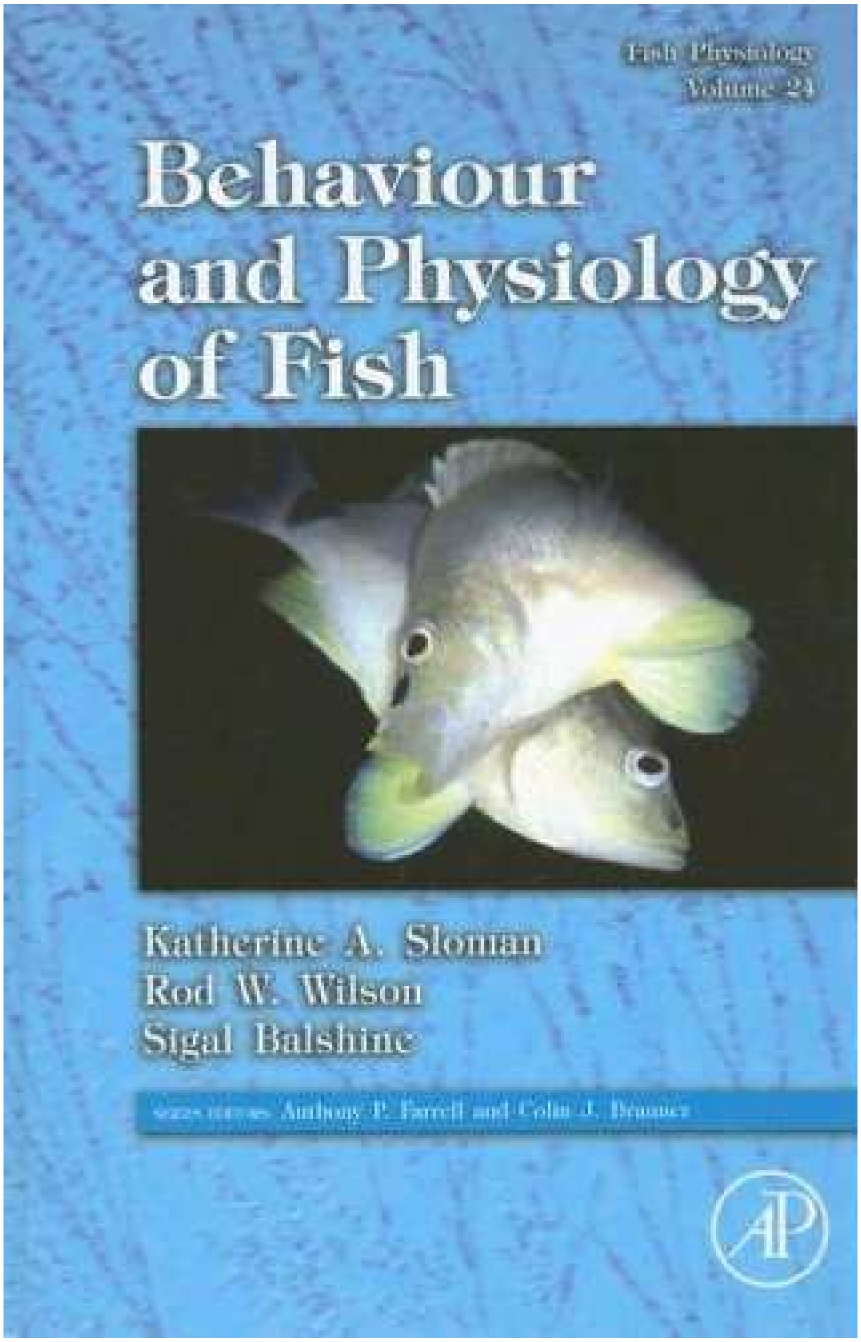

Fish Physiology
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# Behaviour and Physiology of Fish

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# 6

# CIRCADIAN RHYTHMS IN FISH

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## 1. INTRODUCTION

Circadian rhythmicity in behaviour and metabolism is a ubiquitous phenomenon in biology, documented in such diverse species as unicellular organisms, plants, invertebrates, and vertebrates. The reason is quite clear: the survival of all of these organisms depends on adapting to the regular changes of their environment, defined mostly by the 24-hour period of earth's rotation relative to the sun. Importantly, the organisms can immensely benefit from predicting when the day or night comes and, with it, changes in illumination, temperature, or food availability. Anticipating these environmental changes allows organisms to adjust all of their metabolic and behavioural processes in advance and to do everything "on time." Hence, biological clocks have evolved, and even in the absence of any environmental

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cues they autonomously oscillate with a circadian (*circa* = about, *dia* = day) period.

The intrinsic period of circadian clocks can be somewhat shorter or longer than 24 hours and can be adjusted (reset) to the environment by gradually shifting the oscillation phase until it coincides with the environmental cycle and then stabilises (entrains). Such entrainment can be induced by different environmental cues, called *zeitgebers* (“time givers”) or *synchronisers*. Light appears to be the strongest of these synchronisers and, as a result, a large amount of data characterising light-dependent intrinsic oscillations has been collected over the years. In addition, other critical environmental parameters changing daily or annually (such as environmental temperature, food availability, and predation risk) can also affect the phase of intrinsic clocks and, in some species, may even play a more important role than light.

Conceivably, every cell in the body can contain an intrinsic clock mechanism. Although some cells may initiate oscillations only in response to specific internal or external factors, others constantly express this function. The continuously oscillating cells and structures specialising in providing circadian signals to the entire organism are called *central oscillators*. The most renowned of them is the suprachiasmatic nucleus (SCN) of the hypothalamus in mammals, a neuronal structure defining the majority (if not all) of the circadian rhythms in this group The autonomous oscillations displayed by peripheral cells and tissues may remain independent or can synchronise with each other and with the central oscillators, organising complex networks and affecting multiple physiological functions in a species-specific manner.

The circadian system of fish follows the same general design as in other vertebrates and invertebrates; they show circadian rhythms of activity, food intake, and some physiological parameters (Table 6.1). The existence of an elaborate network of coexisting or competing central and peripheral circadian oscillators and a large number of circadian clock genes in fish, when compared to other vertebrates, may explain some specific characteristics such as instability in their circadian rhythms, spontaneous shifts between diurnal and nocturnal activity, and dramatic seasonal changes in activity patterns.

A principal circadian hormone, melatonin, and melatonin-producing organs, the pineal gland and retina, also play a central role in the circadian rhythms of fish and their entrainment to changing environments. Rest in fish is under both circadian and homeostatic control, showing distinct behavioural and pharmacological features of sleep. A sleeplike state can be induced in fish by different hypnotic agents and melatonin, further suggesting that rest in fish is analogous to sleep in higher vertebrates.

**Table 6.1**
Self-Sustained Circadian Rhythms (and Attempts to Find Such) in Fishes

| Parameter | Common name (or family) | Latin name | Lighting and tau | Reference | Comment |
|---|---|---|---|---|---|
| Body colour change | Mummichog | *Fundulus heteroclitus* | LL and dimLL: 22.5–26.5 h | Kavaliers and Abbott, 1977 | Hypophysectomy abolishes Rhythm |
| Cell proliferation in retina | (Cichlid) | *Haplochromis burtoni* | DD: ca. 24 h | Chiu *et al.*, 1995 | |
| Demand-feeding | European sea bass | *Dicentrarchus labrax* | LL: 21.3–26 h | Boujard *et al.*, 2000 | Groups of 50 fish |
| | European sea bass | *Dicentrarchus labrax* | LD 40:40 min: 22.5–24.5 h | Sánchez-Vázquez *et al.*, 1995a | Singles and groups of four |
| | European sea bass | *Dicentrarchus labrax* | DD: no rhythm detected | Sánchez-Vázquez *et al.*, 1995b | After many days under a restricted feeding schedule |
| | Rainbow trout | *Oncorhynchus mykiss* | LL: 24.6–26.0 h | Chen and Tabata 2002 | After many days under a restricted feeding schedule |
| | Rainbow trout | *Oncorhynchus mykiss* | LL: >24 h | Sánchez-Vázquez *et al.*, 2000 | Pinealectomy does not abolish rhythm |
| | Rainbow trout<br>European catfish | *Oncorhynchus mykiss*<br>*Silurus glanis* | LL (trout): 23–30 h<br>DD (catfish): 20–26 h | Bolliet *et al.*, 2001 | Groups and individuals were tested, but no difference detected |
| | Rainbow trout | *Oncorhynchus mykiss* | LL: 16–32 h | Chen *et al.*, 2002a | Longer tau in groups than in individuals |

(*continued*)

Table 6.1 (*continued*)

| Parameter | Common name (or family) | Latin name | Lighting and tau | Reference | Comment |
|---|---|---|---|---|---|
| Demand-feeding (ambulatory) | Bluegill sunfish<br>Largemouth bass | *Lepomis macrochirus*<br>*Micropterus salmoides* | DD: ca. 24 h | Davis, 1964 | Rhythm lasts for only 2 days after a restricted feeding schedule |
| Electric discharge | (Gymnotid) | *Gymnorhamphichthys* hypostomus | DD and LL: 23.5–25.4 h | Schwassmann, 1971 | Well-defined rhythm; also a review of the older literature |
| Locomotion, demand-feeding | Goldfish | *Carassius auratus* | DD: 22.2–27.5 h<br>LD 45:45 min: 23.0–24.8 h | Sánchez-Vázquez *et al.*, 1996 | Rhythms lacked constancy and damped out within a few days |
| | Brown bullhead | *Ictalurus nebulosus* | LD 45:15 min: 21.5–23.8 h | Eriksson and Van Veen, 1980 | No rhythm found in DD, LL, or dimLL |
| | Rainbow trout | *Oncorhynchus mykiss* | LD 45:45 min: 21.9 h (feeding)<br>LL: 26.2 h (feeding) and 25.8 h (locomotion) | Sánchez-Vázquez and Tabata, 1998 | More fish expressed rhythm under LL than LD 45: 45 min or dimLL |
| Locomotion | American shad (Characin) | *Alosa sapidissima* | dimLL: no rhythm found | Katz, 1978 | |
| | | *Anoptichthys jordani* | DD: ca. 24 h<br>LL: ca. 24 h | Erckens and Weber, 1976 | Cave-living population; rhythm damps out after 1–4 day |
| | Sea catfish | *Arius felis* | DD and LL: ca. 24 h | Steele, 1984 | |

| | | | | |
|---|---|---|---|---|
| Mexican Tetra | *Astyanax mexicanus* | DD: 21.9–25.9 h<br>LL: ca. 24 h | Erckens and Martin, 1982a | River-living population |
| Mexican tetra | *Astyanax mexicanus* | DD: no rhythm found | Erckens and Martin, 1982b | Cave-living population |
| Shanny | *Blennius pholis* | DD: 23–25 h | Gibson, 1971 | Only after many days of LD in the lab |
| Goldfish | *Carassius auratus* | DD: 24.4<br>dimLL: 26.0<br>LL: 25.2 h | Iigo and Tabata, 1996 | Only half of all individuals were rhythmic |
| Goldfish | *Carassius auratus* | LL: >24 h | Kavaliers, 1981a | More stable rhythms in groups than in individuals |
| Goldfish | *Carassius auratus* | DD: 21.5–28.8 h | Sánchez-Vázquez *et al.*, 1997 | Rhythm better detected at bottom than at top of tank |
| Goldfish | *Carassius auratus* | DD and LL: ca. 24 h | Spieler and Clougherty, 1989 | After many days under a restricted feeding schedule |
| White sucker | *Catostomus commersoni* | DD: <24 h | Kavaliers, 1981b | Long-lasting rhythm |
| White sucker | *Catostomus commersoni* | DD: 22.4–23.5 h (single) and 24.6–26.0 (groups of 25) | Kavaliers, 1980a | Better defined rhythm in groups of 25 than in individuals |
| Herring | *Clupea harengus* | DD: ca. 24 h | Stickney, 1972 | Rhythm damps out after 2 days |
| Lake chub | *Couesius plumbeus* | DD: 24.8–28.1 h | Kavaliers and Ross, 1981 | Seasonal variation in tau |
| Lake chub | *Couesius plumbeus* | DD: 24.8–28.1 h | Kavaliers, 1978 | Seasonal variation in tau |
| Lake chub | *Couesius plumbeus* | DD: ca. 25 h | Kavaliers, 1980b | In both intact and pinealectomized individuals |

(*continued*)

**Table 6.1** ***(continued)***

| Parameter | Common name (or family) | Latin name | Lighting and tau | Reference | Comment |
|---|---|---|---|---|---|
| | Lake chub | *Couesius plumbeus* | DD: 24.6–26.9 h | Kavaliers, 1979 | In both intact and pinealectomized individuals |
| | Lake chub | *Couesius plumbeus* | DD: >24 h | Kavaliers, 1980c | In both intact and pinealectomized individuals |
| | Zebrafish | *Danio rerio* | DD: many averages, all >24 h | Hurd and Cahill, 2002 | Larvae |
| | Inshore hagfish | *Eptatetrus burgeri* | DD: <24 h | Kabasawa and Ooka-Souda, 1989 | Well defined and long-lasting rhythm |
| | Inshore hagfish | *Eptatretus burgeri* | DD: 22.8–25.1 h | Ooka-Souda and Kabasawa, 1995 | Well defined and long-lasting rhythm; phase-response curve to light |
| | Inshore hagfish | *Eptatretus burgeri* | DD: 23.0–24.7 h | Ooka-Souda *et al.*, 1985 | Nice transient cycles after LD shift |
| | Northern pike | *Esox lucius* | DD: 24 h<br>LL: 25.25 h | Beauchamp *et al.*, 1993 | Actograms not shown |
| | Mummichog | *Fundulus heteroclitus* | LL: >24 h<br>DD: >24 h | Kavaliers, 1980d | Better defined rhythm in groups of 25 than in groups of 5 or in individuals |
| | Yellow wrasse | *Halichoeres chrysus* | dimLL: 24.2 h on average | Gerkema *et al.*, 2000 | 16 tested individually; well defined rhythms; phase-response curve to light |

| | | | | |
|---|---|---|---|---|
| (Wrasse) | *Halichoeres tenuispinnis* | DD: 23.6–24.3 h<br>LL: 23.5–23.7 h | Nishi, 1989 | Well defined rhythm |
| Horn shark | *Heterodontus francisci* | DD and LL: no rhythm for horn shark | Nelson and Johnson, 1970 | Only one individual tested; relation between presence of sleep and of rhythm |
| Swell shark | *Cephaloscyllium ventriosum* | DD and LL: 23.4 h and 24.4 h for swell shark | | |
| Stinging catfish | *Heteropneustes fossilis* | DD: <24 h | Garg and Sundararaj, 1986 | Pinealectomy abolishes rhythm |
| Rosy tetra | *Hyphessobrycon rosaceus* | LL: no rhythm<br>DD: ca. 24 h | Thinès, 1967 | Groups of 12 fish; two cycles only |
| Channel catfish | *Ictalurus punctatus* | DD and LL: no rhythm found | Goudie *et al.*, 1983 | |
| Arctic lamprey | *Lampetra japonica* | DD: 20.0–23.5 h | Morita *et al.*, 1992 | Pinealectomy abolishes rhythm |
| Burbot | *Lota lota* | DD: 21.2–23.5 h | Kavaliers, 1980e | Seasonal variation in tau; well defined and long-lasting rhythms |
| Oriental weatherfish | *Misgurnus anguillicaudatus* | DD: 22.0–28.2 h | Naruse and Oishi, 1994 | No more than 50% of fish showed rhythm |
| (River loach) | *Nemacheilus evezardi* | DD: ca. 24 h | Pati, 2001 | In both cave-dwelling and surface-dwelling populations |
| (River loach) | *Noemacheilus barbatulus* | dimLL: ca. 24 h | Burdeyron and Buisson, 1982 | Groups of 9 fish; individuals are arhythmic |

(*continued*)

**Table 6.1 (*continued*)**

| Parameter | Common name (or family) | Latin name | Lighting and tau | Reference | Comment |
|---|---|---|---|---|---|
| | Pink salmon | *Oncorhynchus gorbuscha* | LL: 20.9–26.4 h<br>dimLL: 20.0–35.6 h | Godin, 1981 | Juveniles; only half the fish were rhythmic |
| | Sea lamprey | *Petromyzon marinus* | dimLL: ca. 23 h | Kleerekoper *et al.*, 1961 | Only one individual |
| | European minnow | *Phoxinus phoxinus* | LL: no rhythm found | Harden Jones, 1956 | |
| | Bluefish | *Pomatomus saltatrix* | dimLL: ca. 24 h | Olla and Studholme, 1972 | One group of 6 fish |
| | (Bagrid catfish) | *Pseudobagrus aurantiacus* | DD and LL: no rhythm found | Mashiko, 1979 | |
| | Longnose dace | *Rhinichthys cataractae* | DD: 21.6–23.6 on average | Kavaliers, 1981c | Seasonal variation in tau |
| | Amur catfish | *Silurus asotus* | DD: 22.5–27.3 h<br>LL: 20.1–27.0 h<br>LD 45:15 min: 20.9–27.5 h | Tabata *et al.*, 1989 | |
| | Amur catfish | *Silurus asotus* | DD: 24.3–26.2 h<br>LL: 21.2–25.6 h<br>dimLL: 25.9–26.3 h | Tabata *et al.*, 1991 | Neither pinealectomy nor blinding abolish rhythm |
| | Slender wrasse<br>Cleaner wrasse | *Suezichthys gracilis* | LL: depends on species, but generally <24h | Nishi, 1990 | Well-defined rhythm |

| | | | | | |
|---|---|---|---|---|---|
| | Threadfin wrasse | *Thalassoma cupido*<br>*Labroides dimidiatus*<br>*Cirrhilabrus temminckii* | DD: activity often suppressed | | |
| | Slender wrasse | *Suezichthys gracilis* | LL: >24 h<br>DD: activity suppressed | Nishi, 1991 | In Japanese with English summary; rhythm dependent on presence of refuge (sand) |
| | (Heptapterid) | *Taunayia sp.* | DD: no rhythm found | Trajano and Menna-Barreto, 2000 | Cave-living |
| | Tench | *Tinca tinca* | LD 40:40 min: 20.8–28.6 h<br>DD: 21.0–26.4 h | Herrero *et al*., 2003 | Rhythm detected in only half the fish |
| | Dark chub | *Zacco temmincki* | DD: 23.9 h<br>dimLL: 26.1 h | Minh-Nyo *et al*., 1991 | |
| | Viviparous blenny | *Zoarces viviparus* | DD: ca. 24 h | Cummings and Morgan, 2001 | Mixed with a stronger circatidal rhythm |
| | Bluegill sunfish | *Lepomis macrochirus* | DD: ca. 24 h | Reynolds and Casterlin, 1976a | Scant details of methods and results |
| | Largemouth bass | *Micropterus salmoides* | LL: ca. 24 h | Reynolds and Casterlin, 1976b | Scant details of methods and results |
| | Atlantic salmon | *Salmo salar* | DD: 23.5–24.2 h<br>LL: no rhythm found | Richardson and McCleave, 1974 | Only 5 out of 30 individuals were rhythmic in DD |
| Locomotion, oxygen consumption | Lemon shark | *Negaprion brevirostris* | Dim LL: ca. 24 h | Nixon and Gruber, 1988 | One individual tested |

(*continued*)

**Table 6.1 (*continued*)**

| Parameter | Common name (or family) | Latin name | Lighting and tau | Reference | Comment |
|---|---|---|---|---|---|
| Oxygen consumption | Nile tilapia | *Oreochromis niloticus* | LL: ca. 24 h<br>DD: ca. 24 h | Ross and McKinney, 1988 | |
| | River puffer fish | *Takifugu obscurus* | DD: 22.7–24.8 h | Kim *et al.*, 1997 | In singles as well as in groups |
| Parental behaviour | Convict cichlid<br>Rainbow cichlid | *Cichlasoma nigrofasciatum*<br>*Herotilapia multispinosa* | DD: ca. 24 h | Reebs and Colgan, 1991 | Rhythm only 2 cycles long |
| | Threespine stickleback | *Gasterosteus aculeatus* | LL: no rhythm found | Sevenster *et al.*, 1995 | Also no rhythm of self-selection of light |
| Response to light | Lake chub | *Couesius plumbeus* | DD: ca. 24 h | Kavaliers, 1981d | In blind and pinealectomized individuals |
| Self-selection of light | Pumpkinseed sunfish | *Lepomis gibbosus* | Self-selected: no rhythm found | Colgan, 1975 | |
| | (River loach) | *Nemacheilus evezardi* | Self-selected: only one cycle measured | Pradhan *et al.*, 1989 | Tested in groups of 16 fish |
| Melatonin production | Northern pike | *Esox lucius* | DD: 24–27 h | Bolliet *et al.*, 1997 | Pineal cell culture |
| | Ayu | *Plecoglossus altivelis* | DD: averages 25.7–26.1 h | Iigo *et al.*, 2003a | Pineal organ culture |
| | Ayu | *Plecoglossus altivelis* | DD: 26.1 h | Iigo *et al*, 2004 | Pineal organ culture |

Many of these rhythms lasted no longer than 10 days. Many were also hard to distinguish visually on actograms and required periodogram analysis for detection.

Tau, period of free-run; DD, constant darkness; LL, constant light; LD, light–dark cycle.

Remarkable intra- and interspecies variability in the design and function of the circadian systems in fish (Table 6.1) add challenge to the study of their circadian rhythmicity, but also could provide unique insights into the general mechanisms of biological timekeeping in vertebrates.

## 2. CIRCADIAN CLOCK GENES

The discovery in insects and mammals of a network of circadian clock genes and the proteins they encode, with a possibility to study them *in vivo* and *in vitro*, provided a remarkable breakthrough in our understanding of the circadian system and its development. Some of these genes define intrinsic circadian oscillations, whereas others influence the distribution of the circadian message. The genetic regulation of circadian rhythm generation in fish appears to be similar to the general scheme described in *Drosophila* and in mice (Dunlap, 1999). It is based on a self-sustaining transcriptional–translational feedback loop, in which the expression of the clock genes is periodically suppressed by their protein products. The oscillation involves heterodimerisation of CLOCK and BMAL proteins, members of the basic helix-loop-helix PAS superfamily of transcription factors, which bind to the E-box DNA motif. This complex activates expression of the circadian clock genes *Period* (*Per*) and *Cryptochrome* (*Cry*). Then, PER and CRY proteins form complexes that enter into the nucleus and repress the CLOCK-BMAL dependent transcription of their own genes, thereby generating approximately a 24-hour period molecular oscillator (see Okamura, 2003 for a review). This loop also controls the rhythmic expression of the repressor REV-ERBα, which is required for rhythmic Bmal1 transcription. Such a second loop appears to promote an overall robustness of the circadian oscillator. The negative feedback loop, reinforced by a positive transcriptional loop, can be reset by external time cues (predominantly a light–dark cycle) synchronising the intrinsic processes with the periodically changing environment (Glossop *et al*., 1999).

Our knowledge of the molecular mechanisms of the fish circadian system is based mainly on studies conducted in zebrafish (Cahill, 2002). A distinct feature of the zebrafish circadian system is a large number of circadian clock genes, although all of them appear to be homologs of the circadian clock genes known in other species. This phenomenon is likely to stem from whole or partial genome duplication in some teleosts (Postlethwait *et al*., 1998; Leggatt and Iwama, 2003; Le Comber and Smith, 2004).

So far, three zebrafish *Clock* genes (*zfClock1, 2,* and *3*) and three *Bmal* genes (*Bmal1*, *2,* and *3*) have been cloned (Whitmore *et al*., 1998; Ishikawa *et al*., 2002). In mammals, *Clock* expression does not oscillate but *Bmal* expression does (Oishi *et al.*, 1998; Shearman *et al.*, 2000). In contrast, in zebrafish, all of the *Clock* and *Bmal* genes show robust rhythmic expression under a light–dark cycle or in constant darkness (Cermakian *et al.*, 2000; Ishikawa *et al.*, 2002).

Three zebrafish *Period* genes are homologs of the mammalian *Per1*, *Per2,* and *Per3*. At least two of them, *Per2* and *Per3*, are expressed early in zebrafish development. Their differential spatiotemporal expression suggests that they play distinct roles in the establishment of the embryonic circadian system (Delaunay *et al.*, 2000, 2003).

Zebrafish have six *Cry* genes (*zCry1a*, *1b*, *2a*, *2b*, *3,* and *4*) (Kobayashi *et al.*, 2000). Four of them (*zCry1a*, *1b*, *2a*, *2b*) have high sequence similarity to mammalian *Cry* genes. They are rhythmically expressed in the retina, pineal, brain, and other zebrafish tissues and their products can inhibit CLOCK-BMAL mediated transcription. z*Cry3 and* z*Cry4* have higher sequence similarity to the Drosophila *Cry* gene and their protein products do not affect CLOCK-BMAL mediated transcription.

Further studies in other fish species would substantiate the data collected in zebrafish and help determine the basis for interspecies variability in circadian rhythms and the circadian plasticity exhibited by these vertebrates.

## 3. ENTRAINMENT TO LIGHT

Three major properties of a light-dependent circadian system include photoreception, intrinsic oscillation, and ability to communicate circadian phase information to the local environment (to peripheral oscillators, for example). Apparently, such a "trio" can be present within one cell because unicellular organisms can show robust intrinsic circadian rhythms. Moreover, all these properties are retained by specialised photosensitive cells in phylogenetically advanced species. Both retinal photoreceptors and photosensitive cells of the pineal gland contain circadian clocks and secrete melatonin, a bioamine that can convey circadian messages either to the nearby surroundings (retinal melatonin) or to the entire organism (pineal melatonin).

Furthermore, it has recently been shown that multiple tissues in vertebrates, including peripheral ones, can directly detect light and entrain to it, and can express circadian clock genes (Whitmore *et al.*, 2000). This suggests that cell-autonomous circadian oscillation modulated by environmental light is a more widespread phenomenon than previously thought.

It is also becoming increasingly clear that the circadian system does not rely only on the cone- or rod-based opsins, although they are likely to play some role in light entrainment. Several new photopigments have been identified in fish retinas, pineal glands, brain and peripheral tissues (see Foster *et al.*, 2003 for a review). Such photopigments include three isoforms of vertebrate-ancient (VA) opsin (Soni and Foster, 1997; Soni *et al.*, 1998; Kojima *et al.*, 2000; Moutsaki *et al.*, 2000; Minamoto and Shimizu, 2002; Jenkins *et al.*, 2003), melanopsin (Bellingham *et al.*, 2002; Jenkins *et al.*, 2003; Drivenes *et al.*, 2003), cryptochromes (Kobayashi *et al.*, 2000; Cermakian and Sassone-Corsi, 2002), and *tmt*-opsin (Moutsaki *et al.*, 2003). These molecules became candidates for a putative ''circadian photoreceptor.'' It remains to be elucidated which of them play critical roles in circadian systems. So far, it appears that several rather than one photopigment might be involved in photic entrainment.

### 3.1. Centralised Circadian Oscillators

In fish, the existence of a centralised neuronal central clock structure, analogous to the mammalian SCN, has not yet been documented. However, another evolutionary conserved circadian structure, the pineal gland (*epiphysis cerebri*) plays an important role in fish circadian rhythmicity via its strictly periodic secretion of melatonin. Melatonin is also produced by the retina, providing a local paracrine signal. Analysis of the temporal parameters of melatonin secretion by the pineal gland and retina and their role in different physiological functions allows interesting comparisons between the centralised and peripheral circadian clocks.

The pineal gland is one of the first brain structures to develop in fish. For example, in zebrafish, the pineal gland develops by 19 hours postfertilisation and, almost immediately, becomes responsive to light and starts secreting melatonin (Kazimi and Cahill, 1999; Danilova *et al.*, 2004). If the embryos are exposed to a light–dark cycle during these early stages of development, their pineal glands secrete melatonin in a distinct circadian pattern, persisting after the embryos are moved to constant conditions. However, if the embryos are kept in constant darkness from the start, the circadian rhythm of melatonin production does not develop and melatonin is secreted continuously at a relatively low level (Kazimi and Cahill, 1999). Thus, the pineal gland in zebrafish has intrinsic circadian oscillators but these may need to be ''turned on'' by the environmental light–dark cycle.

Fish show a surprising variety of tissue-specific circadian adaptations, which are well reflected in peculiarities of melatonin secretion and function. This might be explained by fish having more genes for encoding the same or similar proteins than mammals or birds, presumably due to a duplication of the teleost genome early in the course of evolution. For example, as opposed to mammals having one gene that encodes a limiting melatonin-synthesising enzyme, arylalkylamine-N-acetyltransferase (AANAT), fish have at least two of them (Begay *et al.*, 1998; Mizusawa *et al.*, 1998, 2000; Coon *et al.*, 1999;

Benyassi *et al.*, 2000). Similarly, mammals appear to have two genes for melatonin receptor proteins, but zebrafish have at least five of them (Reppert *et al.*, 1995). Such an abundance of proteins with similar functions may be at the root of the high functional and tissue specialisation shown by fish, resulting in more complex and often unpredictable patterns of circadian adaptations in cells and organs of different fish species.

In the vast majority of vertebrates, including mammals, the pineal gland and the retina secrete melatonin only at night, and in both structures melatonin synthesis is inhibited by bright light. This is not necessarily true in fish, at least for the retina.

Pineal glands in teleosts (e.g., zebrafish and pike) are directly photosensitive and contain intrinsic circadian clocks. Similarly to mammalian pineals, they secrete melatonin exclusively at night under a light–dark cycle, or exclusively during what would be nighttime (subjective night) under constant darkness. Pinealectomy can significantly disrupt circadian rhythmicity in these fish (as has been reported in white suckers, burbot, and catfish), presumably because their pineal glands serve as central circadian clocks (Kavaliers, 1980e; Garg and Sundararaj, 1986).

In contrast, the pineal glands of salmonids, though photosensitive, lack an intrinsic circadian oscillator (Gern and Greenhouse, 1988; Max and Menaker, 1992; Iigo *et al.*, 1997a; Falcon, 1999). In the absence of an SCN-like "master" clock or an intrinsic clock in the pineal gland, melatonin production in these species is under exclusive light control, occurring at any dark period, whether it is during their subjective day or at night (Masuda *et al.*, 2003). Consequently, pinealectomy does not dramatically alter their circadian rhythmicity, as shown by studies conducted in trout (Sánchez-Vázquez *et al.*, 2000).

Even more remarkable are the differences between melatonin rhythms in fish retinas. In some fish (e.g., sea bass, trout, or pike), the retina produces melatonin during the day, contrary to the "rule." In these species, nighttime light pulses stimulate retinal melatonin production and at the same time inhibit melatonin secretion by the pineal gland (Zachmann *et al.*, 1992; Iigo *et al.*, 1997b; Garcia-Allegue *et al.*, 2001; Falcon *et al.*, 2003). Studies in European sea bass show other differences in the pineal-retinal relationship; for example, stable circadian rhythms of nighttime pineal melatonin production can be associated with seasonally-adjustable retinal melatonin synthesis (Garcia-Allegue *et al.*, 2001) and alterations in retinal melatonin production can attenuate the pineal secretory activity, despite independent photosensitivity in this species (Bayarri *et al.*, 2003). Such remarkable variability in melatonin rhythms underscores the overall plasticity of the fish circadian system reflected in circadian patterns of behaviour, as discussed in detail below.

### 3.2. Peripheral Circadian Oscillators

Along with centralised clock structures, such as the pineal gland, fish have multiple peripheral oscillators in a variety of tissues, if not in all of them. This has been shown by documenting periodic expression of zebrafish circadian clock genes in isolated tissues, such as the heart or the kidney (Whitmore *et al*., 1998). Importantly, these peripheral tissue pacemakers, at least in zebrafish, are responsive to light and thus can be reset and entrained independently of the central circadian structures or photic input via the retina (Whitmore *et al*., 2000). In addition, the peripheral clocks appear to be able to entrain to other zeitgebers, such as feeding time (Tamai *et al*., 2003).

Central and peripheral oscillators can retain a similar circadian phase or be out of phase with one another by up to 12 hours. However, peripheral oscillators are likely to have a high degree of independence from central circadian signals, because there appears to be no time lag between pacemakers in the brain and the periphery in responding to a zeitgeber. Such a time lag would be expected in hierarchical structures that feature a leading "master" clock (Figure 6.1).

A complex network of coexisting central and peripheral clocks, coordinated to maintain physiological integrity, poses an interesting and challenging system to decipher. Depending on environmental or internal processes, the relative contribution of centralised circadian signals (such as circulating melatonin) and local clocks in peripheral organs can probably vary. Moreover, some oscillators may stay dormant, allowing a central oscillator to define the major rhythm, until the central clock activity is altered or special events "wake up" the local clocks.

### 3.3. Melatonin: Functional Significance

Conveying a circadian message to the immediate surrounding or to faraway structures and organs requires some delivery mechanisms. Presumably, there are multiple mechanisms, both neuronal and hormonal, that allow central clocks to achieve this. However, we still know very little about those pathways, with the exception of one of them involving the bioamine melatonin. Documenting changes in melatonin secretion proved to be an excellent way to monitor circadian phase and its changes. Similarly, studying the effects of increased or reduced melatonin levels during certain hours of the day provided important data on some of the physiological effects of the circadian clock (for a review, see Zhdanova and Tucci, 2003).

Melatonin produced by the pineal gland and melatonin produced by the retina have different physiological roles. The pineal gland provides its

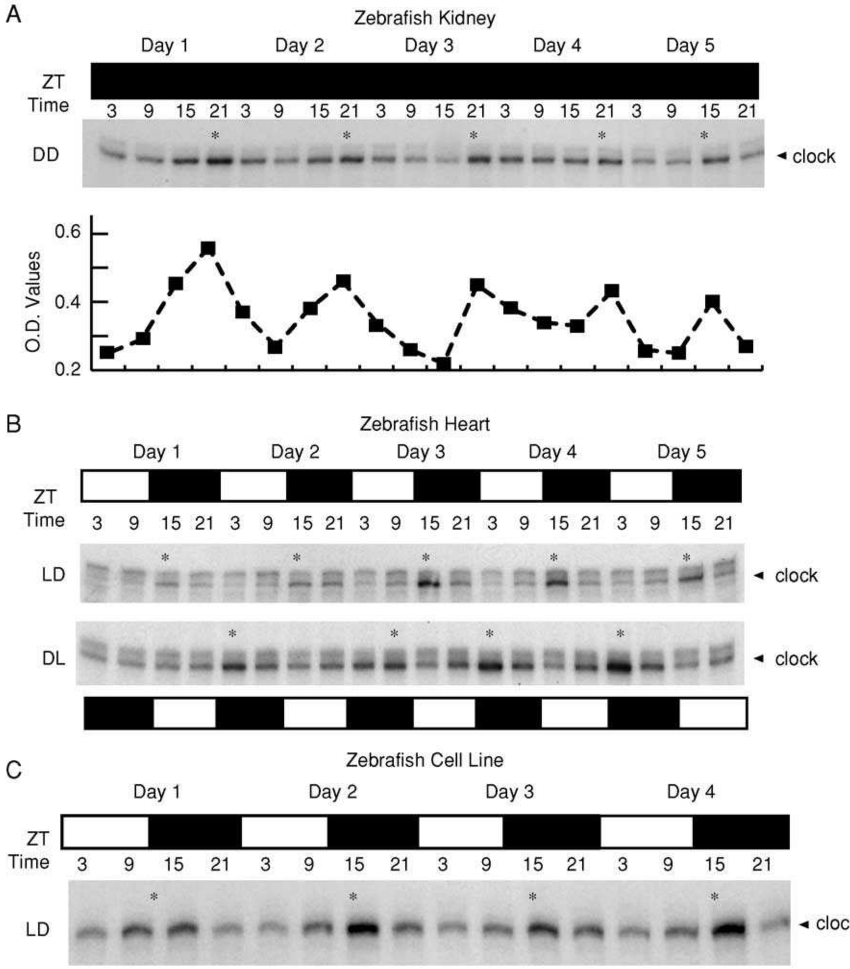

**Fig. 6.1.** Circadian oscillation in *Clock* gene transcript levels in a variety of tissues dissected from zebrafish maintained on 14:10 light-dark cycle (LD). (A) Clock oscillations in cultured zebrafish kidneys in constant darkness over a 5-day period. (B) Re-entrainment of cultured hearts placed on alternate light/dark cycles for 5 days. Hearts were dissected from an identical group of fish, and then placed onto out-of-phase light/dark cycles in ‘‘side-by-side’’ incubators, illuminated with a fiber-optic light source. Note that hearts in the DL reversed cycle re-entrain after only 1 day in the new lighting regime. (C) Clock oscillations in a zebrafish cell line when placed on a light-dark cycle. *Increased *Clock* expression. ZT time, ‘‘zeitgeber time,’’ with ZT0 corresponding to lights on time; OD values, optical density measurements of *Clock* gene expression from (A). (Adapted from Tamai *et al*., 2003.)

hormonal circadian signal to the entire organism, whereas the retina utilises its melatonin mostly for local, paracrine functions. In fish, this is further highlighted by the existence of two forms of the key enzyme for melatonin synthesis and differential expression of the genes encoding them in the pineal gland (AANAT 2) and retina (AANAT 1) (Benyassi *et al*., 2000). This way, not only the physiological functions but also the timing of melatonin production by these organs may differ, as mentioned above.

In the retina, the circadian or light-dependent fluctuations in retinal dopamine and melatonin production define some of the critical light–dark adaptations in this major photoreceptive organ. For example, under a light–dark cycle or in constant darkness, dopamine release from isolated fish retina has a circadian pattern, being high during subjective day and low during subjective night (Li and Dowling, 2000). This daily fluctuation in retinal dopamine enables light adaptation in advance of the actual changes in illumination and can affect light sensitivity. Melatonin, acting via its specific receptors, defines this daily fluctuation in retinal dopamine levels, attenuating nighttime dopamine release (Figure 6.2), activating rod input and decreasing cone input through dopamine-mediated D2-like receptor activation (Ribelayga *et al*., 2004).

The multiple physiological roles of daily variations in circulating melatonin and in the affinity of melatonin receptors from different tissues are only starting to emerge in all of their variety and complexity. Because, in the majority of fish species as well as other vertebrates, melatonin is secreted only at night and is suppressed by bright light, the duration of photoperiod is inversely related to the duration of melatonin production. While providing a circadian signal to multiple tissues and organs, melatonin affects such diverse processes as reproduction, locomotor activity, feeding, or sleep in fish.

Mating and spawning exhibit daily and seasonal variations, promoting offspring survival. Increased melatonin production, associated with short photoperiods, can significantly affect reproduction in fish (Zachmann *et al.*, 1992). In male sea bass, daily rhythms of pituitary LH positively correlate with the duration of melatonin production, and its daily rhythm of storage and release is altered by nighttime light exposure, which suppresses melatonin synthesis (Bayarri *et al.*, 2004). In masu salmon, a short photoperiod is known to stimulate gonadal maturation via activation of the brain-pituitary-gonadal axis. Melatonin treatment administered during long photoperiods, in such a way as to simulate melatonin profile during a short photoperiod, accelerates testicular development in this fish (Amano *et al*., 2000). However, it is important to appreciate that these effects of melatonin depend on the

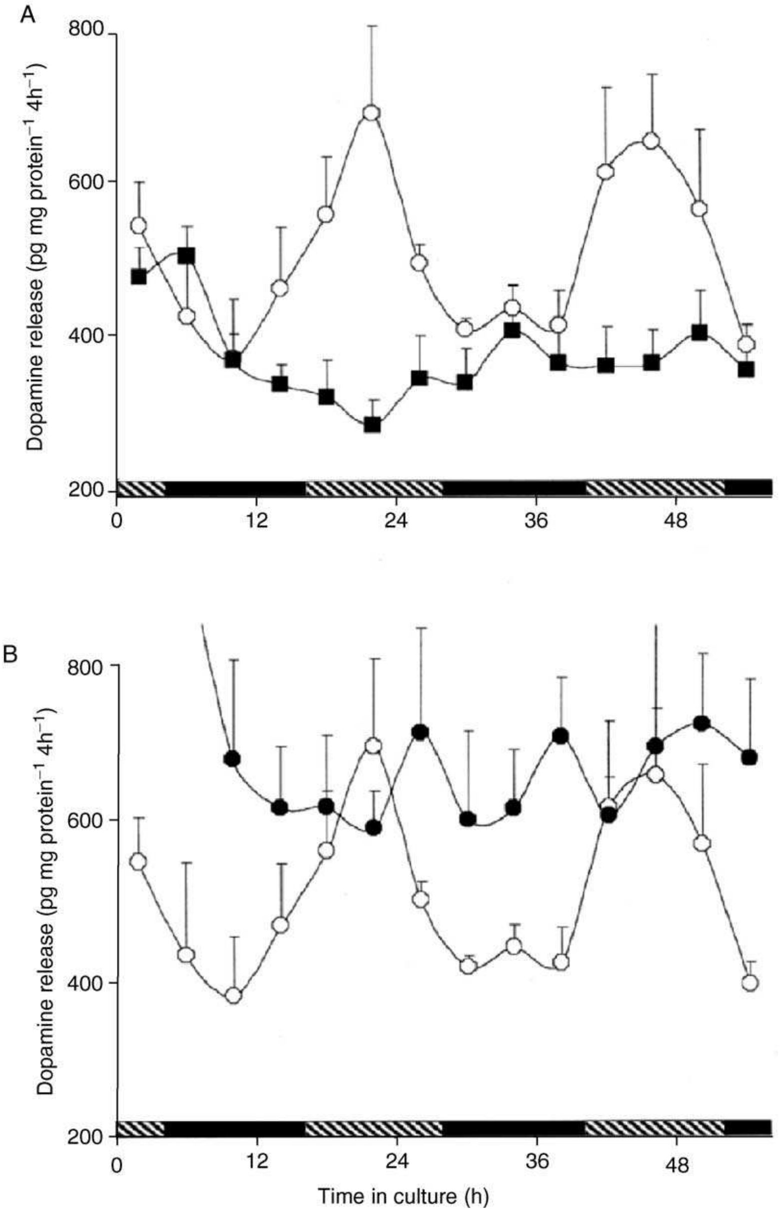

**Fig. 6.2.** The retinal clock uses melatonin to control the circadian release of dopamine. Isolated retinae were maintained for 56 hours in total darkness and constant temperature in a culture medium containing no drugs, melatonin (1 nM), or luzindole (1 $\mu$M). (A) Continuous application of melatonin (filled squares) abolished the rhythm of dopamine release by decreasing

maintenance of its normal circadian pattern. Increasing melatonin to supraphysiological levels and keeping them high throughout the day not only abolishes melatonin's promoting effect on reproduction but also lowers the gonadosomatic index and plasma testosterone levels in fish (Amano *et al*., 2004).

The role of melatonin in fish locomotor activity and sleep has been studied in zebrafish (Zhdanova *et al*., 2001). Similar to diurnal primates (Zhdanova *et al*., 2002), melatonin treatment attenuates locomotor activity in this diurnal fish and induces a sleeplike state. This sleep-promoting effect of the hormone is mediated via specific melatonin receptors because melatonin receptor antagonists attenuate or block its effects (Figure 6.3). The location of the structures responsible for this effect of melatonin remains unknown.

Interestingly, melatonin administration has also been reported to influence food intake and diet selection in fish. In goldfish, intraperitoneal injection of melatonin inhibited food intake, whereas melatonin administration into the cerebral ventricles did not produce such effect (Pinillos *et al*., 2001). Similarly, oral administration of melatonin inhibited total food intake and reduced carbohydrate intake in sea bass (Rubio *et al*., 2004).

Knowledge of specific sites of melatonin actions in fish is critical for understanding its functions. Circadian patterns of melatonin production can be complemented by circadian variations in melatonin receptor density or affinity. In the goldfish brain, for example, a circadian variation in melatonin receptor (binding site) density has been documented under both entrained and constant conditions (i.e., under a light–dark cycle and in constant darkness), whereas the receptor affinity to its ligand remained stable (Iigo *et al*., 2003b; Figure 6.4). It is not yet known whether other fish also exhibit daily or seasonal variations in melatonin receptor density or melatonin receptor affinity, and whether such variations might be coordinated in different tissues.

Further studies are needed to establish whether other circadian phenomena in fish—such as histamine levels in goldfish brain (Burns *et al*., 2003), steroid levels in Japanese char (Yamada *et al*., 2002), or electric discharges in gymnotid electric fish (Deng and Tseng, 2000)—are also under the control of melatonin production.

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daytime levels to the nighttime values. (B) Continuous application of the selective melatonin receptor antagonist luzindole (filled circles) abolished the rhythm of dopamine release by increasing the nighttime values to the daytime levels. Each data point represents mean values ±S.E.M. for 5 independent retinae. Open circles represent a positive control performed at the same time, but with no test drugs added. Hatched and filled bars indicate the subjective day and night, respectively. (Adapted from Ribelayga *et al*., 2004.)

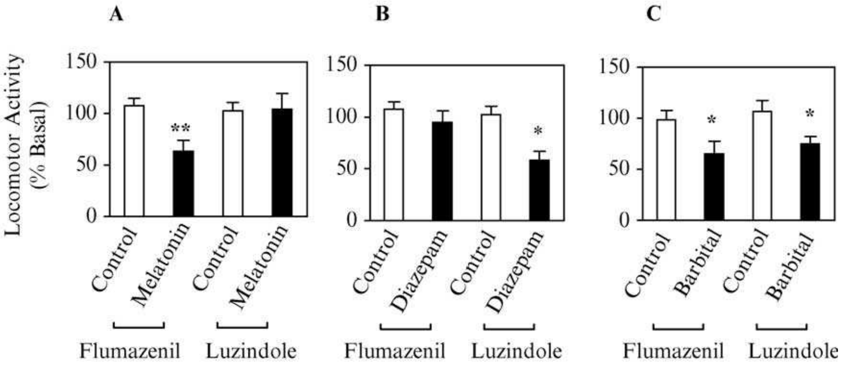

**Fig. 6.3.** Melatonin and diazepam affect locomotor activity in zebrafish via specific membrane receptors. Pretreatment with the specific antagonist for melatonin receptors, luzindole, blocked the decline in locomotor activity induced by (A) melatonin, but not by (B) diazepam or (C) pentobarbital. Pretreatment with specific benzodiazepine receptor antagonist, flumazenil, blocked reduction in locomotor activity following (B) diazepam, but not (A) melatonin or (C) pentobarbital treatment. Control solutions are vehicles for each treatment used. Data are expressed as mean ± S.E.M. group changes (%) in daytime locomotor activity, measured for 2 hours after treatment, relative to basal activity. $N = 30$ for each group. $^{**}P < 0.01$. (Adapted from Zhdanova *et al.*, 2001.)

## 4. ENTRAINMENT TO OTHER ENVIRONMENTAL CUES

In addition to the strong effect of light, other environmental factors such as water temperature and chemistry, food availability, social interaction, or predation risk could be considered as potential synchronisers. So far, there are only limited data available regarding these potentially entraining stimuli in fish. For example, daily variations in water chemistry (most notably oxygen content) have not been tried or reported as synchronisers of fish rhythms, at least to our knowledge.

### 4.1. Temperature

In homeothermic animals, temperature is considered to be a much weaker synchroniser than light. However, in poikilothermic vertebrates, ambient temperature can greatly influence metabolism and behaviour, including circadian periodicity (Rensing and Ruoff, 2002). Surprisingly, however, there seem to be no examples of entrainment by temperature cycles in fish. Only a few chronobiological studies in fish have mentioned temperature, the majority analysing it in conjunction with seasonal variations (e.g., Yokota and Oishi,

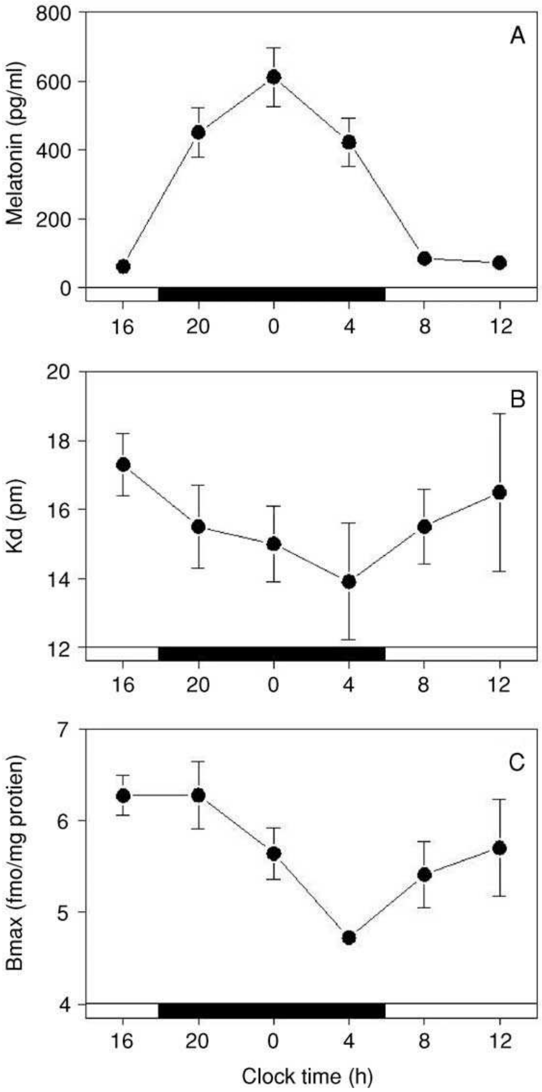

**Fig. 6.4.** Daily variations of melatonin levels in the plasma (A) and the $K_d$ (B) and $B_{max}$ (C) of melatonin-binding sites in the brain of the goldfish reared under LD 12:12. Solid and open bars along the X-axis represent the dark phase and the light phase, respectively. Plasma melatonin levels and the $B_{max}$ of melatonin binding sites in the brain exhibited significant daily variations (ANOVA, $P < 0.05$) with no variation in the $K_d$. $K_d$, melatonin affinity for its receptor in radioligand binding experiments; $B_{max,}$ receptor density. (Adapted from Iigo *et al.*, 2003b.)

1992; Aranda *et al*., 1999a). For example, lake chubs captured in winter display longer free-running periods in constant darkness than individuals captured in summer (Kavaliers, 1978; Kavaliers and Ross, 1981). The reverse relationship is observed in burbot and longnose dace (Kavaliers, 1980e; 1981c). It is not clear whether this reflects an endogenous circannual rhythm of circadian periodicity or simply an aftereffect of temperature and/or photoperiod at the time of capture. Because both photoperiod and temperature change with seasons, it will be necessary to resort to an experimental approach to determine the relative influence of each in seasonal variation.

When studying the effects of temperature on circadian clocks, it is difficult to tell whether the effects represent true entrainment or simply a temperature-dependent change in metabolism that could affect clock outcomes, activity, or endocrine rhythms. For example, melatonin production can be modified by water temperature, producing a masking effect on its endogenous rhythm (Zachmann *et al*., 1992; Max and Menaker, 1992; Iigo and Aida, 1995). Normal melatonin production by the pineal gland typically occurs during the night (i.e., during a colder phase of the 24-hour cycle). On the other hand, studies on isolated pineal glands from white sucker, lamprey, and sea bass show that low temperatures suppress melatonin production and attenuate its circadian rhythm (Zachmann *et al*., 1992; Samejima *et al*., 2000; Garcia-Allegue *et al*., 2001; Masuda *et al*., 2003). Similarly, changes in water temperature are associated with changes in the amplitude of fish plasma melatonin levels *in vivo* (Iigo and Aida, 1995; Garcia-Allegue *et al*., 2001). Because melatonin provides a centralised circadian signal to all the cells of the organism, modification of this signal is one of the ways water temperature could affect the amplitude of circadian responses in fish. However, the extent to which such changes in melatonin secretion may affect the phase of circadian clocks under normal conditions is not yet clear.

### 4.2. Food Availability

When food delivery is restricted to the same time every day, fish, like other animals, display food-anticipatory activity (FAA) under a light–dark cycle (e.g., Spieler and Noeske, 1984; Laguë and Reebs, 2000a,b; Aranda *et al*., 2001; Chen and Purser, 2001; Chen and Tabata, 2002; for a review, see Sánchez-Vázquez and Madrid, 2001). Even when maintained under constant lighting conditions, fish can rapidly synchronise their activity pattern to restricted food availability (e.g., Davis and Bardach, 1965; Gee *et al*., 1994; Naruse and Oishi, 1994).

Studies in mammals suggest the existence of a separate food-dependent circadian oscillator(s) because SCN lesions do not abolish FAA. Fish may also have such a separate entraining pathway. For example, in medaka (Weber and Spieler, 1987) maintained under light–dark cycle and fed once a day, a daily rhythm of agonistic behaviour was entrained to the feeding schedule and persisted during a starvation period. In contrast, the daily rhythms of egg laying and courtship remained entrained to the light–dark cycle and were not affected by the time of food availability in this species. Similarly, trout held under constant light and a food restriction protocol displayed both a free-running rhythm, presumably defined by a light-dependent oscillator, and another one corresponding to the feeding schedule (Bolliet *et al.*, 2001). Goldfish have yielded data that suggest food could be as strong a synchroniser as light (Aranda *et al.*, 2001). Experiments with goldfish and sea bass have also provided data consistent with the existence of a food-entrainable oscillator (Sánchez-Vázquez *et al.*, 1995a,b; 1997).

Thus, light and food-dependent oscillators could coexist and interact with each other. Their relative power may vary between different fish species and this might depend on the habitual diurnal-nocturnal activity patterns and feeding habits. In a diurnally active trout, relying on its visual system to find food, light is a stronger zeitgeber; however, in a nocturnally active catfish, which uses its barbells to detect food, food availability has been shown to be a better entraining factor (Bolliet *et al.*, 2001).

It is also possible, however, to envision a circadian mechanism that would allow FAA based only on a light-entrainable oscillator. In such a model, the animal could store in memory a representation of the circadian phase at which meals are delivered. When clock time approaches the marked phase on a light-entrained oscillator, FAA would take place. Reebs and Laguë (2000) obtained some evidence for such a mechanism in golden shiners: FAA in trained fish disappeared when the light–dark cycle was removed, but persisted for a few days when the daily meals were withheld. Their results, however, could not eliminate the possibility of a food-entrainable oscillator linked to the light-entrainable one, disrupted by the damping out of the latter when the light–dark cycle was removed.

The mechanisms involved in FAA remain unknown, as well as the location(s) of any putative feeding-entrainable oscillator in fish or other animals. Perhaps multiple peripheral oscillators could be synchronised by food intake processes and/or energy availability, providing a powerful enough signal to entrain behavioural patterns. Interestingly, the properties of feeding-entrainable oscillators may depend more on meal size than on the amount of dietary energy supplied, suggesting that part of the FAA mechanism might involve gut distension (Sánchez-Vázquez *et al.*, 2001).

### 4.3. Social Environment

Many fish live in groups, ranging from small aggregates to shoals and schools (see Chapter 5). Social factors might affect the entraining properties of different synchronisers and define circadian patterns of activity and food intake.

When tested in laboratory conditions, groups of fish typically show more robust circadian rhythms than isolated animals, whether they are entrained by light or by a feeding schedule. This has been documented in killifish (Kavaliers, 1980d), white sucker (Kavaliers, 1980a), goldfish (Kavaliers, 1981a), and trout and catfish (Bolliet *et al.*, 2001). It is difficult to evaluate whether these instances reflect a direct effect of social factors on the circadian oscillator of fish, or more simply a social facilitation of movement that increases the chance of detection by the activity-recording devices.

In golden shiners, hungry individuals can discern the FAA of conspecifics and join them (Reebs and Gallant, 1997). They can also follow shoal leaders who know where and when food is available (Reebs, 2000). This attention to the activity of others raises the possibility that fish might display social entrainment of circadian activity and feeding rhythms, as has already been shown in various mammals (Bovet and Oertli, 1974; Crowley and Bovet, 1980; Marimuthu *et al.*, 1981). However, there have been no published attempts thus far to rigourously demonstrate social synchronisation of circadian activity rhythms in fish.

In an opposite vein, intraspecific competition for limited resources may also result in circadian rhythm fragmentation in fish groups. For example, trout were found to be almost exclusively diurnal while individually isolated, but they displayed both diurnal and nocturnal feeding behaviour soon after they were put in groups (Chen *et al.*, 2002a,b). The nocturnal feeding gradually decreased and disappeared after about 10 days of group housing. This phenomenon could be explained either by subordinate individuals initially, but not permanently, being forced to feed at an unfavorable time (night) or by an overall initial stress of resocialisation following isolation, which could temporarily disrupt the circadian rhythms in fish of different hierarchical ranks.

Thus, social environment per se may serve as an entraining signal but can also disrupt entrainment to other synchronisers. High plasticity of the fish circadian system, discussed below, may contribute to this phenomenon.

### 4.4. Predation Risk

Predation risk plays an important part in fishes' lives (Chapter 3; Smith, 1997). However, there is no evidence that predatory attacks occurring daily at the same clock time can entrain circadian rhythms. Time-place learning (the ability to associate specific locations with specific daily times, a process that is known to rely on circadian clocks for the estimation of time; see also Chapter 1) can develop in some fish when food is used as a reward (Reebs, 1996) but not when predatory attacks are simulated (Reebs, 1999). When threatened, fish seem to rely more on a general decrease in activity rather than shifting the timing of activity (e.g., Pettersson *et al*., 2001). Given the abundance of fish predators in nature, probably active at all times of day and night as a whole, it may be unrealistic to expect that a mechanism could have evolved to entrain circadian oscillators to predation risk.

## 5. CIRCADIAN RHYTHMS AND DEVELOPMENT

External development in fish can be successful only if all the critical processes are provided by the egg (e.g., nutrition) or develop very early in ontogenesis. Based on this assumption, in fish the circadian system appears to be critical for the embryo's adaptation.

A study of the expression of one of the circadian clock genes, *Per3,* during zebrafish development showed a remarkable picture of an inherited functional circadian clock (Delaunay *et al*., 2000). A circadian rhythm of *Per3* expression corresponding to that in the female was observed in unfertilised eggs, in the fertilised eggs prior to initiation of embryonic transcription, and in the developing embryos maintained under constant light or constant darkness. This rhythm can be entrained by light to either circadian or ultradian (e.g., light–dark 8:8 hours) periods. It should be noted, however, that the downstream effect of this clock (the expression of specific proteins under circadian regulation) seems to require embryonic development of the pineal gland and axonal connections. These data suggest that the products of the maternal clock gene play an important role in early fish development, along with the newly emerging circadian structures of the embryo itself.

Early onset of melatonin secretion by fish pineal glands, which occurs prior to hatching (Kazimi and Cahill, 1999; Roberts *et al*., 2003; Danilova *et al*., 2004), can provide a unifying neuroendocrine circadian signal, synchronising internal physiological processes with each other and with the periodically changing environmental conditions. This embryonic melatonin may both synchronise and potentiate development. In the zebrafish embryo, melatonin treatment can promote the S phase of the cell cycle and accelerate zebrafish growth and hatching via specific melatonin receptors, abundantly expressed starting 18 hours postfertilisation (Danilova *et al*., 2004).

Circadian entrainment of young zebrafish larvae by light–dark cycle synchronises and enhances the S phase in the skin, heart, and gut, with peak levels observed around 3 hours before lights-on time (Dekens *et al*., 2003).

These data further suggest that circadian rhythmicity plays an important role in early vertebrate development and may synchronise entry into the S phase and mitosis.

## 6. CIRCADIAN RHYTHMS AND PLASTICITY OF BEHAVIOURAL PATTERNS

The existence of a circadian clock within an animal imposes restrictions on the periodicity of this animal's activity, but not necessarily on the phasing of its activity relative to the light–dark cycle. Though this does not happen easily in humans, it is possible for some animals to live a diurnal life one day, and then switch to a nocturnal mode a few days later (or vice versa). Such cases are particularly numerous in fishes (for a review, see Reebs, 2002). Whether a fish is diurnal or nocturnal at any one time seems to depend mostly on food availability. For example, goldfish are diurnal when fed by day and nocturnal when fed at night (Spieler and Noeske, 1984; Gee *et al*., 1994; Sánchez-Vázquez *et al*., 1997) and can change the timing of their general activity when the timing of food availability suddenly changes (Aranda *et al*., 2001; Sánchez-Vázquez *et al*., 2001). Similarly, golden shiners can anticipate the arrival of food day or night, or during both day and night simultaneously (Laguë and Reebs, 2000b; for similar results in rainbow trout, see Chen and Tabata, 2002). Many species appear to be able to feed both visually and nonvisually (Diehl, 1988; Ehlinger, 1989; Collins and Hinch, 1993; Mussen and Peeke, 2001) and can vary their diet so that they are able to feed during the day or at night (Ebeling and Bray, 1976; Johnson and Dropkin, 1995; Pedersen, 2000) or forage at the time when food is more nutritious (Zoufal and Taborsky, 1991).

The choice between day- and night-living can also be influenced by competition, ontogeny, and light intensity, inasmuch as these factors all have a bearing on food availability. In addition to Chen *et al*. (2002a,b) already mentioned in Section 4.3. examples of intraspecific competition resulting in a temporal segregation of activity include Randolph and Clemens (1976) in channel catfish and Alanärä *et al*. (2001) in brown trout. Ontogenic shifts in activity patterns are widely documented (Reebs, 2002) and may reflect a strategy to alleviate competition between age classes, or a change in diet as the gape of a fish increases with growth; unfortunately, neither of these two hypotheses has been formally tested. The role of light intensity in helping or hindering food detection has been invoked to explain diurnal versus nocturnal activity in such studies as Løkkeborg (1998) and Thetmeyer (1997).

Predation risk may also determine whether a fish is diurnal or nocturnal, though the evidence here is weak, being inferential (there is no denying that one sensory modality is less available to predators during the night, and so it may pay for prey to be nocturnal) rather than experimental. One of the most interesting arguments involving predation risk to explain plastic activity rhythms in fish originated from a series of studies on Atlantic salmon. Fraser *et al.* (1993, 1995) experimentally confirmed that Atlantic salmon become proportionally more nocturnal when water temperatures are low, even when photoperiod is held constant. They argued that cold fish were more sluggish and felt more vulnerable to attacks by warm-blooded predators such as birds and mink (see also Chapters 3 and 5). Accordingly, such fish confined their activity to the relative safety of darkness at night. Warm fish could afford the risk of foraging by day and reap the benefit of better foraging due to good lighting conditions. Interestingly, in those individuals for whom foraging success was more important (e.g., salmon with low energy reserves or preparing to migrate at sea), the switch to nocturnalism in the cold was less pronounced, suggesting that the higher imperative for foraging tipped the balance towards increased diurnalism, despite the predation risk (Metcalfe *et al.*, 1998; see also Valdimarsson *et al.*, 1997; Metcalfe *et al.*, 1999; Johnston *et al.*, 2004).

Many other examples are known of switches between diurnal and nocturnal activity as summer makes way for winter (e.g., Andreasson, 1973; Müller, 1978; Cook and Bergersen, 1988; Clark and Green, 1990; Grant and Brown, 1998; Sánchez-Vázquez *et al.*, 1998; David and Closs, 2001, 2003). There is no solid evidence, however, to show whether these shifts are caused by changes in photoperiod, temperature, or food availability. One exception is research by Aranda *et al.* (1999a,b) on sea bass, in which experimental manipulations of photoperiod and temperature were tried. The results indicated that neither factor was at work, suggesting that the switch to nocturnal living shown by sea bass in winter is under the influence of a circannual clock.

It seems that freshwater species are more prone than marine ones to switch back and forth between diurnalism and nocturnalism (Reebs, 2002). Perhaps this reflects the fact that freshwater environments tend to be less stable than the sea, and therefore may have yielded fewer evolutionary cases of sensory specialisation for particular conditions, including daytime or nighttime. Being able to fare relatively well by day or by night, freshwater species can choose to be nocturnal as well as diurnal, depending on food availability and perhaps also temperature (Reebs, 2002).

The physiological mechanism that binds activity (permanently or not) to a particular phase of the circadian clock is unknown for any animal or plant taxon. Because of their flexibility in this regard, fish may represent a promising subject for future studies on this question.

## 7. CIRCADIAN RHYTHMS AND SLEEP

A rest–activity cycle, its regulation by the internal circadian clock, and its entrainment to environmental cues are evolutionary conserved phenomena. However, in higher vertebrates, rest is associated with sleep, a distinct behavioural and physiological state. Brain activity during sleep shows recognisable electrophysiological patterns significantly different from those observed during wakefulness. Moreover, sleep in mammals is not a uniform process but a series of alternating states, called "slow wave" (SWS) and "rapid eye movement" (REM) sleep. In addition to differences in brain activity during SWS and REM sleep, the peripheral organs and systems are in a different functional mode.

So far, the physiological function of sleep and its principal molecular mechanisms remain obscure. However, a substantial body of evidence on the regulation of sleep processes identifies two major forces driving sleep initiation and maintenance. They include a homeostatic control, defining an increase in sleep propensity proportional to the time spent awake, and a circadian control, determining a window of high sleep propensity or of increased wakefulness within each 24-hour period. The circadian mechanisms may synchronise sleep with daytime or nighttime, depending on whether the animal is nocturnal or diurnal.

Typical behavioural features of sleep include prolonged behavioural quietness, species-specific postures, elevated arousal threshold, and rapid reversibility from quietness to activity in response to moderately intense stimulation (Campbell and Tobler, 1984). These features are common to many fish species, with some completely ceasing their activity and others only slowing it down (Clark, 1973; Tauber, 1974; Shapiro and Hepburn, 1976; Karmanova, 1981; for reviews, see Reebs, 1992, 2002). The increase in arousal threshold associated with such sleeplike state can be substantial. For example, blueheads, Spanish hogfish, and several species of wrasses could be lifted by hand to the surface at night before "waking up" (Tauber, 1974).

Zebrafish larvae (7–14 days old) demonstrate sleeplike behaviour even at an early developmental stage (Zhdanova *et al.*, 2001). Long periods of immobility in zebrafish larvae are associated with either floating with the head down or staying in a horizontal position close to the bottom of a tank. A nocturnal decline in motor activity in these diurnal fish is accompanied by a significant increase in arousal threshold relative to daytime

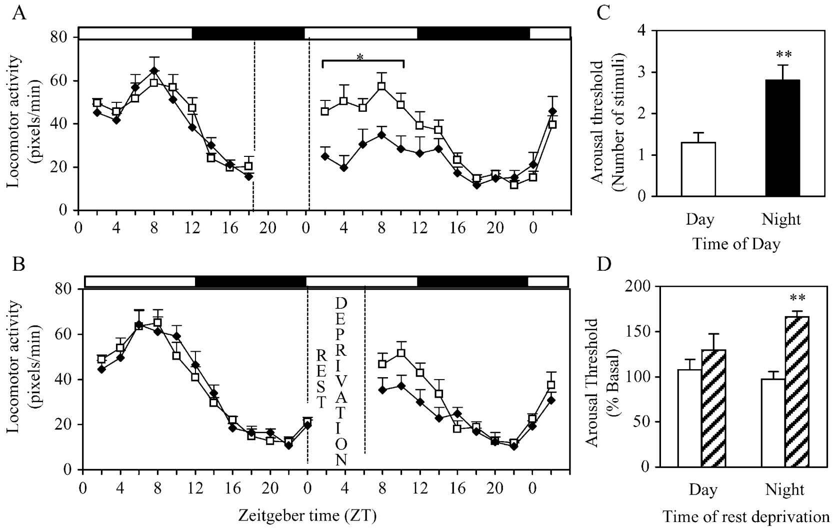

**Fig. 6.5.** Daily variation in locomotor activity and arousal threshold in larval zebrafish maintained in constant darkness and a compensatory reduction in locomotor activity and increase in arousal threshold following rest deprivation. (A, B) Zeitgeber time (ZT) and horizontal white/black bars indicate subjective day versus subjective night, according to 12:12 light–dark cycle prior to the beginning of recording, with ZT0 corresponding to lights on time. Each data point represents mean ± S.E.M. group locomotor activity for preceding 2 hours of recording (computerised image analysis data in pixels per minute). $N = 60$ for each group. The rest deprivation was scheduled either (A) during subjective night (ZT18–ZT24) or (B) during subjective day (ZT0–ZT6). Closed diamonds, rest deprivation group; open squares, control group. (C) Arousal threshold was measured in constant darkness during subjective day (ZT3–5) or subjective night (ZT15–17). $N = 20$ for each group. (D) Changes in daytime arousal threshold (% of basal) starting an hour after daytime or nighttime rest deprivation. White bars, control; striped bars, rest deprivation. $N = 20$ for each group. $^*P < 0.05$; $^{**}P < 0.01$. (Adapted from Zhdanova *et al.*, 2001.)

(Figure 6.5) and is maintained in constant darkness, confirming that sleeplike state in larval zebrafish is under the control of a circadian system.

As in mammals, preventing fish from resting or sleeping results in subsequent increases in sleeplike behaviour, as has been shown in cichlids (Tobler and Borbely, 1985) and zebrafish (Zhdanova *et al.*, 2001). Daytime rest deprivation in zebrafish larvae does not significantly affect rest behaviour thereafter, though some decrease in daytime locomotor activity and elevation in the arousal threshold have been noticed (Figure 6.5, B and D). In contrast, nighttime rest deprivation resulted in a significant decline in daytime locomotor activity and in a heightened arousal threshold, compared

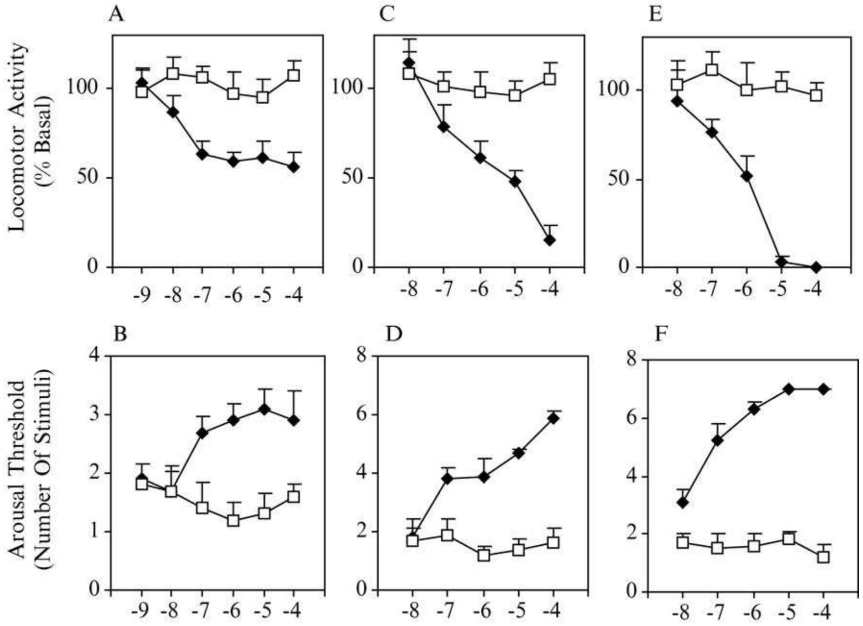

**Fig. 6.6.** Melatonin and conventional sedatives promote rest behaviour in larval zebrafish. Melatonin, diazepam, and sodium pentobarbital (barbital) significantly and dose-dependently reduced zebrafish locomotor activity (A, C, E) and increased arousal threshold (B, D, F). Each data point represents mean ± SEM group changes in a 2-hour locomotor activity relative to basal activity, measured in each treatment or control group for 2 hours prior to treatment administration. Arousal threshold data are expressed as the mean ± SEM group number of stimuli necessary to initiate locomotion in a resting fish. Closed diamond, treatment; open square, vehicle control. $N = 20$ for each group. (Adapted from Zhdanova *et al.*, 2001.)

to basal recordings. These data further confirm that sleeplike states in fish are under both circadian and homeostatic control.

Furthermore, a sleeplike state can be induced in fish with common hypnotic agents, such as benzodiazepines or barbiturates (Figure 6.6), suggesting that at least some of the mechanisms of sleep regulation must be similar in fish and mammals. Diurnal zebrafish are also sensitive to the sleep-promoting effects of melatonin (Figure 6.6), similar to diurnal monkeys and humans.

The lower vertebrates have obvious anatomical limitations for the expression of some of the electrographic patterns commonly found in mammalian sleep. For example, it is unlikely that animals such as fish with only a rudimentary neocortex, if any, would generate the brain waves characteristic of mammalian slow-wave sleep. However, the neurons with sleep-promoting properties are contained in structures within the isodendritic core of the brain, extending from the medulla through the brainstem, hypothalamus, and up into the basal forebrain (see Chapter 1 for details on brain anatomy; for a review, see Jones, 1993). Thus the lower vertebrates, with their "limbic brain," possess most of the brain structures that have been found to regulate the sleep process in mammals.

New methodological approaches, such as monitoring the expression of genes related to spontaneous sleep processes or inducing sleep by hypnotic agents, might help clarify the extent to which sleeplike states in fish are similar to those in mammals.

## 8. SUMMARY

Circadian rhythms play a critical role in fish development and daily activities. Although a major circadian "master" clock, like the SCN of mammals, has not yet been identified in fish, indirect evidence suggests that a light-entrainable oscillator is present in fish brain. Furthermore, the structural and functional design of fish circadian systems is remarkably complicated. Photosensitive CNS-related clock organs (the pineal gland and retina), peripheral photosensitive tissues with autonomic circadian clocks, and presumed food- or temperature-entrainable circadian oscillator(s) all make for complex circadian machinery that must remain well coordinated and still be able to ensure physiological adaptation to a periodically changing environment.

Such a multilevel structure of partially independent oscillators may explain the high interspecies variability observed in piscine circadian systems and substantial individual plasticity in fish behaviour and physiology. Studying these features will continue to contribute to a better understanding of the principal mechanisms involved in circadian clock functions.

Data accumulated so far show that rest in fish has fundamental similarities to the behavioural manifestations of sleep in higher vertebrates. Analogous to sleep in mammals, fish show a compensatory rest rebound, reducing locomotor activity and increasing arousal thresholds after a period of rest deprivation, suggesting that fish exert a homeostatic control on rest behaviour. Furthermore, rest in fish is regulated by the circadian system, because periodic reduction in locomotor activity and increase in arousal threshold are maintained in constant darkness and occur during the subjective night. These observations, together with the hypnotic effects of melatonin and sleep-inducing agents of the benzodiazepine and barbiturate families, indicate that rest behaviour in fish can be considered a sleeplike state. Studying sleep in fish may prove to be very productive in deciphering both the enigmatic function and the physiological mechanisms of sleep.

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## REFERENCES

Alanärä, A., Burns, M. D., and Metcalfe, N. B. (2001). Intraspecific resource partitioning in brown trout: The temporal distribution of foraging is determined by social rank. *J. Anim. Ecol.* **70,** 980–986.

Amano, M., Iigo, M., Ikuta, K., Kitamura, S., Okuzawa, K., Yamada, H., and Yamamori, K. (2000). Roles of melatonin in gonadal maturation of underyearling precocious male masu salmon. *Gen. Comp. Endocrinol.* **120,** 190–197.

Amano, M., Iigo, M., Ikuta, K., Kitamura, S., and Yamamori, K. (2004). Disturbance of plasma melatonin profile by high dose melatonin administration inhibits testicular maturation of precocious male masu salmon. *Zool. Sci.* **21,** 79–85.

Andreasson, S. (1973). Seasonal changes in diel activity of *Cottus poecilopus* and *C. gobio* (Pisces) at the Arctic Circle. *Oikos* **24,** 16–23.

Aranda, A., Sánchez-Vázquez, F. J., and Madrid, J. A. (1999a). Influence of water temperature on demand-feeding rhythms in sea bass. *J. Fish Biol.* **55,** 1029–1039.

Aranda, A., Madrid, J. A., Zamora, A., and Sánchez-Vázquez, F. J. (1999b). Synchronising effect of photoperiod on the dual phasing of demand-feeding rhythms in sea bass. *Biol. Rhythm Res.* **30,** 392–406.

Aranda, A., Madrid, J. A., and Sánchez-Vázquez, F. J. (2001). Influence of light on feeding anticipatory activity in goldfish. *J. Biol. Rhythms* **16,** 50–57.

Bayarri, M. J., Rol de Lama, M. A., Madrid, J. A., and Sánchez-Vázquez, F. J. (2003). Both pineal and lateral eyes are needed to sustain daily circulating melatonin rhythms in sea bass. *Brain Res.* **969,** 175–182.

Bayarri, M. J., Rodriguez, L., Zanuy, S., Madrid, J. A., Sánchez-Vázquez, F. J., Kagawa, H., Okuzawa, K., and Carrillo, M. (2004). Effect of photoperiod manipulation on the daily rhythms of melatonin and reproductive hormones in caged European sea bass (*Dicentrarchus labrax*). *Gen. Comp. Endocrinol.* **136,** 72–81.

Begay, V., Falcon, J., Cahill, G. M., Klein, D. C., and Coon, S. L. (1998). Transcripts encoding two melatonin synthesis enzymes in the teleost pineal organ: Circadian regulation in pike and zebrafish, but not in trout. *Endocrinology* **139,** 905–912.

Bellingham, J., Whitmore, D., Philp, A. R., Wells, D. J., and Foster, R. G. (2002). Zebrafish melanopsin: Isolation, tissue localisation and phylogenetic position. *Brain Res. Mol. Brain Res.* **107,** 128–136.

Benyassi, A., Schwartz, C., Coon, S. L., Klein, D. C., and Falcon, J. (2000). Melatonin synthesis: Arylalkylamine N-acetyltransferases in trout retina and pineal organ are different. *Neuroreport* **11,** 255–258.

Bolliet, V., Begay, V., Taragnat, C., Ravault, J. P., Collin, J.P, and Falcon, J. (1997). Photoreceptor cells of the pike pineal organ as cellular circadian oscillators. *Eur. J. Neurosci.* **9,** 643–653.

Bolliet, V., Aranda, A., and Boujard, T. (2001). Demand-feeding rhythm in rainbow trout and European catfish: Synchronisation by photoperiod and food availability. *Physiol. Behav.* **73,** 625–633.

Boujard, T., Gélineau, A., Corraze, G., Kaushik, S., Gasset, E., Coves, D., and Dutto, G. (2000). Effect of dietary lipid content on circadian rhythm of feeding activity in European sea bass. *Physiol. Behav.* **68,** 683–689.

Bovet, J., and Oertli, E. F. (1974). Free-running circadian activity rhythms in free-living beaver (Castor canadensis). *J. Comp. Physiol.* **92,** 1–10.

Burdeyron, H., and Buisson, B. (1982). On a Circadian Endogenous Locomotor Rhythm of Loaches (*Noemacheilus barbatulus* L., Pisces, Cobitidae). *Zool. Jb. Physiol.* **86,** 82–89.

Burns, T. A., Huston, J. P., and Spieler, R. E. (2003). Circadian variation of brain histamine in goldfish. *Brain Res. Bull.* **59,** 299–301.

Cahill, G. M. (2002). Clock mechanisms in zebrafish. *Cell Tissue Res.* **309,** 27–34.

Campbell, S. S., and Tobler, I. (1984). Animal sleep: A review of sleep duration across phylogeny. *Neurosci. Biobehav. Rev.* **8,** 269–300.

Cermakian, N., and Sassone-Corsi, P. (2002). Environmental stimulus perception and control of circadian clocks. *Curr. Opin. Neurobiol.* **12,** 359–365.

Cermakian, N., Whitmore, D., Foulkes, N. S., and Sassone-Corsi, P. (2000). Asynchronous oscillations of two zebrafish CLOCK partners reveal differential clock control and function. *Proc. Natl. Acad. Sci. USA* **97,** 4339–4344.

Chen, W. M., and Purser, G. J. (2001). The effect of feeding regime on growth, locomotor activity pattern and the development of food anticipatory activity in greenback flounder. *J. Fish Biol.* **58,** 177–187.

Chen, W. M., and Tabata, M. (2002). Individual rainbow trout *Oncorhynchus mykiss* Walbaum can learn and anticipate multiple daily feeding times. *J. Fish Biol.* **61,** 1410–1422.

Chen, W. M., Naruse, M., and Tabata, M. (2002a). The effect of social interactions on circadian self-feeding rhythms in rainbow trout *Oncorhynchus mykiss* Walbaum. *Physiol. Behav.* **76,** 281–287.

Chen, W., Naruse, M., and Tabata, M. (2002b). Circadian rhythms and individual variability of self-feeding activity in groups of rainbow trout *Oncorhynchus mykiss* (Walbaum). *Aquac. Res.* **33,** 491–500.

Chiu, J. F., Mack, A. F., and Fernald, R. D. (1995). Daily rhythm of cell proliferation in the teleost retina. *Brain Res.* **673,** 119–125.

Clark, D. S., and Green, J. M. (1990). Activity and movement patterns of juvenile Atlantic cod, *Gadus morhua*, in Conception Bay, Newfoundland, as determined by sonic telemetry. *Can. J. Zool.* **68,** 1434–1442.

Clark, E. (1973). "Sleeping" sharks in Mexico. *Underwat. Nat.* **8,** 4–7.

Colgan, P. (1975). Self-selection of photoperiod as a technique for studying endogenous rhythms in fish. *J. Interdiscipl. Cycle Res.* **6,** 203–211.

Collins, N. C., and Hinch, S. G. (1993). Diel and seasonal variation in foraging activities of pumpkinseeds in an Ontario pond. *Trans. Am. Fish. Soc.* **122,** 357–365.

Cook, M. F., and Bergersen, E. P. (1988). Movements, habitat selection, and activity periods of northern pike in Eleven Mile Reservoir, Colorado. *Trans. Am. Fish. Soc.* **117,** 495–502.

Coon, S. L., Begay, V., Deurloo, D., Falcon, J., and Klein, D. C. (1999). Two arylalkylamine N-acetyltransferase genes mediate melatonin synthesis in fish. *J. Biol. Chem.* **274,** 9076–9082.

Crowley, M., and Bovet, J. (1980). Social synchronisation of circadian rhythms in deer mice (*Peromyscus maniculatus*). *Behav. Ecol. Sociobiol.* **7,** 99–105.

Cummings, S. M., and Morgan, E. (2001). Time-keeping system of the eel pout, *Zoarces viviparus*. *Chronobiol. Int.* **18,** 27–46.

Danilova, N., Krupnik, V. E., Sugden, D., and Zhdanova, I. V. (2004). Melatonin stimulates cell proliferation in zebrafish embryo and accelerates its development. *FASEB J.* **18,** 751–753.

David, B. O., and Closs, G. P. (2001). Continuous remote monitoring of fish activity with restricted home ranges using radiotelemetry. *J. Fish Biol.* **59,** 705–715.

David, B. O., and Closs, G. P. (2003). Seasonal variation in diel activity and microhabitat use of an endemic New Zealand stream-dwelling galaxiid fish. *Freshwater Biol.* **48,** 1765–1781.

Davis, R. E. (1964). Daily ''predawn'' peak of locomotion in fish. *Anim. Behav.* **12,** 272–283.

Davis, R. E., and Bardach, J. E. (1965). Time-co-ordinated prefeeding activity in fish. *Anim. Behav.* **13,** 154–162.

Dekens, M. P., Santoriello, C., Vallone, D., Grassi, G., Whitmore, D., and Foulkes, N. S. (2003). Light regulates the cell cycle in zebrafish. *Curr. Biol.* **13,** 2051–2057.

Delaunay, F., Thisse, C., Marchand, O., Laudet, V., and Thisse, B. (2000). An inherited functional circadian clock in zebrafish embryos. *Science* **289,** 297–300.

Delaunay, F., Thisse, C., Marchand, O., Laudet, V., Thisse, B., Delaunay, F., Thisse, C., Thisse, B., and Laudet, V. (2003). Differential regulation of Period 2 and Period 3 expression during development of the zebrafish circadian clock. *Gene Expr. Patterns* **3,** 319–324.

Deng, T. S., and Tseng, T. C. (2000). Evidence of circadian rhythm of electric discharge in Eigenmannia virescens system. *Chronobiol. Int.* **17,** 43–48.

Diehl, S. (1988). Foraging efficiency of three freshwater fishes: Effects of structural complexity and light. *Oikos* **53,** 207–214.

Drivenes, O., Soviknes, A. M., Ebbesson, L. O., Fjose, A., Seo, H. C., and Helvik, J. V. (2003). Isolation and characterisation of two teleost melanopsin genes and their differential expression within the inner retina and brain. *J. Comp. Neurol.* **456,** 84–93.

Dunlap, J. C. (1999). Molecular bases for circadian clocks. *Cell* **96,** 271–290.

Ebeling, A. W., and Bray, R. N. (1976). Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. *Fish. Bull.* **74,** 703–717.

Ehlinger, T. J. (1989). Foraging mode switches in the golden shiner (*Notemigonus crysoleucas*). *Can. J. Fish. Aquat. Sci.* **46,** 1250–1254.

Erckens, W., and Martin, W. (1982a). Exogenous and endogenous control of swimming activity in *Astyanax mexicanus* (Characidae, Pisces) by direct light response and by a circadian oscillator. I. Analyses of the time-control systems of an epigean river population. *Z. Naturforsch.* **37,** 1253–1265.

Erckens, W., and Martin, W. (1982b). Exogenous and endogenous control of swimming activity in *Astyanax mexicanus* (Characidae, Pisces) by direct light response and by a circadian oscillator. II. Features of time-controlled behaviour of a cave population and their comparison to an epigean ancestral form. *Z. Naturforsch.* **37,** 1266–1273.

Erckens, W., and Weber, F. (1976). Rudiments of an ability for time measurement in the cavernicolous fish *Anoptichthys jordani* Hubbs and Innes (Pisces Characidae). *Experientia* **32,** 1297–1299.

Eriksson, L.-O., and Van Veen, T. (1980). Circadian rhythms in the brown bullhead, *Ictalurus nebulosus* (Teleostei): Evidence for an endogenous rhythm in feeding, locomotor, and reaction time behaviour. *Can. J. Zool.* **58,** 1899–1907.

Falcon, J. (1999). Cellular circadian clocks in the pineal. *Prog. Neurobiol.* **58,** 121–162.

Falcon, J., Gothilf, Y., Coon, S. L., Boeuf, G., and Klein, D. C. (2003). Genetic, temporal and developmental differences between melatonin rhythm generating systems in the teleost fish pineal organ and retina. *J. Neuroendocrinol.* **15,** 378–382.

Foster, R. G., Hankins, M., Lucas, R. J., Jenkins, A., Munoz, M., Thompson, S., Appleford, J. M., and Bellingham, J. (2003). Non-rod, non-cone photoreception in rodents and teleost fish. *Novartis Found. Symp.* **253,** 3–23.

Fraser, N. H. C., Metcalfe, N. B., and Thorpe, J. E. (1993). Temperature-dependent switch between diurnal and nocturnal foraging in salmon. *Proc. R. Soc. Lond. B* **252,** 135–139.

Fraser, N. H. C., Heggenes, J., Metcalfe, N. B., and Thorpe, J. E. (1995). Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. *Can. J. Zool.* **73,** 446–451.

Garcia–Allegue, R., Madrid, J. A., and Sánchez-Vázquez, F. J. (2001). Melatonin rhythms in European sea bass plasma and eye: Influence of seasonal photoperiod and water temperature. *J. Pineal Res.* **31,** 68–75.

Garg, S. K., and Sundararaj, B. I. (1986). Role of pineal in the regulation of some aspects of circadian rhythmicity in the catfish, *Heteropneustes fossilis* (Bloch). *Chronobiologia* **13,** 1–11.

Gee, P., Stephenson, D., and Wright, D. E. (1994). Temporal discrimination learning of operant feeding in goldfish (*Carassius auratus*). *J. Exp. Anal. Behav.* **62,** 1–13.

Gerkema, M. P., Videler, J. J., de Wiljes, J., van Lavieren, H., Gerritsen, H., and Karel, M. (2000). Photic entrainment of circadian activity patterns in the tropical labrid fish *Halichoeres chrysus*. *Chronobiology International* **17,** 613–622.

Gern, W. A., and Greenhouse, S. S. (1988). Examination of *in vitro* melatonin secretion from superfused trout (Salmo gairdneri) pineal organs maintained under diel illumination or continuous darkness. *Gen. Comp. Endocrinol.* **71,** 163–174.

Gibson, R. N. (1971). Factors affecting the rhythmic activity of *Blennius pholis* L. (Teleostei). *Anim. Behav.* **19,** 336–343.

Glossop, N. R., Lyons, L. C., and Hardin, P. E. (1999). Interlocked feedback loops within the Drosophila circadian oscillator. *Science* **286,** 766–768.

Godin, J.-G. J. (1981). Circadian rhythm of swimming activity in juvenile pink salmon (*Oncorhynchus gorbuscha*). *Mar. Biol.* **64,** 341–349.

Goudie, C. A., Davis, K. B., and Simco, B. A. (1983). Influence of the eyes and pineal gland on locomotor activity patterns of channel catfish *Ictalurus punctatus*. *Physiol. Zool.* **56,** 10–17.

Grant, S. M., and Brown, J. A. (1998). Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland. *Can. J. Fish. Aquat. Sci.* **55,** 1307–1316.

Harden Jones, F. R. (1956). The behaviour of minnows in relation to light intensity. *J. Exp. Biol.* **33,** 271–281.

Herrero, M. J., Madrid, J. A., and Sánchez-Vázquez, F. J. (2003). Entrainment to light of circadian activity rhythms in tench (*Tinca tinca*). *Chronobiol. Int.* **20,** 1001–1017.

Hurd, M. W., and Cahill, G. M. (2002). Entraining signals initiate behavioural circadian rhythmicity in larval zebrafish. *J. Biol. Rhythms* **17,** 307–314.

Iigo, M., and Aida, K. (1995). Effects of season, temperature, and photoperiod on plasma melatonin rhythms in the goldfish, *Carassius auratus*. *J. Pineal Res.* **18,** 62–68.

Iigo, M., and Tabata, M. (1996). Circadian rhythms of locomotor activity in the goldfish *Carassius auratus*. *Physiol. Behav.* **60,** 775–781.

Iigo, M., Hara, M., Ohtani-Kaneko, R., Hirata, K., Tabata, M., and Aida, K. (1997a). Photic and circadian regulations of melatonin rhythms in fishes. *Biol. Signals* **6,** 225–232.

Iigo, M., Sanchez-Vazquez, F. J., Madrid, J. A., Zamora, S., and Tabata, M. (1997b). Unusual responses to light and darkness of ocular melatonin in European sea bass. *Neuroreport* **8,** 1631–1635.

Iigo, M., Mizusawa, K., Yokosuka, M., Hara, M., Ohtani-Kaneko, R., Tabata, M., Aida, K., and Hirata, K. (2003a). *In vitro* photic entrainment of the circadian rhythm in melatonin release from the pineal organ of a teleost, ayu (Plecoglossus altivelis) in flow-through culture. *Brain Res.* **932,** 131–135.

Iigo, M., Furukawa, K., Tabata, M., and Aida, K. (2003b). Circadian variations of melatonin binding sites in the goldfish brain. *Neurosci. Lett.* **347,** 49–52.

Iigo, M., Fujimoto, Y., Gunji-Suzuki, M., Yokosuka, M., Hara, M., Ohtani-Kaneko, R., Tabata, M., Aida, K., and Hirata, K. (2004). Circadian rhythm of melatonin release from the photoreceptive pineal organ of a teleost, ayu (*Plecoglossus altivelis*) in flow-thorough culture. *J. Neuroendocrinol.* **16,** 45–51.

Ishikawa, T., Hirayama, J., Kobayashi, Y., and Todo, T. (2002). Zebrafish CRY represses transcription mediated by CLOCK-BMAL heterodimer without inhibiting its binding to DNA. *Genes Cells* **7,** 1073–1086.

Jenkins, A., Munoz, M., Tarttelin, E. E., Bellingham, J., Foster, R. G., and Hankin, M. W. (2003). VA opsin, melanopsin, and an inherent light response within retinal interneurons. *Curr. Biol.* **13,** 1269–1278.

Johnson, J. H., and Dropkin, D. S. (1995). Diel feeding chronology of six fish species in the Juniata River, Pennsylvania. *J. Freshwat. Ecol.* **10,** 11–18.

Johnston, P., Bergeron, N. E., and Dodson, J. J. (2004). Diel activity patterns of juvenile Atlantic salmon in rivers with summer temperatures near the temperature-dependent suppression of diurnal activity. *J. Fish Biol.* **65,** 1305–1318.

Jones, B. E. (1993). The organisation of central cholinergic systems and their functional importance in sleep-waking states. *Prog. Brain Res.* **98,** 61–71.

Kabasawa, H., and Ooka-Souda, S. (1989). Circadian rhythms in locomotor activity of the hagfish, *Eptatretus burgeri* (IV). The effect of eye-ablation. *Zool. Sci.* **6,** 135–139.

Katz, H. M. (1978). Circadian rhythms in juvenile American shad, *Alosa sapidissima*. *J. Fish Biol.* **12,** 609–614.

Karmanova, I. G., Khomutetskaia, O. E., and Shilling, N. V. (1981). Comparative physiologic analysis of the evolutionary stages of sleep and its regulatory mechanisms. *Usp. Fiziol. Nauk.* **12,** 3–19.

Kavaliers, M. (1978). Seasonal changes in the circadian period of the lake chub, *Couesius plumbeus*. *Can. J. Zool.* **56,** 2591–2596.

Kavaliers, M. (1979). Pineal involvement in the control of circadian rhythmicity in the lake chub, *Couesius plumbeus*. *J. Exp. Zool.* **209,** 33–40.

Kavaliers, M. (1980a). Circadian activity of the white sucker, *Catostomus commersoni*: Comparison of individual and shoaling fish. *Can. J. Zool.* **58,** 1399–1403.

Kavaliers, M. (1980b). Pineal control of ultradian rhythms and short-term activity in a cyprinid fish, the lake chub, *Couesius plumbeus*. *Behav. Neur. Biol.* **29,** 224–235.

Kavaliers, M. (1980c). Retinal and extraretinal entrainment action spectra for the activity rhythms of the lake chub, *Couesius plumbeus*. *Behav. Neur. Biol.* **30,** 56–67.

Kavaliers, M. (1980d). Social groupings and circadian activity of the killifish, *Fundulus heteroclitus*. *Biol. Bull.* **158,** 69–76.

Kavaliers, M. (1980e). Circadian locomotor activity rhythms of the burbot, *Lota lota*: Seasonal differences in period length and the effect of pinealectomy. *J. Comp. Physiol.* **136,** 215–218.

Kavaliers, M. (1981a). Period lengthening and disruption of socially facilitated circadian activity rhythms of goldfish by lithium. *Physiol. Behav.* **27,** 625–628.

Kavaliers, M. (1981b). Circadian organisation in white suckers *Catostomus commersoni*: The role of the pineal organ. *Comp. Biochem. Physiol.* **68A,** 127–129.

Kavaliers, M. (1981c). Seasonal effects on the freerunning rhythm of circadian activity of longnose dace (*Rhinichthys cataractae*). *Env. Biol. Fish* **6,** 203–206.

Kavaliers, M. (1981d). Circadian rhythm of nonpineal extraretinal photosensitivity in a teleost fish, the lake chub, *Couesius plumbeus*. *J. Exp. Zool.* **216,** 7–11.

Kavaliers, M., and Abbott, F. S. (1977). Rhythmic colour change of the killifish, *Fundulus heteroclitus*. *Can. J. Zool.* **55,** 553–561.

Kavaliers, M., and Ross, D. M. (1981). Twilight and day length affects the seasonality of entrainment and endogenous circadian rhythms in a fish, *Couesius plumbeus*. *Can. J. Zool.* **59,** 1326–1334.

Kazimi, N., and Cahill, G. M. (1999). Development of a circadian melatonin rhythm in embryonic zebrafish. *Brain Res. Dev. Brain Res.* **117,** 47–52.

Kim, W. S., Kim, J. M., Yi, S. K., and Huh, H. T. (1997). Endogenous circadian rhythm in the river puffer fish *Takifugu obscurus*. *Mar. Ecol. Prog. Ser.* **153,** 293–298.

Kleerekoper, H., Taylor, G., and Wilton, R. (1961). Diurnal periodicity in the activity of *Petromyzon marinus* and the effects of chemical stimulation. *Trans. Amer. Fish Soc.* **90,** 73–78.

Kobayashi, Y., Ishikawa, T., Hirayama, J., Daiyasu, H., Kanai, S., Toh, H., Fukuda, I., Tsujimura, T., Terada, N., Kamei, Y., Yuba, S., Iwai, S., and Todo, T. (2000). Molecular analysis of zebrafish photolyase/cryptochrome family: Two types of cryptochromes present in zebrafish. *Genes Cells* **5,** 725–738.

Kojima, D., Mano, H., and Fukada, Y. (2000). Vertebrate ancient-long opsin: A green-sensitive photoreceptive molecule present in zebrafish deep brain and retinal horizontal cells. *J. Neurosci.* **20,** 2845–2851.

Laguë, M., and Reebs, S. G. (2000a). Phase-shifting the light-dark cycle influences food-anticipatory activity in golden shiners. *Physiol. Behav.* **70,** 55–59.

Laguë, M., and Reebs, S. G. (2000b). Food-anticipatory activity of groups of golden shiners during both day and night. *Can. J. Zool.* **78,** 886–889.

Le Comber, S. C., and Smith, C. (2004). Polyploidy in fishes: Patterns and processes. *Biol. J. Linnean Soc.* **82,** 431–442.

Leggatt, R. A., and Iwama, G. K. (2003). Occurrence of polyploidy in the fishes. *Rev. Fish Biol. Fish.* **13,** 237–246.

Li, L., and Dowling, J. E. (2000). Effects of dopamine depletion on visual sensitivity of zebrafish. *J. Neurosci.* **20,** 1893–1903.

Løkkeborg, S. (1998). Feeding behaviour of cod, *Gadus morhua*: Activity rhythm and chemically mediated food search. *Anim. Behav.* **56,** 371–378.

Marimuthu, G, Rajan, S., and Chandrashekaran, M. K. (1981). Social entrainment of the circadian rhythm in the flight activity of the microchiropteran bat *Hipposideros speoris*. *Behav. Ecol. Sociobiol.* **8,** 147–150.

Mashiko, K. (1979). The light intensity as a key factor controlling nocturnal action in the catfish, *Pseudobagrus aurantiacus*. *Jap. J. Ichthyol.* **25,** 251–258.

Masuda, T., Iigo, M., Mizusawa, K., Naruse, M., Oishi, T., Aida, K., and Tabata, M. (2003). Variations in plasma melatonin levels of the rainbow trout (*Oncorhynchus mykiss*) under various light and temperature conditions. *Zool. Sci.* **20,** 1011–1016.

Max, M., and Menaker, M. (1992). Regulation of melatonin production by light, darkness, and temperature in the trout pineal. *J. Comp. Physiol. A* **170,** 479–489.

Metcalfe, N. B., Fraser, N. H. C., and Burns, M. D. (1998). State-dependent shifts between \ nocturnal and diurnal activity in salmon. *Proc. R. Soc. Lond. B* **265,** 1503–1507.

Metcalfe, N. B., Fraser, N. H. C., and Burns, M. D. (1999). Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *J. Anim. Ecol.* **68,** 371–381.

Minamoto, T., and Shimizu, I. (2002). A novel isoform of vertebrate ancient opsin in a smelt fish, Plecoglossus altivelis. *Biochem. Biophys. Res. Commun.* **290,** 280–286.

Minh-Nyo, M., Tabata, M., and Oguri, M. (1991). Circadian locomotor activity in kawamutsu *Zacco temmincki*. *Nippon Suisan Gakkaishi* **57,** 771.

Mizusawa, K., Iigo, M., Suetake, H., Yoshiura, Y., Gen, K., Kikuchi, K., Okano, T., Fukada, Y., and Aida, K. (1998). Molecular cloning and characterisation of a cDNA encoding the retinal arylalkylamine N-acetyltransferase of the rainbow trout, *Oncorhynchus mykiss*. *Zool. Sci.* **15,** 345–351.

Mizusawa, K., Iigo, M., Masuda, T., and Aida, K. (2000). Photic regulation of arylalkylamine N-acetyltransferase1 mRNA in trout retina. *Neuroreport* **16,** 3473–3477.

Morita, Y., Tabata, M., Uchida, K., and Samejima, M. (1992). Pineal-dependent locomotor activity of lamprey, *Lampetra japonica*, measured in relation to LD cycle and circadian rhythmicity. *J. Comp. Physiol. A* **171,** 555–562.

Moutsaki, P., Bellingham, J., Soni, B. G., David-Gray, Z. K., and Foster, R. G. (2000). Sequence, genomic structure and tissue expression of carp (*Cyprinus carpio* L.) vertebrate ancient (VA) opsin. *FEBS Lett.* **473,** 316–322.

Moutsaki, P., Whitmore, D., Bellingham, J., Sakamoto, K, David-Gray, Z. K., and Foster, R. G. (2003). Teleost multiple tissue (tmt) opsin: A candidate photopigment regulating the peripheral clocks of zebrafish? *Brain Res. Mol. Brain Res.* **112,** 135–145.

Müller, K. (1978). The flexibility of the circadian system of fish at different latitudes. *In* "Rhythmic Activity of Fishes" (Thorpe, J. E., Ed.), pp. 91–104. Academic Press, New York.

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.

Naruse, M., and Oishi, T. (1994). Effects of light and food as zeitgebers on locomotor activity rhythms in the loach, *Misgurnus anguillicaudatus*. *Zool. Sci.* **11,** 113–119.

Nelson, D. R., and Johnson, R. H. (1970). Diel activity rhythms in the nocturnal, bottom-dwelling sharks *Heterodontus francisci* and *Cephaloscyllium ventriosum*. *Copeia* **1970,** 732–739.

Nishi, G. (1989). Locomotor activity rhythm in two wrasses, *Halichoeres tenuispinnis* and *Pteragogus flagellifera*, under various light conditions. *Jap. J. Ichthyol.* **36,** 350–356.

Nishi, G. (1990). Locomotor activity rhythm in four wrasse species under varying light conditions. *Jap. J. Ichthyol.* **37,** 170–181.

Nishi, G. (1991). The relationship between locomotor activity rhythm and burying behaviour in the wrasse, *Suezichthys gracilis*. *Jap. J. Ichthyol.* **37,** 402–409.

Nixon, A. J., and Gruber, S. H. (1988). Diel Metabolic and Activity Patterns of the Lemon Shark (*Negaprion brevirostris*). *J. Exp. Zool.* **248,** 1–6.

Oishi, K., Sakamoto, K., Okada, T., Nagase, T., and Ishida, N. (1998). Antiphase circadian expression between BMAL1 and period homologue mRNA in the suprachiasmatic nucleus and peripheral tissues of rats. *Biochem. Biophys. Res. Commun.* **253,** 199–203.

Okamura, H. (2003). Integration of molecular rhythms in the mammalian circadian system. *Novartis Found Symp.* **253,** 161–170.

Olla, B. L., and Studholme, A. L. (1972). Daily and seasonal rhythms of activity in the bluefish (*Pomatomus saltatrix*). *In* "Behaviour of Marine Animals" (Wina, H. E., and Olla, B. L., Eds.), Vol. 2, pp. 303–326. Plenum Press, New York.

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 free-running rhythm. *Zool. Sci.* **12,** 337–342.

Ooka-Souda, S., Kabasawa, H., and Kinoshita, S. (1985). Circadian rhythms in locomotor activity of the hagfish, *Eptatretus burgeri*, and the effect of reversal of light-dark cycle. *Zool. Sci.* **2,** 749–754.

Pati, A. K. (2001). Temporal organisation in locomotor activity of the hypogean loach, *Nemacheilus evezardi*, and its epigean ancestor. *Env. Biol. Fishes* **62,** 119–129.

Pedersen, J. (2000). Food consumption and daily feeding periodicity: Comparison between pelagic and demersal whiting in the North Sea. *J. Fish Biol.* **57,** 402–416.

Pettersson, L. B., Andersson, K., and Nilsson, K. (2001). The diel activity of crucian carp, *Carassius carassius*, in relation to chemical cues from predators. *Environ. Biol. Fish* **61,** 341–345.

Pinillos, M. L., De Pedro, N., Alonso-Gomez, A. L., Alonso-Bedate, M., and Delgado, M. J. (2001). Food intake inhibition by melatonin in goldfish (*Carassius auratus*). *Physiol Behav.* **72,** 629–634.

Postlethwait, J. H., Yan, Y. L., Gates, M. A., Horne, S., Amores, A., Brownlie, A., Donovan, A., Egan, E. S., Force, A., Gong, Z., Goutel, C., Fritz, A., Kelsh, R., Knapik, E., Liao, E., Paw, B., Ransom, D., Singer, A., Thomson, M., Abduljabbar, T. S., Yelick, P., Beier, D., Joly, J. S., Larhammar, D., Rosa, F., Westerfield, M., Zon, L. I., Johnson, S. L., and Talbot, W. S. (1998). Vertebrate genome evolution and the zebrafish gene map. *Nat Genet.* **18,** 345–349.

Pradhan, R. K., Pati, A. K., and Agarwal, S. M. (1989). Meal scheduling modulation of circadian rhythm of phototactic behaviour in cave dwelling fish. *Chronobiol. Int.* **6,** 245–249.

Randolph, K. N., and Clemens, H. P. (1976). Some factors influencing the feeding behaviour of channel catfish in culture ponds. *Trans. Am. Fish. Soc.* **105,** 718–724.

Reebs, S. G. (1992). Sleep, inactivity and circadian rhythms in fish. *In* "Rhythms in Fishes" (Ali, M. A., Ed.), pp. 127–135. Plenum Press, New York.

Reebs, S. G. (1996). Time-place learning in golden shiners (Pisces, *Notemigonus crysoleucas*). *Behav. Proces.* **36,** 253–262.

Reebs, S. G. (1999). Time-place learning based on food but not on predation risk in a fish, the inanga (*Galaxias maculatus*). *Ethology* **105,** 361–371.

Reebs, S. G. (2000). Can a minority of informed leaders determine the foraging movements of a fish shoal? *Anim. Behav.* **59,** 403–409.

Reebs, S. G. (2002). Plasticity of diel and circadian activity rhythms in fishes. *Rev. Fish Biol. Fish* **12,** 349–371.

Reebs, S. G., and Colgan, P. W. (1991). Nocturnal care of eggs and circadian rhythms of fanning activity in two normally diurnal cichlid fishes, *Cichlasoma nigrofasciatum* and *Herotilapia multispinosa*. *Anim. Behav.* **41,** 303–311.

Reebs, S. G., and Gallant, B. (1997). Food-anticipatory activity as a cue for local enhancement in golden shiners (Pisces, Cyprinidae, *Notemigonus crysoleucas*). *Ethology* **103,** 1060–1069.

Reebs, S. G., and Laguë, M. (2000). Daily food-anticipatory activity in golden shiners: A test of endogenous timing mechanisms. *Physiol. Behav.* **70,** 35–43.

Rensing, L., and Ruoff, P. (2002). Temperature effect on entrainment, phase shifting, and amplitude of circadian clocks and its molecular bases. *Chronobiol. Int.* **19,** 807–864.

Reppert, S. M., Weaver, D. R., Cassone, V. M., Godson, C., and Kolakowski, L. F., Jr. (1995). Melatonin receptors are for the birds: Molecular analysis of two receptor subtypes differentially expressed in chick brain. *Neuron* **15,** 1003–1015.

Reynolds, W. W., and Casterlin, M. E. (1976a). Locomotor activity rhythms in the bluegill sunfish, *Lepomis macrochirus*. *Amer. Midl. Nat.* **96,** 221–225.

Reynolds, W. W., and Casterlin, M. E. (1976b). Activity rhythms and light intensity preferences of *Micropterus salmoides* and *M. dolomieui*. *Trans. Am. Fish. Soc.* **105,** 400–403.

Richardson, N. E., and McCleave, J. D. (1974). Locomotor activity rhythms of juvenile Atlantic salmon (*Salmo salar*) in various light conditions. *Biol. Bull.* **147,** 422–432.

Ribelayga, C., Wang, Y., and Mangel, S. C. (2004). A circadian clock in the fish retina regulates dopamine release via activation of melatonin receptors. *J. Physiol.* **554,** 467–482.

Roberts, D., Okimoto, D. K., Parsons, C., Straume, M., and Stetson, M. H. (2003). Development of rhythmic melatonin secretion from the pineal gland of embryonic mummichog (Fundulus heteroclitus). *J. Exp. Zool. Part A Comp. Exp. Biol.* **296,** 56–62.

Ross, L. G., and McKinney, R. W. (1988). Respiratory cycles in *Oreochromis niloticus* (L.), measured using a six-channel microcomputer-operated respirometer. *Comp. Biochem. Physiol.* **89A,** 637–643.

Rubio, V. C., Sanchez-Vazquez, F. J., and Madrid, J. A. (2004). Oral administration of melatonin reduces food intake and modifies macronutrient selection in European sea bass (*Dicentrarchus labrax, L.*). *J. Pineal Res.* **37,** 42–47.

Samejima, M., Shavali, S., Tamotsu, S., Uchida, K., Morita, Y., and Fukuda, A. (2000). Light- and temperature-dependence of the melatonin secretion rhythm in the pineal organ of the lamprey, *Lampetra japonica*. *Jap. J. Physiol.* **50,** 437–442.

Sánchez-Vázquez, F. J., and Madrid, J. A. (2001). Feeding anticipatory activity. *In* "Food Intake in Fish" (Houlihan, D., Boujard, T., and Jobling, M., Eds.), pp. 216–232. Blackwell Science, London.

Sánchez-Vázquez, F. J., and Tabata, M. (1998). Circadian rhythms of demand-feeding and locomotor activity in rainbow trout. *J. Fish Biol.* **52,** 255–267.

Sánchez-Vázquez, F. J., Madrid, J. A., and Zamora, S. (1995a). Circadian rhythms of feeding activity in sea bass, *Dicentrarchus labrax* L.: Dual phasing capacity of diel demand-feeding pattern. *J. Biol. Rhythms* **10,** 256–266.

Sánchez-Vázquez, F. J., Zamora, S., and Madrid, J. A. (1995b). Light-dark and food restriction cycles in sea bass: Effect of conflicting zeitgebers on demand-feeding rhythms. *Physiol. Behav.* **58,** 705–714.

Sánchez-Vázquez, F. J., Madrid, J. A., Zamora, S., Iigo, M., and Tabata, M. (1996). Demand feeding and locomotor circadian rhythms in the goldfish, *Carassius auratus*: Dual and independent phasing. *Physiol. Behav.* **60,** 665–674.

Sánchez-Vázquez, F. J., Madrid, J. A., Zamora, S., and Tabata, M. (1997). Feeding entrainment of locomotor activity rhythms in the goldfish is mediated by a feeding-entrainable circadian oscillator. *J. Comp. Physiol. A* **181,** 121–132.

Sánchez-Vázquez, F. J., Azzaydi, M., Martínez, F. J., Zamora, S., and Madrid, J. A. (1998). Annual rhythms of demand-feeding activity in sea bass: Evidence of a seasonal phase inversion of the diel feeding pattern. *Chronobiol. Int.* **15,** 607–622.

Sánchez-Vázquez, F. J., Iigo, M., Madrid, J. A., and Tabata, M. (2000). Pinealectomy does not affect the entrainment to light nor the generation of the circadian demand-feeding rhythms of rainbow trout. *Physiol. Behav.* **69,** 455–461.

Sánchez-Vázquez, F. J., Aranda, A., and Madrid, J. A. (2001). Differential effects of meal size and food energy density on feeding entrainment in goldfish. *J. Biol. Rhythms* **16,** 58–65.

Schwassmann, H. O. (1971). Biological rhythms. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 6, pp. 371–428. Academic Press, New York.

Sevenster, P., Feuth-de Bruijn, E., and Huisman, J. J. (1995). Temporal structure in stickleback behaviour. *Behaviour* **132,** 1267–1284.

Shapiro, C. M., and Hepburn, H. R. (1976). Sleep in a schooling fish, *Tilapia mossambica*. *Physiol. Behav.* **16,** 613–615.

Shearman, L. P., Sriram, S., Weaver, D. R., Maywood, E. S., Chaves, I., Zheng, B., Kume, K., Lee, C. C., van der Horst, G. T., Hastings, M. H., and Reppert, S. M. (2000). Interacting molecular loops in the mammalian circadian clock. *Science* **288,** 1013–1019.

Smith, R. J. F. (1997). Avoiding and deterring predators. *In* "Behavioural Ecology of Teleost Fishes" (Godin, J.-G. J., Ed.), pp. 163–190. Oxford University Press, Oxford.

Soni, B. G., and Foster, R. G. (1997). A novel and ancient vertebrate opsin. *FEBS Lett.* **406,** 279–283.

Soni, B. G., Philp, A. R., Foster, R. G., and Knox, B. E. (1998). Novel retinal photoreceptors. *Nature* **394,** 27–28.

Spieler, R. E., and Clougherty, J. J. (1989). Free-running locomotor rhythms of feeding-entrained goldfish. *Zool. Sci.* **6,** 813–816.

Spieler, R. E., and Noeske, T. A. (1984). Effects of photoperiod and feeding schedule on diel variations of locomotor activity, cortisol, and thyroxine in goldfish. *Trans. Am. Fish. Soc.* **113,** 528–539.

Steele, C. W. (1984). Diel activity rhythms and orientation of sea catfish (*Arius felis*) under constant conditions of light and darkness. *Mar. Behav. Physiol.* **10,** 183–198.

Stickney, A. P. (1972). The locomotor activity of juvenile herring (*Clupea harengus harengus* L.) in response to changes in illumination. *Ecology* **53,** 438–445.

Tabata, M., Minh-Nyo, M., Niwa, H., and Oguri, M. (1989). Circadian rhythm of locomotor activity in a teleost, *Silurus asotus*. *Zool. Sci.* **6,** 367–375.

Tabata, M., Minh-Nyo, M., and Oguri, M. (1991). The role of the eyes and the pineal organ in the circadian rhythmicity in the catfish *Silurus asotus*. *Nippon Suisan Gakkaishi* **57,** 607–612.

Tamai, T. K., Vardhanabhuti, V., Arthur, S., Foulkes, N. S., and Whitmore, D. (2003). Flies and fish: Birds of a feather. *J. Neuroendocrinol.* **15,** 344–349.

Tauber, E. S. (1974). The phylogeny of sleep. *In* "Advances in Sleep Research" (Weitzman, E. D., Ed.), Vol. 1, pp. 133–172. Spectrum Public, New York.

Thetmeyer, H. (1997). Diel rhythms of swimming activity and oxygen consumption in *Gobiusculus flavescens* (Fabricius) and *Pomatoschistus minutus* (Pallas) (Teleostei, Gobiidae). *J. Exp. Mar. Biol. Ecol.* **218,** 187–198.

Thinès, G. (1967). Étude d'un dispositif actographique permettant de mesurer l'activité des poissons: Examen de quelques résultats obtenus sur *Carassius auratus*, *Pygocentrus piraya* et *Hyphessobricon rosaceus*. *In* "La Distribution Temporelle des Activités Animales et Humaines" (Médioni, J., Ed.), pp. 65–77. Masson, Paris.

Tobler, I., and Borbely, A. A. (1985). Effect of rest deprivation on motor activity of fish. *J. Comp. Physiol. A* **157,** 817–822.

Trajano, E., and Menna-Barreto, L. (2000). Locomotor activity rhythms in cave catfishes, genus Taunayia, from eastern Brazil (Teleostei: Siluriformes: Heptapterinae). *Biol. Rhythm Res.* **31,** 469–480.

Valdimarsson, S. K., Metcalfe, N. B., Thorpe, J. E., and Huntingford, F. A. (1997). Seasonal changes in sheltering: Effect of light and temperature on diel activity in juvenile salmon. *Anim. Behav.* **54,** 1405–1412.

Weber, D. N., and Spieler, R. E. (1987). Effects of the light-dark cycle and scheduled feeding on behavioural and reproductive rhythms of the cyprinodont fish, Medaka, *Oryzias latipes*. *Experientia* **43,** 621–624.

Whitmore, D., Foulkes, N. S., and Sassone-Corsi, P. (2000). Light acts directly on organs and cells in culture to set the vertebrate circadian clock. *Nature* **404,** 87–91.

Whitmore, D., Foulkes, N. S., Strahle, U., and Sassone-Corsi, P. (1998). Zebrafish Clock rhythmic expression reveals independent peripheral circadian oscillators. *Nat. Neurosci.* **1,** 701–707.

Yamada, H., Satoh, R., Ogoh, M., Takaji, K., Fujimoto, Y., Hakuba, T., Chiba, H., Kambegawa, A., and Iwata, M. (2002). Circadian changes in serum concentrations of steroids in Japanese char *Salvelinus leucomaenis* at the stage of final maturation. *Zool. Sci.* **19,** 891–898.

Yokota, T., and Oishi, T. (1992). Seasonal change in the locomotor activity rhythm of the medaka, *Oryzias latipes*. *Int. J. Biometeorol.* **36,** 39–44.

Zachmann, A., Falcon, J., Knijff, S. C., Bolliet, V., and Ali, M. A. (1992). Effects of photoperiod and temperature on rhythmic melatonin secretion from the pineal organ of the white sucker (*Catostomus commersoni*) *in vitro*. *Gen. Comp. Endocrinol.* **86,** 26–33.

Zhdanova, I. V., Geiger, D. A., Schwagerl, A. L., Leclair, O. U., Killiany, R., Taylor, J. A., Rosene, D. L., Moss, M. B., and Madras, B. K. (2002). Melatonin promotes sleep in three species of diurnal nonhuman primates. *Physiol. Behav.* **75,** 523–529.

Zhdanova, I. V., Wang, S. Y., Leclair, O. U., and Danilova, N. P. (2001). Melatonin promotes sleep-like state in zebrafish. *Brain Res.* **903,** 263–268.

Zhdanova, I. V., and Tucci, V. (2003). Melatonin, Circadian Rhythms, and Sleep. *Curr. Treat. Options Neurol.* **5,** 225–229.

Zoufal, R., and Taborsky, M. (1991). Fish foraging periodicity correlates with daily changes of diet quality. *Mar. Biol.* **108,** 193–196.