

Endogenous activity rhythms in tomcod (*Microgadus tomcod*) post-yolk-sac larvae¹

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Received April 17, 1990

MASSICOTTE, B., and DODSON, J. J. 1991. Endogenous activity rhythms in tomcod (*Microgadus tomcod*) post-yolk-sac larvae. *Can. J. Zool.* **69**: 1010–1016.

Post-yolk-sac tomcod (*Microgadus tomcod*) larvae were caught in a spawning river. They were held in the laboratory under three different environmental conditions: (i) constant conditions; (ii) exposure to a simulated tidal cycle; and (iii) exposure to simulated tidal and diel cycles. Swimming activity determinations made under constant conditions revealed significant endogenous rhythms in each group. Chronobiological flexibility affected by simulation of the basic cycles of the estuarine habit was demonstrated. Groups of larvae exposed to simulated tidal signals demonstrated modified rhythmic patterns relative to control groups held under constant conditions. Rhythms of groups exposed to both tidal and diel light signals included a low-frequency component in the 20-h region. Examination of the metabolic effects of feeding on endogenous activity patterns revealed lower activity levels when larvae were deprived of food. However, control groups exhibited the same period length whether fed or unfed, and entrained groups did not show consistent trends in period change related to feeding. This is not consistent with the hypothesis that metabolic conflict between digestion and aerobic swimming should modify the period length of endogenous activity rhythms.

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Des larves du Poulamon atlantique (*Microgadus tomcod*) ont été capturées dans une rivière de fraye. Ces larves ont été gardées au laboratoire sous trois conditions environnementales: (i) conditions constantes; (ii) exposées à un cycle tidal simulé; et (iii) exposées à des cycles tidal et journalier simulés. L'observation de l'activité nataoire a révélé l'existence de rythmes endogènes pour chaque groupe. L'exposition de ces larves à des simulations de cycles de leur habitat estuarien a mis en lumière une certaine plasticité chronobiologique. Les groupes de larves exposées à des cycles tidaux simulés ont exhibé des patrons d'activité modifiés comparativement à ceux des groupes maintenus sous conditions constantes. Les rythmes des groupes exposés à la fois à des signaux tidaux et journaliers incluaient une composante de basse fréquence, d'environ 20 h. L'activité des larves était moins intense lorsque celles-ci étaient privées de nourriture durant la période d'observation. Cependant, les rythmes endogènes des larves des groupes témoins, aussi bien à jeun que nourries, avaient la même périodicité. De plus, aucune tendance définie de changement de périodicité ne se dégage de l'observation des groupes soumis à l'entraînement. Ce résultat n'appuie pas l'hypothèse selon laquelle un conflit métabolique entre la digestion et la locomotion aérobie doit modifier la périodicité des rythmes endogènes d'activité.

Introduction

In many fishes, various behavioral rhythms have been observed in the field and in the laboratory (Rusak 1981). However, few laboratory observations have been made under constant conditions. This approach is necessary for demonstrating an endogenous component in a rhythm. Experiments by Gibson (reviewed in Gibson 1984) demonstrated circadian and (or) circatidal locomotory rhythms in adult and juvenile fishes of the littoral zone. Other recent experiments have demonstrated endogenous activity rhythms in adult goldfish (Spieler and Noeske 1984) and killifish (*Fundulus heteroclitus*) (Kavaliers 1980a). Juvenile stages of various species also exhibited endogenous activity rhythms. These include burbot, *Lota lota* (Kavaliers 1980b), white sucker, *Catostomus commersoni* (Kavaliers 1980c), and pink salmon, *Oncorhynchus gorbuscha* (Godin 1981). In other studies, however, juvenile fishes failed to demonstrate activity rhythms under constant conditions, which suggests that the rhythms observed under cyclical conditions were mostly exogenous (Varanelli and McCleave 1974; Katz 1978).

Few studies have demonstrated endogenous behavioral rhythms in the early life stages of fishes. Whippelhauser and McCleave (1988) performed experiments with migrating glass eels (*Anguilla rostrata*) which are observed in the field to exhibit tidal vertical migrations (McCleave and Kleckner

1982). This locomotory pattern, known as selective tidal stream transport, allows glass eels to migrate upstream in fresh water by staying on the bottom during ebbs and occupying nonbottom waters during floods. The results of experiments under constant conditions suggest that this rhythm is endogenous and can be entrained by exposing the fish to a horizontal current cycle with a 12-h periodicity. This work also demonstrates the ecological significance of endogenous rhythmicity in the early life history of fishes.

Tomcod (*Microgadus tomcod*) spawn in January in tributaries of the St. Lawrence River (Léveillé 1985). Hatching occurs in early spring and the larvae then drift downstream to the St. Lawrence estuary, where they remain for at least 3 months (Lapris and Dodson 1990). The estuarine retention area is associated with a maximum turbidity zone and is affected by strong and complex tidal features (D'Anglejan and Smith 1973). Such a cyclical environment (e.g., diel and tidal cycles) may be expected to favor the evolution of rhythmic behavior, possibly under the control of an internal clock. Thus, the primary objective of this study was to investigate the possible existence of endogenous activity rhythms in post-yolk-sac larvae of the tomcod. The second objective was to test the hypothesis that exposure to simulated diel or tidal cycles modifies the activity pattern.

The third objective was to investigate the effect of feeding on the endogenous activity pattern. Previous chronobiological studies have shown that food can act as a Zeitgeber in fishes (Spieler and Noeske 1984) and mammals (Moore-Ede et al. 1982). Also, Reid (1988) demonstrated that feeding may affect

¹Contribution to the program of the Groupe interuniversitaire de recherches océanographiques du Québec (GIROQ).

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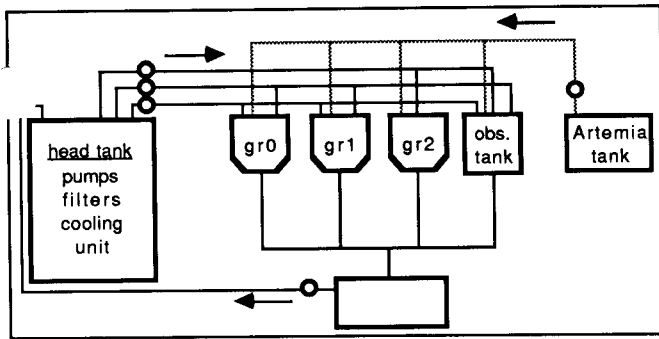


FIG. 1 Organization and circulation of rearing and observation tanks. Group 0 was kept under constant conditions; group 1 was exposed to current cycle; group 2 was exposed to current and diel light cycles. Arrows indicate the direction of recirculating water flow and *Artemia* pumping.

the entrainment mechanism itself in the isopod *Eurydice pulchra*: individuals fed prior to entrainment exhibited circatidal rhythms characterized by a diurnal modulation. The diurnal modulation was absent if the isopods were unfed, or fed after entrainment. However, the influence of feeding on periodicity due to energetic constraints is not documented. In fishes, power consumption capacity exceeds respiratory capacity, resulting in metabolic conflict between locomotion and "digestion" (including mastication, digestion, and assimilation) (Priede 1985). Locomotion should be reduced during digestion, to reduce the relatively high cost associated with anaerobic pathways. The power demand during digestion, generally evaluated in fishes by measuring respiration rate, is then referred to as "apparent specific dynamic action." Reduced or absent aerobic locomotory power during digestion has been observed in the blenny *Blennius pholis* (Vahl and Davenport 1979) and juvenile cod *Gadus morhua* (Soofiani and Priede 1985). We proposed that such metabolic conflict may also affect the locomotory pattern of tomcod larvae. We hypothesized that feeding larvae may exhibit a new locomotory pattern resulting from a metabolically imposed feeding-swimming cycle dominating the basic endogenous rhythm of unfed larvae.

Materials and methods

The demonstration of endogenous rhythmicity in fish larvae requires some modification of traditional chronobiological procedures. Exposure to specific conditions must be short, since rapid changes in larval morphology and behavior occur during the early ontogeny of fishes (Balon 1985). Observations under constant conditions may not be pursued over long periods for the same reason. In addition, post-yolk-sac larvae cannot be kept alive during many days of food deprivation. In the present experiment, different experimental manipulations were conducted simultaneously because of rapid growth, and because the larvae were available only during short periods of the annual cycle. Observing these small and often translucent organisms required the use of particular techniques. Finally, observations were made on groups of larvae because their fragility resulted in too great a probability of death of individuals, resulting in loss of observation time and possible loss of annual observation periods.

Collection and holding

Tomcod larvae were collected in brief plankton-net (1.0 m diameter) tows on April 8, 1988, from the St. Anne River, the principal spawning site of tomcod in the St. Lawrence River basin, located 100 km upstream from Québec City. All larvae were at the yolk-sac stage. As yolk resorption was completed 3 days after

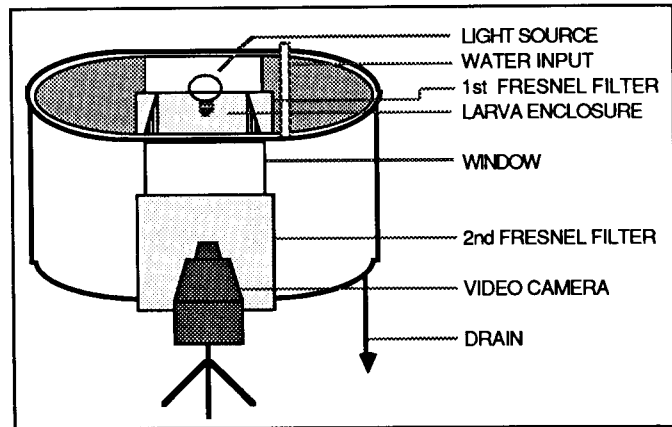


FIG. 2. Observation tank. Larvae were confined in the larva enclosure. The observation sessions were videotaped using the shadow videography technique, in which the use of two Fresnel filters caused the larvae to appear as silhouettes on a clear background.

capture, it was assumed that the larvae were hatched approximately 2 days before capture, as yolk-sac depletion occurs within 5 days at 5°C.

Approximately 720 yolk-sac larvae were transported to the Aquarium du Québec, Québec City, where they were kept in three 35-L circular holding tanks in fresh water and under dim light. Each tank was thermally isolated and supplied with recirculating filtered and dechlorinated municipal water (Fig. 1). At least one-quarter of the total water volume was replaced each day. Toxic nitrogen compounds were determined every 2nd day and were generally not detectable. Salinity was below 1 g/kg.

A peristaltic pump allowed continual input of *Artemia* nauplii into each rearing tank. A current cycle was generated in two of the tanks by two pumps alternately switched on and off every 6 h, yielding a 6-h current pulse in each direction (12-h cycle). Each pump was controlled by a time switch and was connected to one of two 1/2 in. diameter (1 in. = 25.4 mm) pierced chlorinated polyvinyl chloride pipes fixed vertically in the tanks. One pipe was oriented so as to generate a clockwise current, the other to generate a counterclockwise current. Pumping water alternately through the two pipes thus generated a reversing horizontal circular current in the tank.

Rearing conditions

Three experimental conditions were applied: group 0 was held under constant conditions in dim light; group 1 was held in a reversing current cycle of a 12-h periodicity and constant dim light; group 2 was exposed to the same current cycle and the natural photoperiod (13.5 h L : 10.5 h D). Exposure of groups 1 and 2 to cyclic signals began when feeding was established 3 days after capture. Durations of rearing periods are given in Table 1. All groups were fed continuously throughout the rearing period. Water temperature was held at $5 \pm 1^\circ\text{C}$.

Observation conditions

The observation tank (Fig. 2) was designed to allow use of the shadow cinematography technique (Arnold and Nuttall-Smith 1974), which we used with a video system. In this technique the object is backlit so that its contour is silhouetted on a clear background. One Fresnel lens was placed on each side of the larva enclosure, i.e., one adjacent to the front window of the tank and the other in the middle of the tank in a Plexiglas box. The tungsten light source was located behind the tank so that its filament was at the focal distance of the first lens (23 cm). The camera was located at the focal distance of the second lens. Everything between the Fresnel lenses was in focus, as the first renders the light rays horizontal and the second converges them on the camera retina. This technique was used because of its efficiency in revealing small transparent organisms at very low light levels. The dimensions of the tank were $57 \times 38 \times 28$ cm (width \times

TABLE 1. Description of the experimental groups used for the study of the effects of food and rearing conditions on endogenous activity rhythms in post yolk sac larvae of tomcod

Beginning of observation session		Group	Rearing conditions	No. of days	Observation condition
Date	Time				
April 20	15:30	U2	Current cycle Light cycle	9 10	Constant conditions, no food
April 22	17:00	F2	Current cycle Light cycle	11 12	Constant conditions, food
April 24	19:15	U1	Current cycle	13	Constant conditions, no food
April 27	08:30	F1	Current cycle	15	Constant conditions, food
April 29	10:30	U0	Constant conditions	20	Constant conditions, no food
May 1	12:30	F0	Constant conditions	22	Constant conditions, food

TABLE 2. Mean number of bursts/5 min, coefficient of variation of activity series, normality of activity data, and stationarity order of detrended activity series

Group	Mean activity (bursts/5 min)	Coefficient of variation (%)	Normality ($p < 0.05$)	Stationarity order ($p < 0.05$)
U0	256	16	Y	1
F0	401	14	Y	1 and 2
U1	261	25	Y	1 and 2
F1	322	13	Y	1
U2	149	20	N	1 and 2
F2	236	16	Y	1

NOTE: Y, yes; N, no; 1, stationarity of the mean; 2, stationarity of the variance.

depth \times height) and those of the larva enclosure $20 \times 16 \times 25$ cm. A strongly underrun 10-W red light bulb was used as the light source for the video camera, which had an extended sensitivity for low intensities and red light.

The observation tank was connected to the water line that fed the rearing tanks so that the water temperature ($5 \pm 1^\circ\text{C}$) was the same in all tanks. The only light striking the observation tank was from the light source used for video taping. For each observation session, 50 larvae of a given group were transferred from their rearing tank to the larva enclosure of the observation tank. Each session was integrally videotaped using a time-lapse video recorder (1 frame/1.2 s). All observation sessions were performed under constant conditions. Two groups of 50 larvae from each of the three rearing conditions were videotaped for 48 h. Preliminary observations revealed that longer observation periods were not suitable, as about 50% of the individuals died between the 2nd and 3rd days under constant conditions and food deprivation. One of the two groups from each of the rearing conditions was observed without food. The second group was observed with food continually delivered to the observation tank (Table 1).

For observation sessions conducted in the presence of food, an output tube of the peristaltic pump used for the rearing tanks was connected to the observation tank, yielding a continual flow of live *Artemia* nauplii. The rate of *Artemia* input exceeded the predation rate, causing the prey to accumulate gradually in the tank. Six hours before such an observation session, *Artemia* input to the appropriate rearing tank was stopped and prey already present were siphoned out of the tank. The 6-h starvation period was intended to synchronize the larvae in the case of an activity rhythm in which food was involved. Although each larva may have acted according to a rhythmic pattern, it is possible that the resulting pattern involving all 50 individuals

would have been arrhythmic because of variance in the phase.

After each observation session, 25 larvae were measured live (to the nearest millimetre), using a graduated pipette. In experiments with food, all living larvae were visually inspected at the end of the session to determine the proportion of larvae without prey in the digestive tract. This operation was quite easy to perform on living larvae because of the transparency of the tissues and the bright orange color of *Artemia* nauplii.

Analysis

Locomotor activity was quantified by measuring the rate of burst swimming which was the principal locomotory mode of the larvae. Video tapes were viewed using the frame by frame mode and the number of "burst events" (larvae exhibiting burst swimming) was counted for the first 5 min of each half-hour of recording. Elimination of trend for achievement of first- and second-order stationarity was done using polynomial regression models. Mean stationarity was achieved for every series but variance stationarity could not be reached in three cases out of six (Table 2).

Autocorrelation (SAS Institute Inc. 1984, procedure ARIMA) was performed to test the significance of rhythmicity (Dowse and Ringo 1989). The periodicity was analysed with spectral analysis, using the maximum entropy method (MESA) described by Dowse and Ringo (1989). Spectral analysis is a powerful method for analysing serial data. The graphical presentation of the computations, or spectrum, plots the relative contribution of oscillations of different frequencies to the total series, expressed as spectral density. These values represent the proportion of the total variance of the series introduced by the corresponding periodicities (Legendre and Legendre 1984). The traditional method of spectral analysis uses the Fourier transformation of the autocorrelation (or autocovariance) for calculation of the spectrum. The MESA method is more appropriate when the series to be analysed is short and noisy (Legendre and Legendre 1984; Dowse and Ringo 1989) and in the presence of irregular cycles. This method appeared to be appropriate, given the short data series dictated by the use of fish larvae as subjects. Wippelhauser and McCleave (1988) used the MESA method in chronobiological experiments on juvenile eels.

Results

Length and mortality of larvae

For all groups, the lengths were similar (11.0 mm total length). Larvae belonging to a given group were of the same size for experiments performed with or without food (Table 3). We thus assumed that swimming abilities were the same for all groups of larvae. The total mortality during the 48-h observation sessions never exceeded 12% and was similar for fed and unfed groups of larvae (Table 3).

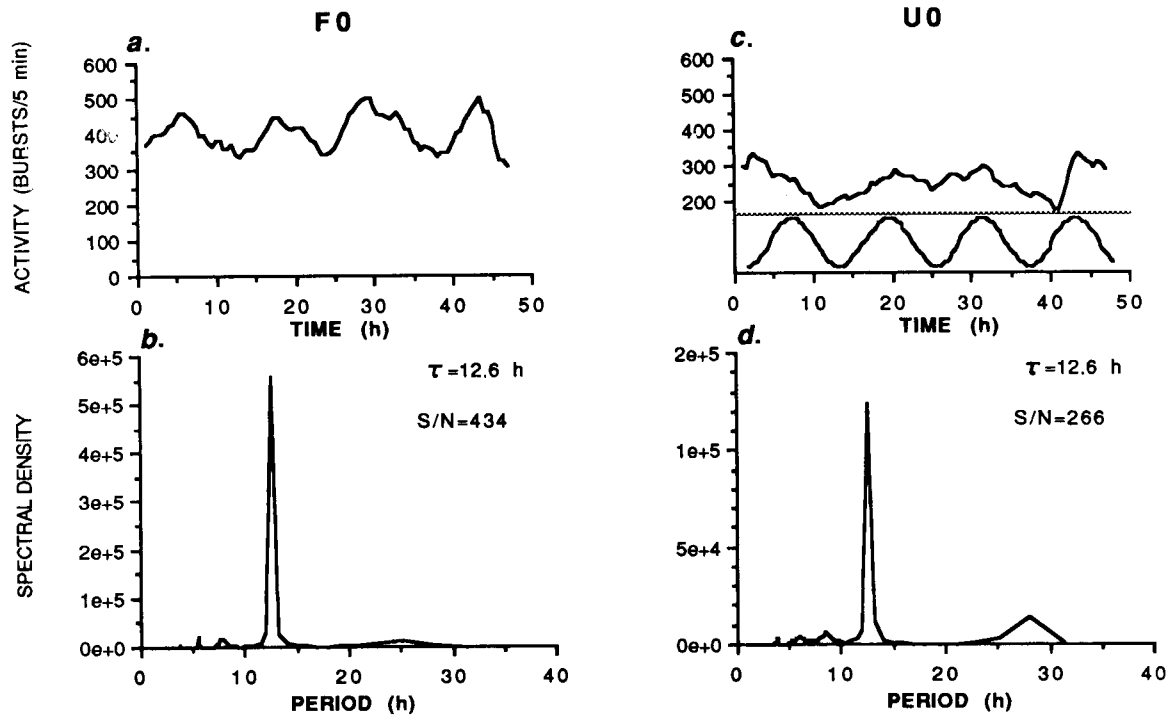


FIG. 3. Series (a, c) and spectra (b, d) for groups F0 and U0, respectively. These groups were kept and observed under constant conditions (F, fed during the observation session; U, unfed during the observation session). The series (a, c) of this and the following figures were smoothed with a 5-point moving average. τ , period length; S/N, signal to noise ratio. A simulation of series F0 is represented in c to facilitate comparison of the phase. This convention is repeated in subsequent figures.

TABLE 3. Length (mean \pm SD), mortality, and number of fed larvae at the end of the observation sessions

Group	Length (mm)	Number dead	With food	
			Number	%
U0	11.0 \pm 0.8	6	—	—
F0	11.2 \pm 0.9	6	42/44	95
U1	11.2 \pm 0.7	1	—	—
F1	11.1 \pm 0.8	3	43/47	91
U2	10.6 \pm 0.8	4	—	—
F2	11.0 \pm 0.8	2	43/48	90

NOTE: U, unfed during observation session; F, fed during observation session; group 0, reared under constant conditions; group 1, exposed to current cycle; group 2, exposed to current and light cycles.

Feeding

Larvae fed well during observations with food, as 90% or more of living individuals had food in the gut at the end of the sessions (Table 3). This high feeding incidence was independent of time and corroborated the observation of continuous feeding of larvae in the rearing tanks.

Activity level

Mean activity values of each group are presented in Table 2 and varied (Kruskal-Wallis, $p < 0.05$) according to the following pattern (from the lowest to the highest mean value):

$$U2 < F2 < U0 < U1 < F1 < F0$$

These values indicate that under constant conditions, the presence of food increased the level of locomotor activity. Analysis of activity values (Mann-Whitney U -test, $p < 0.05$) for each session revealed that the level of locomotor activity

was significantly higher when food was available:

$$(U1 \ U2 \ U0) < (F1 \ F2 \ F3)$$

A group effect was detected, group 2 being the less active whether fed or unfed (Kruskal-Wallis, $p < 0.05$):

$$U2 < U0 \ U1 \\ F2 < F1 < F0$$

For all series, activity never reached very low values, as illustrated by coefficients of variation, which never exceeded 25%.

Rhythms

Autocorrelation and spectral analysis revealed that each group exhibited a rhythmic swimming pattern. Series and spectra are presented in Figs. 3-5. Relative phasing of the tide and light cycles used for groups U2 and F2 is shown in Fig. 5. Groups U0 and F0 were reared for 3 weeks under constant conditions before observation, indicating that the rhythm persisted for at least this period of time.

Except for group U2 (unfed, both cycles), each group exhibited a dominant or exclusive periodicity of about 12 h (range 10.5-13.3 h). The absolute phase of the rhythms expressed is difficult to establish because of the necessarily short duration of the observation sessions. It is thus not possible to determine whether the rhythms are circatidal or semicircadian on the basis of the calculated values of period length. In addition, the tidal signal we used as Zeitgeber had a periodicity of 12.0 h (rather than the traditional 12.4 h). This is not unnatural, as the period length of the tidal cycle in the St. Lawrence estuary varies during the lunar month and is asymmetrical (e.g., night tides are of longer duration and

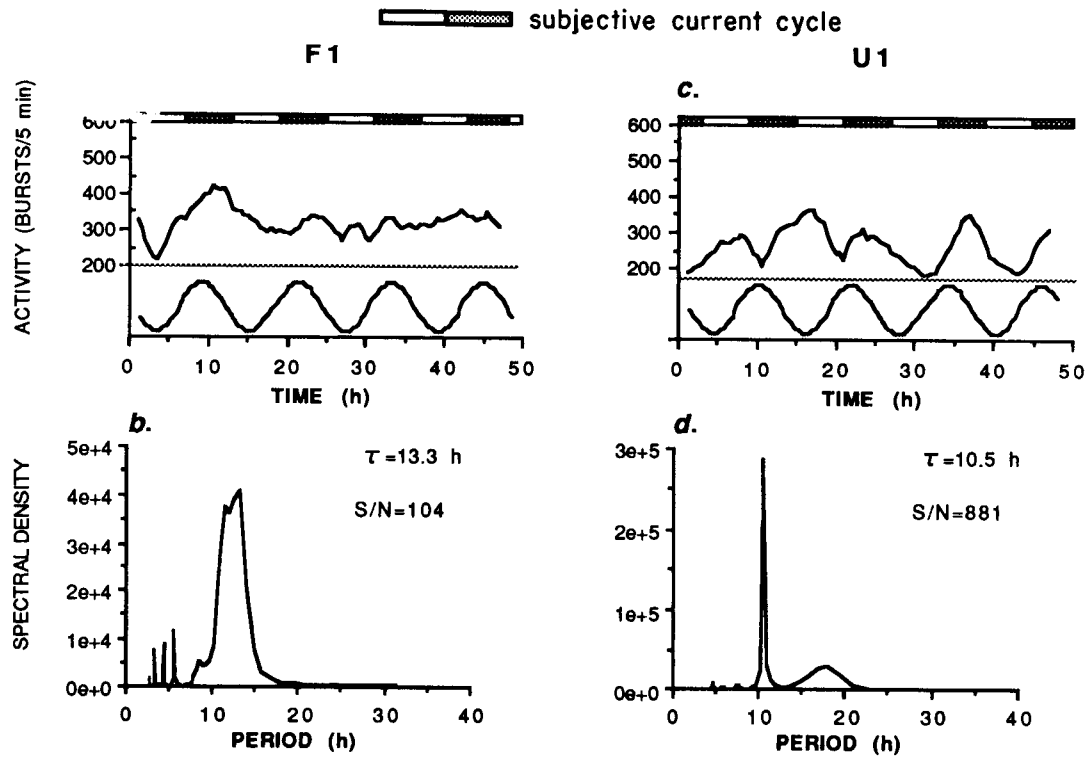


FIG. 4. Series (a, c) and spectra (b, d) for groups F1 and U1, exposed to current cycle (F, fed during the observation session; U, unfed during the observation session).

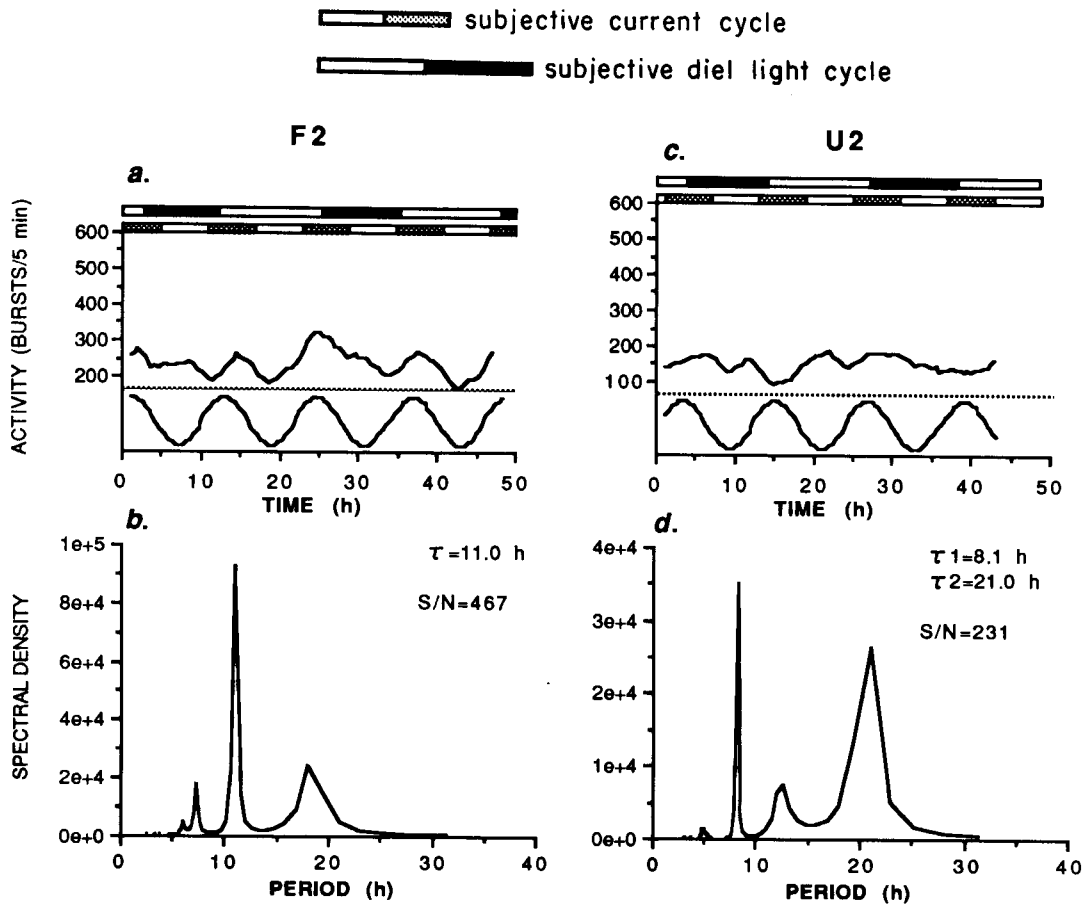


FIG. 5. Series (a, c) and spectra (b, d) for groups F2 and U2 exposed to current and light cycles (F, fed during the observation session; U, unfed during the observation session).

higher amplitude). The phases of the experimental groups are thus evaluated on a relative basis. For this purpose, a simulated version of the rhythm exhibited by group F0 (control group) is represented below the series of the other groups in Figs. 3–5.

Groups F0 and U0 exhibited similar phasing. While the phase of F1 is difficult to establish owing to high noise level (signal to noise ratio = 104), series U1 was out of phase with the control group, suggesting an effect of entrainment. Groups F2 and U2, exposed to both current and diel light cycles, yielded more complex spectra. In both cases, peaks occurred at approximately 8, 11, and 20 h, the dominant one being around 11.0 for F2 and 8.1 h for U2. Owing to these shorter period lengths, these groups were out of phase with control groups. The peaks at about 20 h were lacking in the other groups that were not exposed to diel light cycles.

Discussion

Significant rhythmicity appeared from the activity records of groups of tomcod larvae. The results of the control groups (U0 and F0) kept for 20 and 22 days, respectively, under constant conditions before observation, suggest that rhythmicity can persist for at least 3 weeks. Though endogenous rhythmicity has been observed in different species at the adult or juvenile stages (see Introduction), to our knowledge this is the first demonstration of such behavior in post-yolk-sac fish larvae.

Soon after hatching, tomcod larvae drift to the St. Lawrence estuary where they are retained for at least 3 months (Laprise and Dodson 1990). In addition to the diel cycle, this zone is affected by strong tidal features: mean tidal amplitude 3–5 m, advective displacement of water masses up to 24 km, tidal currents up to $250 \text{ cm} \cdot \text{s}^{-1}$ (D'Anglejan and Smith 1973). Groups of larvae exposed to simulated tidal and diel light signals demonstrated modified rhythmic patterns in relation to control groups, which is suggestive of entrainment. Control groups exhibited activity patterns peaking around subjective sunrise and sunset. Though it may be spurious, exposure to cyclic signals yielded more variable phasing. Groups U1 and U2 were approximately 180° out of phase relative to control groups. In addition, the rhythms of groups F2 and U2 exposed to both tidal and diel light signals included a low-frequency modulation in the 20-h region. Exact characterization of entrainment effects required the use of replicate groups, which was not possible because of the methodological constraints stated previously. Nevertheless, our results reveal the existence of some chronobiological flexibility affected by simulation of the basic cycles of the natural habitat.

Correspondence between local tidal amplitude and fish activity rhythms has been documented by Gibson and Hesthagen (1981). Sand goby (*Pomatoschistus minutus*) collected from a zone of high tidal amplitude exhibited circatidal rhythms under constant conditions. On the other hand, gobies caught in a zone of low tidal amplitude demonstrated no or weak circatidal rhythms in constant darkness. Adjustment of activity rhythms to local conditions was also suggested by Wipplhauser and McCleave (1988). These authors proposed that upstream migrating glass eels no longer express endogenous circatidal rhythms when the zone of tidal influence of the river is passed. Tomcod larvae are exposed to changing environmental conditions during the drift and retention periods, and this possibly accounts for their apparent reactivity to simulated cycles.

Observing larvae in groups rather than in isolation was a

protection against aborted observation sessions caused by the eventual death of the subject. However, social synchronization may have contributed to the expression and (or) persistence of the rhythms. Wipplhauser and McCleave (1988) observed that only 2 glass eels out of 100 demonstrated endogenous rhythms, whereas the fish were generally rhythmic when observed in groups. Kavaliers (1980c) reported that groups of 25 juvenile white suckers demonstrated rhythms in which period lengths were less variable ("more precise") and periods were longer than in isolated subjects, suggesting that the activity patterns of these shoaling fish were synchronized to a certain degree. Tomcod larvae are not known to form shoals, but grouping them may have caused social synchronization.

Examination of the metabolic effects of feeding on activity patterns revealed lowered activity levels when larvae were not fed during observation. Furthermore, it appears that feeding did not modify the parameters of the rhythms expressed by unfed larvae. Control groups exhibited the same period length whether fed or unfed, and the groups exposed to cycles did not show a consistent trend in period change related to feeding. This is contrary to our preliminary hypothesis that a metabolic conflict between feeding and aerobic swimming may lead to a modification in the period length of the endogenous activity rhythm.

The absence of such an effect cannot be related to intragroup variability in endogenous rhythmicity. Numerical simulations performed with combinations of perfect sine and white noise functions revealed that the emergence of significant rhythmicity (tested with autocorrelation) required synchronization of the majority of individuals clustered in groups of 50. Thus, intragroup variations cannot explain the absence of the hypothesized effect of food, and we concluded that this effect did not occur under the conditions of investigation.

The period length of endogenous rhythms is essentially thermo-independent owing to compensation mechanisms (Edmunds 1983). On the other hand, the digestion rate is expected to increase with temperature in ectothermic animals. The possibility of a metabolic conflict modifying the expression of an endogenous locomotory rhythm remains to be investigated under different temperature conditions.

Acknowledgements

We thank the Aquarium du Québec for logistic support, P. Gagné for help in the laboratory, and P. Couture and P. Veillet for field assistance. H. Dowse and J. M. Ringo provided us with their MESA and SNR programs. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada.

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