# Plasticity of diel and circadian activity rhythms in fishes

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## Contents

## Abstract

In many fish species, some individuals are diurnal while others are nocturnal. Sometimes, the same individual can be diurnal at first and then switch to nocturnalism, or vice-versa. This review examines the factors that are associated with such plasticity. It covers the breakdown of activity rhythms during migration, spawning, and the parental phase; reversals of activity patterns during ontogeny or from one season to the next; effects of light intensity, temperature, predation risk, shoal size, food availability, and intraspecific competition. Case studies featuring goldfish (*Carassius auratus*), golden shiner (*Notemigonus crysoleucas*), lake chub (*Couesius plumbeus*),

salmonids, sea bass (*Dicentrarchus labrax*), and parental sticklebacks and cichlids illustrate some of these influences. It is argued that most species have a circadian system but that having such a system does not necessarily imply strict diurnalism or nocturnalism. Rigidity of activity phase seems more common in species, mostly marine, that display behavioral sleep, and for these animals the circadian clock can help maintain the integrity of the sleep period and ensure that its occurrence takes place at that time of day to which the animal's sensory equipment is not as well adapted. However, in other fishes, mostly from freshwater habitats, the circadian clock seems to be used mainly for anticipation of daily events such as the arrival of day, night, or food, and possibly for other abilities such as time-place learning and sun compass orientation, rather than for strict control of activity phase. In these species, various considerations relating to foraging success and predation risk may determine whether the animal is diurnal or nocturnal at any particular time and place.

## Introduction

The activity patterns of animals over a 24-h period can usually be described as nocturnal, diurnal, or crepuscular. In the case of mammals or birds, assigning such labels is not problematic, as these animals typically display activity patterns that are consistent both within species and within individuals (but there are exceptions: Stebbins, 1972; Johnston and Zucker, 1983; Curtis, 1997; Fernandez-Duque and Bravo, 1997; Blanchong et al., 1999; Kas and Edgar, 1999). Consistency of activity patterns is also found in many fish species (Helfman, 1993) but certainly not in all. In a fair number of fish species, some individuals are diurnal while others are nocturnal. Sometimes, the same individual can be diurnal at first and then switch to nocturnalism in just a few days. For this reason, activity patterns in fishes are often said to be plastic (Ali, 1992).

In past reviews of activity patterns in fishes (e.g. Thorpe, 1978; Ali, 1992; Helfman, 1993; Madrid et al., 2001), plasticity has been mentioned along with a few examples, but the phenomenon was not covered in detail because little was known about its causes and possible ecological implications. In the present review, I bring some order to our knowledge of plasticity in activity rhythms by listing the factors that seem to cause within-species or within-individual dualism in activity phases. I take advantage of recent progress in the understanding of some of the systems that are characterized by plasticity in activity patterns, such as the increased nocturnalism shown by salmonids under cold temperature and the food-anticipatory activity exhibited by various species.

The review is structured as follows: first, a few words about its scope; then some consideration of how activity levels are measured in fishes; then a definition of the terms circadian and diel (both of these types of activity patterns are covered in the review).

There follow six case studies, each one centered on one species or on a particular set of species. These case studies introduce some of the factors that underlie plasticity in activity rhythms, and these factors are treated in more detail at the end of the review.

### Scope of the review

This paper deals only with patterns of *activity levels*. In the great majority of studies, locomotion or feeding activities have been measured. In a few cases, spawning and parental activities (fanning the eggs, aggressive acts to protect a nest) have also been studied on a 24-h basis.

The review does not thoroughly cover diel or circadian patterns of habitat preference (that is, patterns of absence/presence from specific habitats; e.g. Hanych et al., 1983; Crook et al., 2001). In the same vein, the review does not look at daily migration patterns (for a review with marine species, see Neilson and Perry, 1990; and for an example of plasticity, see Bennett et al. 2002). Neither does the review cover diel or circadian patterns of physiological parameters such as hormone levels (e.g. Peter et al., 1978; Spieler and Noeske, 1984), oxygen consumption (e.g. Shekk, 1986; Nixon and Gruber, 1988; Thetmeyer, 1997), heart rate (e.g. Priede, 1978; Belich, 1984; Armstrong et al., 1989; see also references in Briggs and Post, 1997a), colour changes (e.g. Kavaliers and Abbott, 1977; Lythgoe and Shand, 1983; Nemtzov et al., 1993) or electric discharges (e.g. Schwassmann, 1971).

### Measurement of activity in fishes

In the laboratory, locomotor activity is usually recorded automatically via interruptions of infrared light beams set across the aquarium. Direct observations (Tobler and Borbély, 1985; Massicotte and Dodson, 1991; Zhdanova et al., 2001), automated

video image analysis (Cahill et al., 1998; Hurd and Cahill, 2002), disruptions of standing ultrasound waves (Kavaliers, 1978, 1980a, b, c, d), and automatically recorded hits on obstacles (Davis, 1964; Davis and Bardach, 1965) are less common methods.

In the field, locomotor activity is often inferred from capture in fishing gear. This of course is valid only for passive gear, such as minnow traps, whose efficiency is dependent on action by the fish themselves. Active methods such as electrofishing or trawling can give information on presence/absence of fish but not necessarily on their activity levels, as active gear can potentially capture resting as well as wakeful fish. Other methods in the field involve telemetry to record electromyograms, which can tell us when muscles are in action (e.g. Demers et al., 1996; Weatherley et al., 1996; Briggs and Post, 1997a, b), or to perform radiotracking, which can reveal hour-by-hour displacement and therefore activity (e.g. Clark and Green, 1990; Guy et al., 1994; Matheney and Rabeni, 1995; Bunnel et al., 1998; Cooke et al., 2001; David and Closs, 2001). A final method is direct observation, but care must be exerted at night. Shining a bright light on a fish at night sometimes causes a "light shock effect" whereby the otherwise active fish stops moving and sinks to the bottom, giving the false impression that it is resting (interestingly, the intensity of this reaction seems to vary according to time of night, at least in bluegill sunfish [*Lepomis macrochirus*]; see Davis, 1962). Several researchers have reported that diurnal as well as nocturnal species become immobilized and can even be approached and touched in the beam of a light at night (Hobson, 1965; Emery, 1973a). The fact that both diurnal and nocturnal species react in this way suggests a direct effect of light. To complicate things even further, some species do not show this light shock reaction, quickly darting away when illuminated at night (Emery, 1973a). It is advisable to use very dim light and light-magnifying scopes (Reebs et al., 1984), or infrared light and cameras (Hinch and Collins, 1991; Collins and Hinch, 1993; Popiel et al., 1996; Mussen and Peeke, 2001) when making observations at night.

In the laboratory, feeding activity is usually recorded through demand feeders, i.e. feeders operated by the fish themselves after proper conditioning (Wright and Eastcott, 1982; Boujard et al., 1992; Sánchez-Vázquez et al., 1994, 1998a). Periodically collecting and measuring the amount of food not eaten by fish under a regular food delivery regime is also valid (Juell, 1991; Madrid et al., 1997). Interruptions of light beams set up at the specific location where food normally appears could also be seen as a measure of feeding activity, or at least motivation to feed, even though it is in fact locomotion (Sánchez-Vázquez et al., 1997; Reebs and Laguë, 2000).

In the field, feeding activity is usually inferred from gut fullness at the moment of capture. Direct observations (e.g. Emery, 1973a; Hobson et al., 1981; Zoufal and Taborsky, 1991; Collins and Hinch, 1993) and electromyograms of jaw muscles (Oswald, 1978) can also be used.

*Circadian versus diel*

The term circadian refers to an endogenous mechanism that cycles with a periodicity of approximately 24 h. The term diel, which can be used interchangeably with daily, refers to any 24-h cyclic pattern, usually in the presence of a light-dark (LD) cycle. Diel patterns of activity may or may not be generated by an endogenous circadian clock.

When an endogenous circadian mechanism is involved, exogenous factors can still exert an influence as zeitgebers, that is, as synchronizers of the endogenous oscillator, entraining the often-imprecise clock to exactly 24 h. Light-dark cycles, patterns of food availability, and daily temperature variations are possible zeitgebers. If, on the other hand, diel activity patterns are not under the influence of an endogenous circadian clock (something that may be hard to prove, given that it is always hard to prove a negative), then these patterns would directly reflect constraining or promoting effects by light intensity, temperature, food availability, social interactions, and perhaps predation risk, all of which can cycle on a 24-h basis.

Rigorously demonstrating the existence of a circadian mechanism usually requires that a cyclic pattern of approximately, but not exactly, 24-h periodicity be displayed by an animal under constant conditions such as constant light (LL), constant darkness (DD), very short light-dark cycles (in the range of a few hours at most; see Eriksson and van Veen, 1980; Sánchez-Vázquez et al., 1995a), constant water temperature and oxygen content, food always present or always absent. The importance of a non-24 h periodicity is that no overlooked daily factor (e.g. people's entrances into the laboratory) can then be said to have caused the rhythm.

There are other ways to suggest the existence of endogenous timing mechanisms, and although these

do not strictly prove the existence of a circadian clock (instead of, say, an hourglass mechanism – an internal timer set for a specific duration and triggered by a daily event such as lights-on), it is often reasonably assumed that they do. One of these demonstrations is to phase-shift the zeitgeber (most commonly the light-dark cycle), advancing or delaying it by a few hours, and observing transient cycles of activity, that is, activity which on the first day following the shift starts at the old time of light or dark and that slowly, day after day, drifts across clock times until it is resynchronized with the new phase of the light-dark cycle. As opposed to laboratory rodents which often, but not always (e.g. Reebs and Mrosovsky, 1989), exhibit 3-4 days of transients after a 6-h advance or delay of their zeitgebers, fish usually display only one day of transient activity before complete resynchronization (Nelson and Johnson, 1970; Godin, 1981; Tabata et al., 1989; Sánchez-Vázquez et al., 1995a). However, Reebs (1996) and Laguë and Reebs (2000a) observed transients for 2–3 days in most of their golden shiners (*Notemigonus crysoleucas*) after a 6-h shift of the light-dark cycle, and Ooka-Souda et al. (1985) observed smooth transitions lasting for 7–13 days after a 12-h shift of the light-dark cycle in inshore hagfish (*Eptatretus burgeri*). Still, the preponderance of cases where the number of transients is rather low indicates that the circadian system of most fishes is easily readjusted, or perhaps easily masked by light (masking is a technical term in chronobiology that denotes a direct effect of an exogenous factor on the expression of an endogenously-generated activity pattern).

Another way to suggest the existence of circadian clocks is to observe the anticipation of regular daily events such as the arrival of night or day (Helfman, 1986; Reebs, 1994b) or the arrival of food. Boujard and Leatherland (1992a), Spieler (1992), Mistlberger (1994) and Sánchez-Vázquez and Madrid (2001) provide good reviews of food-anticipatory activity. Recent studies on food anticipation include Zafar and Morgan (1992), Gee et al. (1994), Naruse and Oishi (1994), Sánchez-Vázquez et al. (1995b), Reebs and Gallant (1997), Sánchez-Vázquez et al. (1997), Azzaydi et al. (1998), Reebs (2000), Reebs and Laguë (2000), Aranda et al. (2001), Chen and Purser (2001), Purser and Chen (2001), and Chen and Tabata (in press).

A final but indirect way to demonstrate circadian rhythmicity is to demonstrate the existence of sun compass orientation, as it is generally accepted that such a compass is based on circadian timekeeping. In fish, sun compasses have been reported in at least a dozen species (Hasler et al., 1958; Schwassmann and Hasler, 1964; Winn et al., 1964; Groot, 1965; Goodyear and Ferguson, 1969; Goodyear, 1970, 1973; Loyacano et al., 1977; Goodyear and Bennett, 1979). The work by Goodyear and Bennett (1979) is a particularly good experimental demonstration of the circadian clock's role in sun compass orientation, as opposed to the possible role of sun height and sun position (though these two variables may also have some effect: see Schwassmann and Hasler, 1964).

## Case studies

### Case study #1: Goldfish (Carassius auratus)

A popular aquarium species, goldfish seem to have been studied exclusively in the laboratory. Goldfish can show circadian activity under constant conditions but their rhythms are messy in the sense that they are not visually obvious on actograms (actograms are a day-by-day representation of hourly activity levels) and often require sophisticated statistical analysis, such as periodograms, to be revealed. Moreover, not all individuals exhibit detectable circadian rhythmicity. Iigo and Tabata (1996) reported that only 57%, 57%, and 67% of their goldfish were rhythmic under DD, LL, and dim LL respectively. Some individuals were rhythmic under DD but not LL, while others were rhythmic under LL but not DD. Sánchez-Vázquez et al. (1996) reported that less than 50% of their goldfish had detectable demand-feeding or locomotor rhythms in DD, and those rhythms lacked consistency and disappeared easily within a few days. Rhythms may appear more reliably when goldfish are tested in shoals: Sanchez-Vázquez et al. (1997) found that only 13 of 20 single goldfish expressed free-running food-anticipatory activity rhythms in DD, whereas Spieler and Clougherty (1989) found such rhythms in DD or LL in 15 of their 17 shoals (12 fish per shoal) – but there were other slight methodological differences between the two studies. Kavaliers (1981a) found that groups of 20 goldfish displayed circadian rhythms in LL that were "slightly more precise" and of significantly longer period than those of single fish.

The phase that is maintained between this endogenous mechanism and the light-dark cycle is very flexible. Tobler and Borbély (1985) deemed their

goldfish's timing of activity as too erratic for their purpose in a study of rest deprivation in fish. In Iigo and Tabata (1996), 83% of the goldfish were diurnal, 7% nocturnal, and 10% aphasic (that is, constant levels of activity 24 h a day); some individuals changed their activity patterns from one type to another. Unfortunately, no information was given on the feeding schedule. In Sánchez-Vázquez et al. (1997), where food was given at irregular intervals day and night, 21% were diurnal, 16% mostly nocturnal, and 63% aphasic; the clearly nocturnal patterns were only detected in the upper layer of the aquarium, whereas four of the five clearly diurnal patterns took place in the lower layer. A few individuals were at once nocturnal in the upper layer and diurnal in the lower level. Sanchez-Vázquez et al. (1996) also witnessed some individuals demand-feeding diurnally but moving nocturnally, and others with the reverse pattern. Sanchez-Vázquez et al. (1998a) reported on goldfish that demand-fed all day-long, but mostly on carbohydrate-rich diets during the day and on protein-rich diets at night.

Time of food availability can have a great effect of the phase of goldfish activity. Sánchez-Vázquez et al. (1997) found that single goldfish which were either nocturnal, diurnal or aphasic when fed at random times of day and night became almost exclusively nocturnal when fed at mid-night only, and almost exclusively diurnal when fed at mid-day only. Spieler and Noeske (1984) found that groups of 12 goldfish were active mostly around the single daily time of food delivery, be it mid-day, mid-night, dawn, or dusk, and that this daily peak of activity persisted for 3–10 days after food was withheld altogether; this was for total activity throughout the tank, not just near the spot of food delivery, as movement was measured with an ultrasonic motion detector. Gee et al. (1994) found that goldfish can express food-anticipatory lever presses in the middle of the night as well as in the middle of the day. Aranda et al. (2001) reported that food-anticipatory activity can track 4-h shifts in the daily timing of food availability under LD 0.25:23.75 h. Sánchez-Vázquez et al. (2001) similarly observed that food-anticipatory activity followed 12-h shifts of meal time in LL, adding that resynchronization was faster when meal size was reduced, but that dilution of meal energy content did not have this effect.

From these studies, one gets the impression that the goldfish is an animal whose sensory abilities enable it to operate efficiently during either day or night. Accordingly, it does not need to maintain a particular phase between the day-night cycle and its internal clock. It can react directly to external factors such as food availability. However, the fact that some fish can be diurnal while others are nocturnal under the same set of laboratory conditions suggests that internal factors may also be at play. There is currently no evidence that genetic factors are involved in determining a preferred activity phase, though studies designed to specifically address this question are not available. Artificial selection experiments based on activity patterns would be enlightening. Another hypothesis is that prior experience, with food availability in particular, plays a role. It would be interesting to measure the influence of food availability or the timing of competition for food early in life on the tendency of adult fish to maintain a certain phase of activity later in life (see Alanärä and Brännäs, 1997; Brännäs and Alanärä, 1997).

Given the little impact that day or night seems to have on the phasing of activity in goldfish, what is the use of the goldfish's circadian clock? Here again, food availability may be important. The internal clock could help the animal anticipate the daily arrival of a temporally predictable food source and limit food-searching to the most profitable time of day. Goldfish do show food-anticipatory activity when food is always scheduled at the same daily time (Spieler and Noeske, 1984; Gee et al., 1994; Sánchez-Vázquez et al., 1997; Aranda et al., 2001). The circadian system of the goldfish, though not strongly self-sustained, can nevertheless be sustained and entrained by the light-dark cycle (an indirect way to remain in phase with a food source that might vary according to a diel pattern) or more directly by the food itself, perhaps overriding the influence of the light-dark cycle (Aranda et al., 2001).

*Case study #2: Golden shiner* (Notemigonus crysoleucas)

Like its fellow cyprinid the goldfish, the golden shiner does not express circadian activity very reliably under constant conditions (Laguë and Reebs, unpublished data). However, it can easily anticipate daily food arrival, at any time of day or night (Reebs and Laguë, 2000). At the shoal level, it can anticipate up to three daily food deliveries, even when these deliveries are in different places (time-place learning: Reebs, 1996), or even when one of these deliveries takes place during the day and another at night (Laguë and Reebs, 2000b; see also Azzaydi et al., 1998, for

similar results in another species); it is not known whether this is caused by some individuals within the shoal specializing on one daily time and place while other individuals specialize on another time and place, or whether individual fish could anticipate more than one time (however, see Chen and Tabata, in press, for an example of double anticipation by single trout). The anticipation is clearly based on an endogenous circadian mechanism because transients in food-anticipatory activity are expressed for 2–3 days when the light-dark cycle is advanced or delayed by 6 h (Reebs, 1996; Laguë and Reebs, 2000a). There is some evidence that golden shiners can learn the daily phase of food availability relative to the oscillation of an endogenous circadian clock, and that this circadian clock is entrained and sustained mostly by the light-dark cycle (Reebs and Laguë, 2000).

In contrast to the goldfish, there is information on the diel activity pattern of golden shiners in the field. Populations feeding on zooplankton appear to be crepuscular (Zaret and Suffern, 1976; Hall et al., 1979; Keast and Fox, 1992). Gascon and Legget (1977) examined gut fullness in a number of species and they reported that golden shiners were diurnal in one part of the study lake where they preyed on flying insects, but in another more productive part of the lake where benthic organisms as well as flying insects were found in the fish's stomach, gut fullness index was high day and night, at least at the population level (the same observation applied to bluntnose minnows [*Pimephales notatus*], but not to silvery minnows [*Hybognathus nuchalis*], johnny darters [*Etheostoma nigrum*], or mimic shiners [*Notropis volucellus*], all of which were crepuscular in both parts of the lake).

Golden shiners can feed on a variety of small organisms in the wild (flying insects, zooplankton, benthos: Harnois et al., 1992) and they are not particular in the laboratory either (floating, sinking, or crumbled pellets: unpublished data; Gatlin and Phillips, 1988). They can feed on bottom substrate, submerged macrophytes, in the water column or at the surface (Paszkowski, 1986). They can locate individual prey items visually, or they can filter-feed on high densities of zooplankton without using visual cues (Ehlinger, 1989; see also Diehl, 1988, for a similar observation in other cyprinids). They can attack the nests of pumpkinseed sunfish (*Lepomis gibbosus*) at night and eat their eggs (Popiel et al., 1996).

All of the above paints the picture of an adaptable animal that can feed both during the day and at night,

and therefore may not always maintain the same phase of activity, depending on food availability. It may still, however, use a weak circadian clock to anticipate food arrival if the availability of food happens to be periodical on a daily basis.

Another modulator of activity phase may be predation risk. Helfman (1981a) observed that young-of-the-year golden shiners fed by day in his study lake, whereas adults appeared more crepuscular. Based on witnessed predation events, Helfman invoked the young fish's susceptibility to crepuscular predation as a possible explanation for their divergent activity pattern. On the other hand, Hall et al. (1979) wondered why their shiners fed on plankton only at dawn and dusk even though plankton was available during the day also, and as a possible explanation the authors posited diurnal predation risk from largemouth bass (*Micropterus salmoides*) and northern pike (*Esox lucius*). The fact that predation risk can be invoked to explain one type of activity pattern in one study and a different type in another study on the same species points to an already recognized problem (Helfman, 1993): predation risk is a rather easy post-hoc explanation, no matter what activity pattern is expressed, and it has seldom been the specific subject of rigorous study as a possible determinant of the prey's activity pattern.

*Case study #3: Lake chub* (Couesius plumbeus)

Of all the cyprinids studied to date, the lake chub has yielded the most clear-cut free-running circadian rhythms in constant conditions (Kavaliers, 1979a, b, 1980d) but these rhythms seldom lasted for more than 2–3 weeks, and many individuals had messier rhythms than those shown in the published papers (Kavaliers, personal communication). In the laboratory under DD, Kavaliers (1978) measured longer free-running periods from fish that had been captured in winter as opposed to summer, but it is not clear whether this was an endogenous (circannual) effect or a lasting consequence of water temperature and photoperiod at the time of capture. Subsequently, Kavaliers and Ross (1981) indicated that this seasonal variation could be seen only when twilight was included in the seasonally-varying photoperiod.

Kavaliers (1980a, 1981b) has also reported seasonal plasticity in circadian periodicity for burbot (*Lota lota*) and for longnose dace (*Rhinichthys cataractae*); for those species, in contrast to the lake chubs, the period was longer in summer. It is not clear why

there is such seasonal variation in circadian periodicity, and why species differ in the direction of this variation. Perhaps in fishes, as in some mammals (Mrosovsky et al., 1976), there are circannual rhythms of metabolic activity and body weight that are adapted to the conditions of each season and that could affect the workings of the circadian clock.

In the laboratory, lake chubs are diurnal (Kavaliers and Ross, 1981; Reebs, unpublished data). In an Ontario lake, Emery (1973a) observed lake chubs feeding at night, but he could not say that they fed more at night than during the day or twilight. In a New Brunswick stream, Reebs et al. (1995) observed that lake chubs entered *unbaited* traps at dawn and dusk only, that they entered *baited* traps not only at dawn and dusk but also during the daylight hours, but that during in-stream and out-stream migration they were intercepted by a counting fence only at night. Diurnal piscivorous birds (kingfishers and common mergansers) were present over the study stream and the authors postulated (another post-hoc explanation) that lake chubs were crepuscular to avoid detection by birds under the bright light of day while still taking advantage of some light to catch their own prey, that they were nevertheless alert by day and could be enticed to enter traps if the food stimulus was strong enough, but that they became nocturnal at migration time to avoid detection in the shallow riffles over which they had to swim. Here again we have a fish that appears quite adaptable in terms of light requirements, and for which food and predation risk have been suggested as major determinants of activity patterns.

*Case study #4: Salmonids*

Like the cyprinids above, salmon and trout sometimes express circadian rhythmicity under constant conditions, but not always and never for long. In Richardson and McCleave (1974), periodogram analysis revealed that only 5 of 30 individual Atlantic salmon (*Salmo salar*) were rhythmic in DD, and none in LL. Only half of Godin's (1981) pink salmon (*Oncorhynchus gorbuscha*) were rhythmic in LL, and this for no longer than 10 days.

There is also variability in activity phase. In Godin (1981), under LD 12:12 h and in the total absence of food, swimming activity was diurnal in 68% of 38 captive pink salmon; the rest were nocturnal (for similar findings in rainbow trout, *Oncorhynchus mykiss*, see Alanärä and Brännäs, 1997; Brännäs and

Alanärä, 1997; Bolliet et al., 2001). Still in the lab but under natural summer temperatures and photoperiod, Godin's (1984) pink salmon were diurnal; under winter conditions, the fish became aphasic as daytime activity decreased to levels similar to those of nighttime. In a summer experiment by Richardson and McCleave (1974) on Atlantic salmon, 35 individuals were diurnal, 20 nocturnal, and 32 crepuscular (this was in the laboratory for 10 days without food); these respective numbers became 30, 1, 11 in another summer replicate, but changed greatly to 5, 19, and 21 in a winter–spring replicate.

Despite the great variability, these numbers show a trend for increased nocturnalism in winter. Indeed, many studies have shown that salmon tend to become more nocturnal, or at least less diurnal, at the end of summer and through the fall (Landless, 1976; Eriksson, 1978a; Heggenes et al., 1993; Riehle and Griffith, 1993; Amundsen et al., 2000; Bremset, 2000; Jakober et al., 2000). Linnér et al. (1990) noted the same phenomenon in young Arctic char (*Salvelinus alpinus*), though in general there was much variation in activity patterns throughout the year (see also Adams et al., 1988).

Fraser et al. (1993, 1995) provided experimental evidence that cold temperatures are involved in increased nocturnalism. In their laboratory studies, Atlantic salmon that were active day and night suppressed daytime activity – and therefore became proportionally more nocturnal – when they were exposed to cold water, even under a summer photoperiod. These authors also mention that juvenile salmon in glacial streams, where water is cold all year round, are mostly nocturnal throughout the year, further suggesting the role of cold temperature. Fraser et al. (1993, 1995) proposed that in the warm temperatures of summer, the higher metabolism of salmon helps them escape from predators, and so they can afford the risk of foraging during the day when they reap the benefit of better success because of higher light intensity. Under cold temperatures, the salmon are slow, which makes them vulnerable to their warm-blooded diurnal predators (birds, mink), and this forces them to become more nocturnal (i.e. better hidden in the dark), even if this means less efficient foraging (reduced foraging success in the dark has been demonstrated by Fraser and Metcalfe, 1997). Interestingly, in those individuals for whom foraging success is more crucial (e.g. salmon with low energy reserves, or preparing to migrate to sea), the fall switch to nocturnalism is less pronounced, suggesting

that the importance of foraging tips the balance towards increased diurnalism, despite the predation risk (Metcalfe et al., 1998; see also Valdimarsson et al., 1997; Metcalfe et al., 1999).

In late-August and early-September, in a New England river, Gries et al. (1997) also found that young-of-the-year Atlantic salmon were proportionally more nocturnal under lower temperatures. However, post-young-of-the-year were always nocturnal, even at relatively high temperatures (15–23 °C). Bradford and Higgins (2001) also found year-round nocturnalism in some (but not all) juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) in the wild. These results indicate that low temperatures may not be the only cause of nocturnalism for salmonids in nature. (The fact that some individuals can be diurnal while others are nocturnal under the same laboratory conditions, as in Alanärä and Brännäs (1997) and Bolliet et al. (2001) shows that internal factors are involved in phase dualism.) Conversely, low temperatures do not always result in nocturnalism. For example, Boujard and Leatherland (1992b) observed that rainbow trout demanded food only diurnally at 7–10 °C, under a variety of photoperiods. In this experiment, the trigger of the demand-feeder was positioned just above the water surface and it was completely dark at night. The fish therefore could use neither eye or lateral line to find the feeders at night, and this probably explains the rainbow's diurnal activity despite the low temperatures.

Once again, we have here an example of a fish that can function both by day and by night, though it seems to prefer the daytime when constrained mostly by foraging considerations, and nighttime when predator avoidance is more important.

*Case study #5: Sea bass* (Dicentrarchus labrax)

Sánchez-Vázquez et al. (1995a) moved sea bass from net cages to laboratory tanks, and found that about half of the fish, whether they were kept in groups or singly, demanded food at feeders during the day while the other half did so at night. When light and darkness were made to continuously alternate every 40 minutes, the fish kept on feeding during the same illumination phase (light or dark) as before. However, the quick alternation meant that the conditions could be considered constant over 24 h, and free-running circadian rhythms were expressed. These rhythms, however, were of low amplitude, with variable activity onsets and changing periodicity. Back under LD 12: 12 h, activity promptly followed 12-h phase-shifts of the light-dark cycle, with only one transient cycle showing, and the authors concluded that the circadian system of sea bass was delicate and capable of being masked by the external LD cycle.

Sánchez-Vázquez et al. (1995b) showed that food-demand rhythms could be synchronized by periodic feeding (food available at the feeders only during the same 4 h every day). Some fish (individuals or groups) that were diurnal could be made nocturnal by restricting food availability at night, and vice-versa. However, not all fish reacted in this way, and so food appears to be an important but not over-powering determinant of diurnalism or nocturnalism in this species. What other factors are involved is unknown.

When sea bass are held in natural conditions of photoperiod and temperature, and in groups (they are a shoaling species), their demand-feeding behavior is predominantly diurnal in summer and mostly nocturnal in winter (Sánchez-Vázquez et al., 1998b). Experimental manipulations of the photoperiod and water temperature were tried but did not induce the seasonal inversion, which suggests that an endogenous circannual clock may be at work (Aranda et al., 1999a, b). The adaptive significance of seasonal inversions in activity phase may reside in the tracking of seasonally variable food availability (Sánchez-Vázquez et al., 1998b).

*Case study #6: Parental sticklebacks and cichlids*

It is probably fair to say that, historically in the field of fish ethology, sticklebacks (family Gasterosteidae) and cichlids (family Cichlidae) have been the most popular subjects of study. Part of their attraction resides in their well-developed parental behavior. Given this popularity, it is surprising that circadian rhythmicity has never been reported for these fishes. Perhaps this is an indication that circadian rhythmicity is not easily revealed – or is absent altogether – in these species, and that negative results have not been submitted for publication. The only example of reported negative results I am aware of is Sevenster et al. (1995): these authors placed parental male three-spined sticklebacks (*Gasterosteus aculeatus*) in LL and found no evidence of circadian rhythmicity for a variety of parental behavior.

Non-parental three-spined sticklebacks tend to feed diurnally (Worgan and FitzGerald, 1981; Allen

and Wootton, 1984; but see Mussen and Peeke, 2001), enter minnow traps mostly – but not exclusively – during the day (Worgan and FitzGerald, 1981; Sjöberg, 1985; Reebs et al., 1995), and are more active in aquaria during the day (Sjöberg, 1985; Westin and Aneer, 1987). However, parental males in the field fan their eggs not only during the day but also at night; in fact, levels of fanning are somewhat – but not significantly – higher at night (Reebs et al., 1984). So sticklebacks need not be strictly diurnal, at least during the reproductive season. Their sensory equipment may create a bias for day foraging, but it does not prevent them from finding their nest and eggs in the dark.

Cichlids are usually recognized as diurnal fishes. New World species such as the convict cichlid (*Archocentrus nigrofasciatus*, ex-*Cichlasoma nigrofasciatum*), severum cichlid (*Heros severus*, ex-*Cichlasoma severum*), and rainbow cichlid (*Herotilapia multispinosa*) are usually quiescent at night, though slow promenades through the aquarium commonly occur (Tobler and Borbély, 1985; Reebs, unpublished data). However, during the parental phase the female fans her eggs and attacks nest intruders both day and night (Reebs and Colgan, 1991; Reebs, 1994a). In the convict cichlid, parental females seem to use visual cues to orient towards their eggs or towards intruders during the day, but they rely on chemical cues in the complete darkness of night (Reebs and Colgan, 1992; Reebs, 1994a). Continuous 24-h care is also present during the wriggler and fry stage (Lavery and Reebs, 1994). Fanning levels are significantly higher at night, probably because the female is not interrupted as often as during the day by her mate. There might also be an endogenous influence, as in DD lone parental females still show 24-h patterns in the percentage of time spent fanning, with high levels corresponding to what would be nighttime (Reebs and Colgan, 1991). However, due to the short duration of the egg stage, these patterns were measured only over a few days and the periodicity of the rhythm could not be ascertained; therefore, in the absence of non-24-h rhythmicity, the circadian nature of this cycle cannot be strictly demonstrated.

There is better evidence for endogenous circadian mechanisms in parental cichlids in the form of night anticipation. Female convicts retrieve their young into a central pit at the end of the day, just before nightfall, and they can do so even when night arrival is not preceded by a dimming of light levels (Reebs, 1994b). This points to the existence of an endogenous clock that "tells" the fish when the day is about to end.

Light intensity still plays a role however, mainly as a modulator of retrieving intensity (Reebs, 1994b).

Like sticklebacks, cichlids have the sensory equipment necessary to provide the full panoply of parental behaviors at night, though they prefer the day for foraging. At least in convict cichlids, a circadian clock seems to be present, and one of its demonstrated roles is to anticipate night arrival.

## Developmental factors influencing activity patterns

### Ontogeny

It is not uncommon for juveniles and adults to have diametrically opposed activity phases in the field (Emery, 1973a; Hobson and Chess, 1976; Johnson and Müller, 1978; Helfman, 1978, 1981a; Kelso, 1978; Hobson et al., 1981; Helfman et al., 1982; Magnan and FitzGerald, 1984; Reebs et al., 1995). Three explanations have been proposed for this state of affairs. First, juveniles may be more vulnerable to predators, forcing them to be quiet at those times when predators are presumed to be most active; owing to their large size, adults may be more impervious to attacks and could afford to be active concurrently with predators. Second, as a fish grows and its gape develops, prey choice changes, possibly leading to a change in activity phase. Third, there could be competition (or even outright cannibalism) between age classes, and temporal segregation might alleviate this. All of these hypotheses are reasonable, but I am aware of no strong experimental evidence in support of them.

### Breakdown during migration

In rivers, larval drift and juvenile or adult migration usually take place at night (Geen et al., 1966; Bardonnet et al., 1993; Johnston, 1997, and references therein; Robinson et al., 1998; Gadomski and Barfoot, 1998, and references therein; Reichard et al., 2002a; but see Ledgerwood et al., 1991). This does not involve a change in activity phase for nocturnal species (e.g. American eels, *Anguilla rostrata*: Dutil et al., 1989), but some of these nocturnal migrants are otherwise mostly active during the daytime (e.g. lake chub, see case study #3). In young fish, nocturnal drift may be a passive process resulting from the loss of visual orientation at night (Brown and Armstrong, 1985). However, recent evidence in cyprinids supports

the alternative view that drift is an active decision on the part of the fish to travel under the cover of darkness (Reichard et al., 2002b). The most obvious, albeit hard to test, hypothesis to explain the advantage of moving at night is that it reduces the risk of capture by visually-oriented predators. Other factors, harder to identify, may also be involved in some cases, such as the observation by Iguchi and Mizuno (1990) that goby larvae migrate at night in gentle to intermediate gradients, but during the day in steep upper-part watercourses.

Daily patterns may also break down during migration in marine species. Olla and Studholme (1978) observed that captive adult tautog (*Tautoga onitis*) were normally diurnal, but when one group was subjected to simulated fall conditions of photoperiod and temperature, they swam day and night, with a tendency for more movement at night. This probably reflected the natural habit of the species to migrate offshore in the fall. Interestingly, juvenile tautog do not migrate offshore in the fall in the wild, and in the laboratory they did not increase their nocturnal activity when exposed to fall conditions.

Fishes are not the only animals whose activity patterns break down during migration. Many species of birds are typically diurnal but fly day and night, and sometimes at night only, during the spring and fall migration.

### Breakdown during the spawning season

During the spawning season, fishes that normally tend to be strictly diurnal or nocturnal often become active day and night. Helfman (1981a) has reported this for a number of temperate lake species: pumpkinseed sunfish, largemouth bass, bluntnose minnow, yellow perch (*Perca flavenscens*), brown bullhead (*Ictalurus nebulosus*), and rock bass (*Ambloptiles rupestris*). Olla and Studholme (1978) observed it in their tautog as well: the fish were unresponsive and easy to capture at night at all times of the year, except during migration (see above) and during the spawning season, at which times they were always alert. With infra-red equipment, I have witnessed normally diurnal convict cichlids occasionally spawning in the complete darkness of night in the laboratory (the egg batches deposited on the inside of a flower pot were more scattered than in daytime-spawners, but did not comprise more unfertilized eggs; see also Noble and Curtis, 1939). Other examples of activity breakdown during the spawning season can be found in Harden Jones (1956), Sjöberg (1977), Nash (1982), and Baade and Fredrich (1998). Strict inversions of activity phase are less common than continuous activity, but Naruse and Oishi (1996) reported that loach fed nocturnally during the non-breeding season and diurnally at spawning time, and Baras (1995) wrote that the common barbel (*Barbus barbus*) is normally crepuscular but that it spawns diurnally under low temperatures and nocturnally under high temperatures.

### Breakdown during the parental phase

Case study #6 introduced two fish families (the sticklebacks and the cichlids) where species that were active mostly during the day could be seen to fan their eggs day and night, and sometimes even more at night. Albrecht (1969) also witnessed night fanning (and some night spawning) in the sergeant major (*Abudefduf saxatilis*). Emery (1973b) also observed night fanning in the sergeant major, and saw many other species hovering near their nest at night, apparently alert (*Microspathodon chrysurus, Chromis multilineata, Eupomacentrus fuscus, E. leucosticus, E. partitus, E. planifrons*). Hinch and Collins (1991) reported that male smallmouth bass (*Micropterus dolomieui*) actively defend their nest day and night, even though they are inactive at night outside of the reproductive season. Cooke et al. (2002) observed the same in both smallmouth and largemouth bass.

Fanning and guarding eggs 24 h a day makes sense, as the function of this behavior is to provide well-oxygenated water to the eggs, and eggs do not seem to have less of a need for oxygen at night (Reebs et al., 1984). Continuous guarding is also adaptive, as egg predators can be present day and night (Hinch and Collins, 1991; Reebs, 1994a). This being said, two species of anemonefish have been said not to fan their eggs at night, though one at least did so on the night of hatching (Moyer and Bell, 1976) and the other report did not mention how the night observations were made and therefore how intrusive they may have been (Ross, 1978).

## Environmental factors influencing activity patterns

### Effect of seasons

There are many examples of activity patterns changing between summer and winter. Case study #4 presented

the situation for salmon. There, the proximate cause for the phase inversion in activity seems to be low temperature and the ultimate function may be to decrease predation risk in individuals rendered sluggish by this low temperature. In sea bass (case study #5), the proximate factor may be an endogenous circannual clock (see also case study #3 on lake chub) and the ultimate function may be to follow changes in food availability.

Other examples include wild northern pike (Cook and Bergersen, 1988) and dusky farmerfish (*Stegastes nigricans*; Letourneur et al., 1997) going from crepuscular in summer to diurnal in winter, and giant kokopu (*Galaxias argenteus*) going from continuously active in summer to nocturnal in winter (David and Closs, 2001). Juvenile Atlantic cod (*Gadus morhua*) are nocturnal in summer and diurnal in winter; being nocturnal in summer may help avoid cannibalism by adult cods but changes in food sources cannot be excluded as a possible cause for the seasonal switch (Clark and Green, 1990; Grant and Brown, 1998). A number of planktivorous cyprinids feed at night in temperate lakes during the summer, but show empty stomachs day and night under the low temperatures of winter, a possible reflection of reduced energy needs because of low metabolism (Bohl, 1980).

At high latitudes, under natural photoperiod and temperature, some nocturnal species (e.g. several freshwater sculpins, burbot) become diurnal during the very short days of winter; in contrast, populations from temperate latitudes remained nocturnal throughout the year (Andreasson, 1973; Müller, 1978a; Westin and Aneer, 1987). There has been no explanation for this phenomenon which, it must be said, has been studied in captive individuals only. The diel activity patterns of free-living individuals at high latitudes are poorly documented.

Most published papers resort to the usual candidates of predation risk and food availability as ultimate causes of seasonal activity reversal, but strong experimental evidence is lacking. As to the proximate causes, in addition to low temperatures and endogenous circannual rhythms, there is the possibility that fish may be tracking food sources directly, but again there is little supporting evidence of this in the literature, probably because of the relative scarcity of winter field work.

## Effect of light intensity

Even in animals with solid circadian systems (such as the laboratory rodents commonly used in chronobiology studies), light can have strong masking effects, markedly increasing (positive masking) or decreasing (negative masking) activity levels, irrespective of what the internal clock might dictate at that particular daily time (Mrosovsky, 1999). There is no reason to believe that the same could not apply to fishes and contribute to variability in activity patterns. Eriksson (1978a) observed that 4 out of 6 captive brown bullheads that swam only at night became diurnal when daylight intensity was lowered to 1 lux (however, all of the six bullheads fed mostly around dawn and dusk, irrespective of daylight intensity). Walleye (*Stizostedion vitreum*) are normally crepuscular (Kelso, 1978; Prophet et al., 1989), but they can also feed during the daytime when at great depth or in turbid areas where light intensity remains low all day long (Ryder, 1977). Nocturnal sculpins can become diurnal when the day is short (i.e., in winter), but only if the light intensity is weak (Andreasson, 1969; Müller, 1978a). Løkkeborg and Fernö (1999) noted that wild cod were active and responsive to food odors day and night, but that they moved more during the day, possibly because of a facilitating effect of light on prey detection (see also Løkkeborg, 1998). Müller (1978b) reported that the length of daily activity in single or grouped whitefish (*Coregonus lavaretus*) matched exactly the varying length of the photoperiod throughout the year. Müller (1978a) also observed this relationship in the European minnow (*Phoxinus phoxinus*), as did Eriksson (1978b) in the Eurasian perch (*Perca fluviatilis*). Beitinger (1975) reported that activity in captive bluegill sunfish matched the times when the lights were on, even under LD 6:6 h. Jennings et al. (1998) observed that diurnal reef fishes reacted to the decreasing light levels of a total solar eclipse by seeking shelter like they normally do at dusk. The exact timing of twilight migration is also influenced by light intensity (McFarland et al., 1979; Helfman, 1981a; Hobson et al., 1981).

Relatively small changes in light intensity can affect foraging success (Harden Jones, 1956; Mills et al., 1986; Fraser and Metcalfe, 1997; Metcalfe et al., 1997; see Grecay and Targett, 1996, for more examples and also exceptions), predation risk (Cerri, 1983; Howick and O'Brien, 1983), refuge use (Helfman, 1981b; Contor and Griffith, 1995; McCartt et al., 1997), courtship (Long and Rosenqvist, 1998),

territorial defense (Valdimarsson and Metcalfe, 2001), parental care (Reebs, 1994b), and shoaling (Harden Jones, 1956; Sogard and Olla, 1996; Vilizzi and Copp, 2001). Depending on species-specific requirements and the synergy between all of those influences, diurnal fish could conceivably be prompted to become more crepuscular, or vice-versa. Also, when the full moon is out, visual feeders could become more active nocturnally (e.g. Hobson, 1965; Elston and Bachen, 1976; Allen and Wootton, 1984). Diurnal feeders could also extend activity into the night around artificial sources of illumination (Hobson et al., 1981).

### Effect of temperature

Few studies have looked directly at the relationship between temperature and activity rhythms. Temperature is usually included as a variable in the study of seasonal changes (see case studies #4 and 5). Outside of such research, there is the work of Greenwood and Metcalfe (1998) who showed that during the daytime single European minnows were more often found outside of a refuge at warmer temperatures, whereas refuge use at night was consistently low and unaffected by temperature. There was no mention, however, of whether the fish were truly active while outside of their refuge and therefore these results are difficult to interpret within the context of activity rhythms. Similarly, diel movements in some cases may be interpreted as a mechanism to remain at fairly constant temperatures day and night (e.g. Gibson et al., 1998), but again this does not concern activity/inactivity cycles.

### Effect of shoal size

Case study #1 on goldfish introduced the notion that groups may express "better" (more stable, less variable) circadian rhythmicity in constant conditions than single fish (Kavaliers, 1981a). Kavaliers (1980c) reported a similar phenomenon in white sucker (*Catostomus commersoni*): groups of 25 fish displayed free-running rhythms in DD that were longer-lasting and less variable than those of single individuals. In the mummichog (*Fundulus heteroclitus*, Kavaliers, 1980b), groups of 1 and 25 had similar rhythms in both DD and LL, while groups of 5 showed more variability (as opposed to the groups of 25, the groups of 5 displayed no cohesive shoaling behavior; rather each fish dispersed through the tank and acted as an individual). Groups of rainbow trout and European catfish, *Silurus glanis*, have been observed to synchronize more quickly to photoperiod and restricted feeding schedules than single fish (Bolliet et al., 2001).

In the laboratory under LD, groups of 25 white suckers were mostly light-active while individuals were mostly night-active (Kavaliers, 1980c). In an outdoor earthen pond, sea bass have also been reported to be diurnal in groups of 60 but nocturnal when single (Anras et al., 1997).

Social facilitation of movement and increased chances of detection by the recording system may explain why activity rhythms are better expressed in larger groups. Nocturnalism in single individuals as opposed to diurnalism in groups may stem from an increased feeling of vulnerability in single fish, leading to avoidance of bright light and a corresponding shift towards night-living. These explanations remain to be tested.

### Effect of predation risk

Avoidance of predators is often postulated to explain why a certain fish is diurnal, nocturnal, or crepuscular (e.g. Wurtsbaugh and Li, 1985; Cochran, 1986; Naud and Magnan, 1988; Culp, 1989) or why the activity phase sometimes changes (e.g. Bowen and Allanson, 1982; Clark and Green, 1990; Grant and Brown, 1998; case studies #2, 3 and 4; discussion above on the effects of ontogeny, migration, shoal size, temperature and season).

There are several problems with this: (1) as noted already, this influence of predation risk is often invoked post hoc, and few experimental studies have been attempted with the specific objective of testing it; (2) it may prove difficult in nature to separate the effects of predator avoidance and food availability (see Bowen and Allanson, 1982; Clark and Green, 1990); (3) invoking predation risk as an explanation for activity shifts in prey tends to overlook the possibility that predators could adjust their own activity patterns to follow that of their prey (see Sjöberg, 1985, 1989); and (4) there may be so many different piscivorous animals in nature that shifting the timing of activity may not guarantee safety for a prey: day and night there might be a predator of one type or another present in the environment (see Reebs, 1999). This being said, nocturnalism should at least greatly reduce the risk of getting caught by visually-oriented predators. In systems where such predators are the main threat, it seems reasonable to assume that a switch to nocturnalism by the prey should confer a degree of protection.

One recent experimental study that looked at the effect of predator cues on the diel activity of prey is that of Pettersson et al. (2001). These authors measured the diel activity of crucian carp (*Carassius carassius*) exposed to water coming from a tank where a northern pike was housed. Unexposed controls were nocturnal, but the exposed carp exhibited low levels of activity day and night. These results suggest negative masking of normal activity by the presence of a predator rather than a fundamental shift in the diel pattern. A few other studies, this time in the field, have failed to find significant changes in diel activity patterns of prey in the presence or absence of a predator (Tonn and Paszkowski, 1987; MacKenzie and Greenberg, 1998).

The lack of experimental evidence for predator-induced shifts in prey activity patterns is in sharp contrast to the great number of studies documenting shifts in habitat use when predator presence is manipulated (e.g. Werner et al., 1983; Schlosser, 1988; Gotceitas, 1990; He and Kitchell, 1990; Tonn et al., 1992; Jacobsen and Berg, 1998). Predator presence seems to lead to spatial adaptations rather than temporal ones on the part of the prey (Smith, 1997).

The general influence of predation risk on fish behavior may pose a problem for the interpretation of activity rhythms displayed in laboratory conditions where the fish may feel particularly vulnerable because of high light levels or lack of cover. In Harden Jones (1956), European minnows kept in rather small groups (2–4) within a glass aquarium on a window sill moved less during the day than at night when cover was made available (presumably they cowered in the refuge during the day) but they moved more during the day than at night when there was no cover. It is not clear whether the increased diurnal movement was normal swimming and food-searching activity, or if it came from the exposed fish being spooked by outside stimuli. Notwithstanding this uncertainty, these results suggest a possible interaction between shoaling, cover availability, and timing of activity which is worth pursuing in future studies.

On the whole, the effect of predation risk on activity patterns is still murky. A case can be made that nocturnalism is promoted by predation risk, based on reasonable inference rather than experimental evidence. However, many species seem to decrease activity at all times or to move elsewhere in response to predator presence rather than fundamentally alter the phasing of their activity.

## Effect of food availability

Just like predation risk, food availability and foraging ability can serve as post-hoc explanations for why certain fishes display certain activity phases. For example, based on his comparison of two gobies, one planktivorous and diurnal, the other benthivorous and nocturnal, crepuscular or aphasic, Thetmeyer (1997) suggested that benthivorous species may be more flexible than zooplankton feeders because they are less dependent on light for detecting and catching their prey. Certainly, many species appear to be able to feed both visually and non-visually (e.g. case studies #1 and 2; 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 (e.g. case study #2; Ebeling and Bray, 1976; Johnson and Dropkin, 1995; Pedersen, 2000). And in contrast to predation risk, there is good experimental evidence that activity rhythms, or at least food anticipatory activity, can be influenced by the timing of food availability (e.g. case studies #1 and 2; references above on food-anticipatory activity). Even temporal differences in food quality rather than quantity can influence activity patterns (Zoufal and Taborsky, 1991).

## Effect of intraspecific competition

Kadri et al. (1997) invoked competitive interactions to explain why differently-sized Atlantic salmon fed at different daily times in an indoor seawater tank. Randolph and Clemens (1976) reported that, in culture ponds, the largest channel catfish (*Ictalurus punctatus*) monopolized the demand feeders in late afternoon and early night; the smaller fish had to wait until the rest of the night and the early morning to feed. A similar temporal segregation was observed by Alanärä et al. (2001) in captive brown trout (*Salmo trutta*), with the improvement that individual dominance rank could be determined beforehand (during competition for limited food). Alanärä and Brännäs (1997) also resorted to competition as an explanation for the nocturnal-diurnal dualism observed within their groups of Arctic char and rainbow trout; however, a further experiment where dominants were removed failed to provide support for this idea (that is, the subordinates did not change their activity phase after the dominants were forced to vacate their temporal niche: Brännäs and Alanärä, 1997). Chen et al. (2002) placed diurnally feeding rainbow trout together and observed that some nocturnal feeding suddenly appeared, but this nocturnal feeding did not persist

over many days and the authors concluded that temporal segregation between dominants and subordinates was flexible.

The influence of competition on activity patterns in the field remains to be determined. Competition has been invoked to explain temporal differences between juvenile and adult activity (see Ontogeny above) but without corroborating evidence so far.

## Relationship with sleep patterns

Sleep is harder to define operationally in fishes than in mammals or birds. Fishes do not have eyelids, and therefore eye closure cannot be used as a criterion for sleep. Fishes also lack the brain cortex from which the brainwave patterns characteristic of sleep are usually detected. But we can follow Meddis' (1975) suggestion of using purely behavioral criteria to define sleep. Most people would agree that a fish is 'sleeping' when it (1) remains quiet for a long portion of the 24-h day, (2) spends that time of day in a typical rest posture and in a typical shelter, and (3) is more difficult to arouse at that time.

Some fishes seem to swim 24 h a day and to remain alert at all times, and therefore cannot be said to sleep (for a review, see Kavanau, 1998). But Weber (1961, cited in Tauber, 1974) observed approximately 200 different species in European public aquaria, and many fulfilled all three of the above behavioral criteria. Many others fulfilled the criteria at least partially. Tauber et al. (1969) and Tauber (1974) reported that blueheads (*Thalassoma bifasciatum*), Spanish hogfish (*Bodianus rufus*), and many species of wrasses (family Labridae) could be lifted by hand to the surface at night before they finally 'woke up' and escaped. Clark (1973) reported the same for requiem sharks. While diving, Ryder (1977) was able to sneak up on resting walleyes and grab them by the tail. Zhdanova et al. (2001) described a sleep-like state in zebrafish larvae, *Danio rerio*. Sleep has also been reported for Mozambique mouthbrooders (*Tilapia mossambica*; Shapiro and Hepburn, 1976; Shapiro et al., 1981), tench (*Tinca tinca*; Peyrethon and Dusan-Peyrethon, 1967) and brown bullheads (*Ictalurus nebulosus*; Titkov, 1976; Karmanova et al., 1981; Karmanova and Belich, 1983). Both Weber (1961) and Tauber (1974) indicated that behavioral sleep seems to be more common in marine than freshwater species.

The most stable and precise free-running circadian rhythms ever reported in fishes came from species that sleep well. For example, it takes solid rhythms to establish a phase-response curve to light (a phase-response curve plots the size and direction of phase-shifts in response to light pulses administered at different times of the circadian day). I am aware of only two phase-response curves obtained with fish, the first one (Ooka-Souda and Kabasawa, 1995) coming from the inshore hagfish (*Eptatretus burgeri*), for which Ooka-Souda et al. (1985) reported complete inactivity during the day coupled with what seems to be sleep postures (see also Kabasawa and Ooka-Souda, 1989, for more examples of steady and long-lasting rhythms in this species). The second phase-response curve (Gerkema et al., 2000) came from the yellow wrasse (*Halichoeres chrysus*), a fish that sleeps buried in sand.

Nelson and Johnson (1970) observed that a sound-sleeping nocturnal shark was rhythmic in both LL and DD, but that another species, also nocturnal but not a sound sleeper, was arrhythmic in constant conditions. This suggests a link between the presence of sleep and the strength and self-sustaining ability of the circadian system. There is little doubt that circadian clocks are an older evolutionary development than sleep (circadian rhythms are present in unicellular organisms), but once sleep appeared on the scene, with its concurrent decrease in sensitivity to both food and predators, there probably was a selective pressure for the circadian system to become (or to remain) strong and precise, as it would be imperative that sleep be limited to the right time of day. Unfortunately, with the exception of Nelson and Johnson (1970) and to a certain extent Zhdanova et al. (2001), I am aware of no studies that have examined sleep characteristics and circadian rhythms concurrently in the same species. The following fishes have yielded fairly nice circadian rhythms in the past and could be good candidates for sleep studies: various wrasses (Nishi, 1989, 1990, 1991), the burbot (Kavaliers, 1980a), the Arctic lamprey (*Lethenteron camtschaticum*, ex-*Lampetra japonica*, Morita et al., 1992), and various gymnotids (Schwassmann, 1971, 1978; Stopa and Hoshino, 1999).

To my knowledge, species that sleep very soundly are strictly nocturnal or strictly diurnal, and do not show plasticity in that respect (i.e., there has been no reported cases of intra-individual switches between diurnalism and nocturnalism, or inter-individual differences in activity phases for strong

sleepers; however, note that in the previous paragraph I mention the burbot as a good candidate for sound sleeping, and Müller [1978a] described a seasonal phase inversion in that species: nocturnal in spring and fall, diurnal in winter, aphasic in midsummer). Sleep can serve to immobilize an animal and help it conserve energy (Meddis, 1975) or process information (Kavanau, 1998, 2001) during a time of day for which it is ill-equipped either sensorily, physiologically or ecologically. If this is true, then it makes sense that fishes which show good signs of sleep are also the ones whose activity is restricted to only one part of the day. (Along the same line of reasoning, fishes that live in constant environments, such as permanently dark caves, should show neither sleep nor circadian rhythmicity, and this seems to be the case, at least for circadian rhythmicity: Erckens and Martin, 1982; Parzefall, 1993; but see Zafar and Morgan (1992) for a cave fish example of circadian rhythmicity sustained by periodic food delivery). It should be noted however that while we could expect soundly sleeping fish to be strictly diurnal of nocturnal, the reverse (strictly diurnal or nocturnal species being sound sleepers) is not necessarily true, as other forms of behavior, such as quiet schooling, could conceivably fulfill some of the same ecological or physiological functions as sleep (Kavanau, 1998).

## Conclusion

It is probably naive to attempt generalizations with fishes, given their great number of species and diversity. I nevertheless suggest that we can establish a crude dichotomy between marine, sound sleeping, strongly circadian, and less plastic (in terms of activity phase) species on the one hand, and freshwater, quietly resting, sloppily circadian, and plastic species on the other hand. Although harder to quantify, the parameter of sensory specialization can be superposed on this dichotomy, with the freshwater species being less specialized.

Many fish species, most of them marine, are relatively sound sleepers. Though the relationship between sleeping and sensory specialization has not been formally studied, it is tempting to hypothesize that piscine sleep has evolved in species that became sensorily specialized for either day-living or night-living (such specialization may be more likely in a more stable environment like the sea). The sensory specialization may have increased the need for the

storing into memory of detailed sensory inputs and of the relationship between the perceived events and their consequences. Sleep could fulfill this function (Kavanau, 2001). The sensory specialization also meant that the animals were at a disadvantage during the other half of the 24-h cycle, and sleep could be useful in forcing the animal into immobility so as to decrease the risk of detection by predators, while saving energy at the same time (Meddis, 1975). But by reducing awareness, sleep decreases the chance of evading a predator, and therefore sleep has to be performed in a protected shelter (see examples in Reebs, 1992), or in a quiet protective shoal. Foraging cannot be done in such a situation, and it is therefore important that sleep be performed at that time of the day during which foraging would not be profitable anyway because of the sensory specialization. Also, the timing of sleep should not be under the direct influence of light because the movement of the sun is not the only cause of darkness (imagine a diurnal fish that would automatically fall asleep whenever it is dark; venturing underneath a rock or big log where it is always dark would make it sleep permanently). These considerations about the benefits of sleep, and the importance of its proper timing, may explain the development in sound sleepers of a more precise and robust circadian system to maintain the integrity of the sleep period. Only at particular moments of hormonal upheaval (migration, spawning, parental phase) could the dictates of this clock, with regards to the timing and occurrence of sleep, be overruled in the individual fish.

On the other hand, in the relatively unstable freshwater environment, sensory specialists may not be as common as sensory generalists. Sleep may not hold as many benefits for these generalists. Quiet but alert resting, whenever the circumstances allow (full stomach, reduced chances of finding food at the moment, no apparent predators in the vicinity), may suffice. In the absence of sleep and of a time of day during which the fish is helpless, the need for a precise circadian system is not felt. This could explain why circadian rhythms are so unstable and why sound sleepers are less frequently found among freshwater species. On the other hand, circadian timekeeping, even a crude one, could still be useful in other ways (night anticipation, day anticipation, food anticipation, sun compass orientation, time-place learning) and therefore it is not absent altogether. Still, immutably linking activity to a particular phase of the light-dark cycle would not be one of the functions of

this circadian clock. The fish could learn to associate certain daily events with a particular phase of their circadian oscillator (Gallistel, 1990) and plan their daily routine accordingly, but this association would not necessarily be permanent. If the circumstances change, the fish could make new associations and modify their activity pattern, even switching from day-living to night-living if needs be, because their sensory generalism allows them to. In my view, foraging success (modulated by food availability, competition, ontogenetic changes, and ease of food detection depending on the lighting conditions) is the strongest candidate to explain why freshwater fishes are active when they are, and why they sometimes change their activity patterns. Predation risk (modulated by temperature, cover availability, body size, and shoal size) is another candidate, albeit one on which much work remains to be done.

## Acknowledgements

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