

Diel activity rhythm of seabass tracked in a natural environment: group effects on swimming patterns and amplitudes

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Abstract: Seabass swimming behavior was investigated in a salt-marsh area located along the Atlantic coast north of La Rochelle, France. Seabass is a natural inhabitant of this coastal zone and is farmed there as well. During its 3rd year, seabass can move about either singly or in small groups. Swimming activity of single fish and fish in a group was studied using an acoustic telemetry recording system. This study demonstrates that swimming activity levels and patterns of this species are modified by a group effect. Single fish were mainly nocturnal and fish in a group adopted a diurnal activity rhythm and lower maximum swimming activity levels.

Résumé : Le comportement natatoire du bar a été étudié dans un marais maritime du littoral atlantique localisé au nord de La Rochelle, France. Le bar est une espèce naturellement hôte de ces zones littorales et son élevage s'y développe également. Dans sa troisième année, il évolue soit seul soit en groupe de taille variable. Le comportement natatoire a été étudié par télémétrie acoustique avec des animaux évoluant soit seuls soit en groupe. Cette étude montre que les niveaux d'activité natatoire de ce poisson et leur expression rythmique sont affectés par un effet de groupe. Des individus isolés sont nocturnes alors que des individus en groupe adoptent un patron de nage diurne et une activité natatoire dont l'amplitude maximale est plus faible.

Introduction

Analysis of fish activity patterns in relation to light represents an important part of the literature dealing with fish behavior (Woodhead 1966; Thorpe 1978; Helfman 1986). Such analyses often lead to the classification of fish with regard to the time of day when their swimming activity, which is strongly linked to active searching for food including exploration of the surroundings, is at its maximum (Helfman 1978, 1986). Most animals can then be classified as being either diurnal, nocturnal, or crepuscular, with adaptation for activity at one light level leading to reduced efficiency at another. Thus, the specific pattern of daily activity is considered a reflection of an animal's behavioral adaptation to its environment (Manteifel et al. 1978; Müller 1978a). A review by Eriksson (1978) of activity rhythms of several fish species indicated that variability in activity pattern was mainly dependent on light intensity and photoperiod, but it is also well known that fish locomotor activity responds to natural environmental oscillations as well as social interactions (Breder 1959; Kavaliers 1980; Reynolds 1977); fish activity is also sensitive to anthropogenic contaminants (Scherer 1992) and to stress imposed in fish farming (Fernö et al. 1988). How group size affects the circadian activity of fish and other vertebrates is not well known (Aschoff

1979); effects of fish density on activity patterns have seldom been investigated (Müller 1978b; Kavaliers 1980). The importance of fish density and its linked group effect have mainly been studied under laboratory conditions, where growth, basal metabolism, and oxygen consumption have been linked to swimming activity. Thus, we chose to conduct an eco-ethological study at the individual level aiming to evaluate the effects of social interaction and seasonal variability on the swimming behavior of seabass in salt marshes.

Juvenile seabass, *Dicentrarchus labrax* (L.), have generally been considered visual predators reported to feed both by day and night (Barnabé 1980). Furthermore, seabass are described as group hunters when they are juveniles, becoming more solitary when they mature late in their 3rd year. Juveniles prefer to forage in groups by day and scatter at night, at which time individuals remain immobile in sight of the bottom (scuba diving observations; Barnabé 1980). For these reasons, individual seabass were tracked, both alone or in a monospecific group, using acoustic telemetry techniques (Lagardère et al. 1990); such an approach avoids experimental bias linked to laboratory conditions (Reynolds 1977). This study took place in salt-marsh ponds, which are the natural habitat of seabass. Fish swimming and feeding behavior and environmental factors were simultaneously recorded. This paper focuses on the effects of being member of a group on the swimming pattern and amplitude of seabass.

Materials and methods

Experimental site

The study took place north of La Rochelle, France, in a salt-marsh area located 46°9'N and 1°9'W. It was conducted in an earthen pond of 250 m² (18 × 14 m). The pond was supplied with marine water to a depth of 0.8 m via an inlet pipe connected to a channel opening to the sea. During experiments, the ponds were isolated from the tides

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Table 1. Data collection and experimental setup for each study year.

	1992	1993
No. of trackings	15	12
No. of individuals tracked	7	6
Total no. of hours	1225	865
Total no. of fish in the pond	1	60
Area of the pond (m ²)	250	250

by closing the pipes and thus limiting any potential tidal effect. Light was measured in the pond using bottom spherical irradiance (Quantameter, Biospherical Instruments Inc. QSP 170) in 1992; atmospheric plane irradiance (Pyranometer) was measured by an automatic weather station (Aanderaa) located on site in January 1993. These light measurements were used to assign dawn, dusk, day, and night treatments.

Acoustic telemetry technique and acoustic data processing

The acoustic positioning system used to observe fish movements without disturbance consisted of a miniature ultrasonic transmitter attached to the back of the fish and a reception antenna made of four spatially separated hydrophones (Brüel & Kjaer, type 8103) with their associated preamplifiers (Brüel & Kjaer, type 2634). Measurement of the arrival time of the signal transmitted by the acoustic transmitter to three of the four hydrophones supplied the information to estimate the position of the fish (Lagardère et al. 1990). The arrival time differences of the signals amplified by four automatic high dynamic gain amplifiers were measured by the time-counter calculation channel with an accuracy of 1 μ s. Specially developed software, LOCA62, installed on a portable computer, was used to interrogate the time-counter calculation channel at regular intervals of 5 s, with storage on diskette of the arrival time differences as well as date and time. This system allows studies in ponds of up to 500 m² with position determination of the fish every 5 s over 10 days (the maximum lifetime of the battery of the transmitter V2B from Vemco Ltd) and with an accuracy of 20 cm.

The relative arrival time signals were processed by the trajectory software TRACKBAR (GISTEM CREMA L'Houmeau) at the laboratory. This software provides listings of instantaneous fixes, swimming speed, residence time per surface unit, and distance traveled during the time step of 60 min in this study. The tracks were also plotted graphically.

Experimental design and data treatments

Fish (age 3+, between 230 and 580 g) were externally fitted with an ultrasonic transmitter under light anesthesia. The transmitter was attached to the back of the fish anterior to the dorsal fin using two linen thread sutures. The fish was then released into a 250-m² pond either alone or with 59 other fish (Table 1). Tracking was carried out over 2 or 3 days in each experiment after an habituation phase of 3 days.

To permit individual identification, fish were cold branded on one side (after Lajeune and Bergerhouse 1991). Most of the fish were used for more than one behavioral recording.

Using these position recordings, swimming activity was calculated and expressed in metres per hour. First a graphical display of each actogram was made. Behavioral recording No. 2 for fish E, Nos. 2 and 3 for fish F, and No. 1 for fish M, which were interrupted because of a tag loss or failure, were removed from further analysis and graphical representation except in Figs. 1 and 3. Thus, mean swimming activity for each hour of the day was assessed for each individual, seven in the single-fish experiment and six in the group experiment. For each study condition, these means were then averaged among fish and confidence limits calculated. An analysis of variance (ANOVA) was performed using one factor (hour of the day) and post-hoc comparisons of pairwise differences between means were done using the Tukey-Kramer honestly significant difference

(HSD) method (Kirby 1993). Normality and homoscedasticity assumptions required for ANOVA were checked and met for each data set (single fish or fish in group).

The temporal distribution of swimming activity during the day was evaluated by calculating the daily activity budget (Baras 1992). This was determined by calculating mean swimming speed for each of the four components of a day: dawn and dusk (light levels between 5 and 10 μ W·m⁻²), day (light levels above 10 μ W·cm⁻²), and night (light levels below 5 μ W·cm⁻²). These activity budgets were calculated over all recordings of each study condition.

Results

Activity rhythms of single fish in a 250-m² pond

Seven fish (A–G) were tracked in 1992, of which six were tracked two or three times over several months (Fig. 1). A strongly rhythmic pattern over 24 h was apparent, with swimming activity three to six times higher at night than by day. Nocturnal swimming activity often showed a small midnight decrease. However 3 of the 15 recordings did not show an obvious rhythm (C2, F2, and F3). Fish C was tracked over three periods, displaying rhythmic patterns in March and December but no obvious pattern in August. Fish F and G showed lightly rhythmic actograms but with a high diurnal basal level of swimming activity. The F2 and F3 recordings were interrupted by the loss of the transmitter; this fish had to be captured, the transmitter reattached, and then the fish immediately released into the pond. Tracking immediately resumed. The actograms for this fish illustrate the length of recovery from surgical external implantation of the transmitter. In both cases, swimming was abnormal during the first 12 h, but thereafter returned to levels comparable with those of other fish. Interruption for E2 was solely due to a recording failure.

Mean swimming activity over each hour is shown in Fig. 2A. ANOVA ($F_{[23,144]} = 6.80, P < 0.001$) and Tukey HSD multiple means comparisons confirmed that mean nocturnal swimming activity (789 m·h⁻¹ between 19:00 and 04:00 UT) exceeded mean diurnal swimming levels (293 m·h⁻¹ between 08:00 and 17:00 UT). Transition periods between those two phases occurred between 04:00 and 07:00 UT and between 17:00 and 19:00 UT with mean levels of 468 and 498 m·h⁻¹, respectively.

Activity rhythms of fish in a group of 60 in a 250-m² pond

Six fish (H–M) within a group of 60 were tracked separately on two or three separate occasions in 1993 (Fig. 3). Swimming activity was strongly rhythmic within this group, with diurnal swimming activity 2 to 10 times higher than nocturnal activity. Diurnal activity levels were quite variable among fish, with maxima ranging from 600 to 1200 m·h⁻¹.

Three of 12 actograms were only slightly rhythmic over 24 h. These recordings took place in July for fish J and K. Fish M, tracked in August, showed very irregular diurnal swimming activity. However, during this last recording, the transmitter failed after a few hours. The fish was captured, re-equipped with a transmitter, and released into the pond. Swimming activity of fish M was irregular for 20 h after release. In all three cases, the second set of behavioral recordings (in October for fish J and K and November for fish M) showed an obvious rhythmic pattern.

Fig. 1. Swimming speeds of solitary fish recorded between March 1992 and January 1993. In this and subsequent figures, swimming speed is expressed as metres per hour and time is given in UT. Panel coding is as follows: A to F denote individual fish; numbers indicate repeated recordings for the same individual. Grey blocks in F2 and F3 indicate technical interruptions for re-attachment of the tag and, in E2, recording failure.

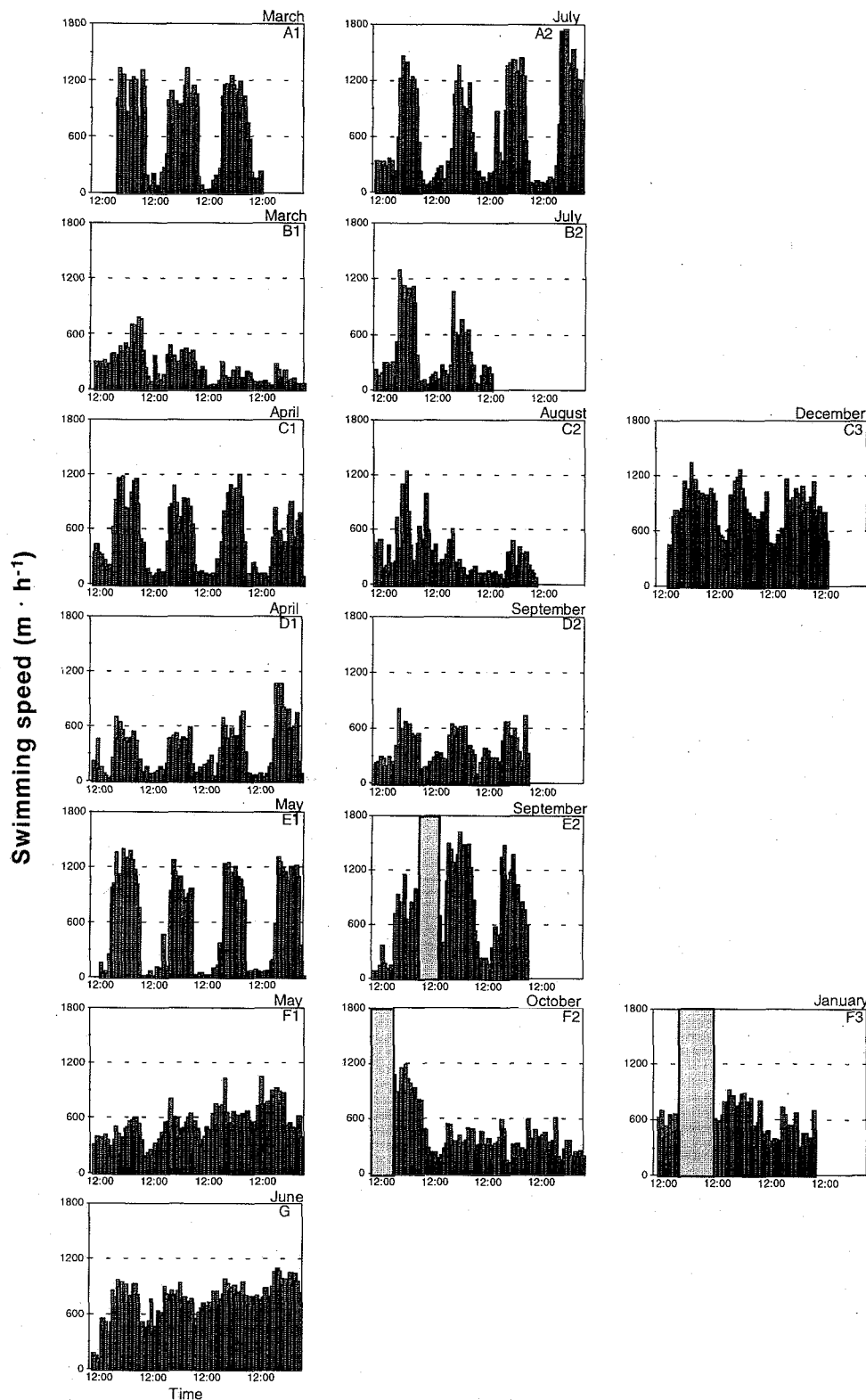
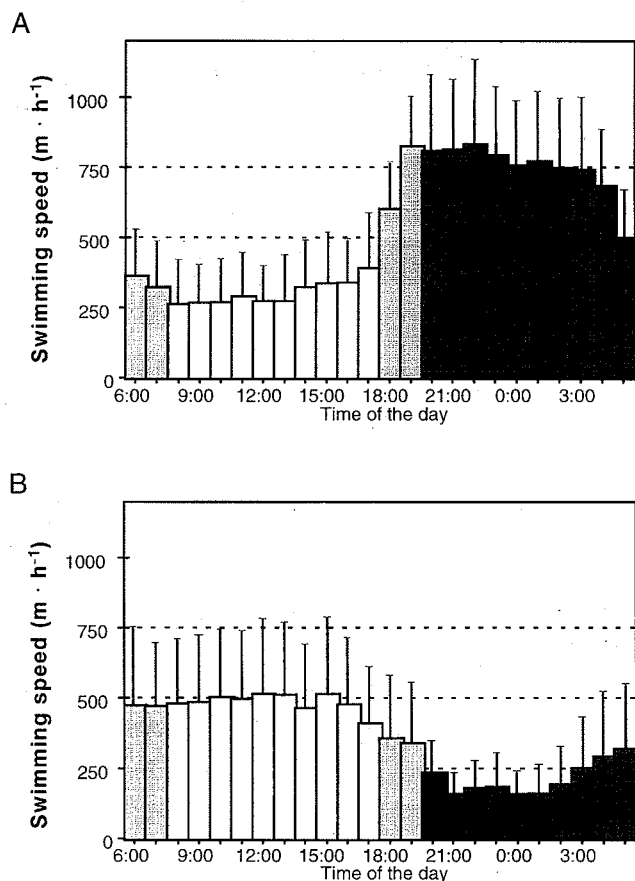


Fig. 2. Mean swimming speed and confidence interval ($\alpha = 0.05$) calculated among individuals for each hour of the day for (A) single fish ($N = 7$) and (B) fish in a group ($N = 6$). Light grey bars correspond to twilight hours and black bars to nighttime.



ANOVA ($F_{[3,120]} = 7.05$, $P < 0.001$) and Tukey HSD multiple means comparisons confirmed that, in contrast to single fish, the mean diurnal swimming levels of grouped fish ($491 \text{ m} \cdot \text{h}^{-1}$ between 06:00 and 17:00 UT) exceeded mean nocturnal swimming levels ($183 \text{ m} \cdot \text{h}^{-1}$ between 20:00 and 03:00 UT). Transition periods between those two phases occurred between 03:00 and 06:00 UT, and between 17:00 and 20:00 UT with mean levels of 288 and $370 \text{ m} \cdot \text{h}^{-1}$, respectively.

Group effect on daily activity budget

Swimming activity in terms of the temporal distribution of activity over the day is presented in Fig. 4 as activity budgets calculated over all behavioral recordings made for each study condition. When seabass were alone in a 250-m^2 area, activity was highest at dusk and at night ($750 \text{ m} \cdot \text{h}^{-1}$), and when individuals were swimming in a group of 60, diurnal activity was the highest ($500 \text{ m} \cdot \text{h}^{-1}$), followed by the dawn and dusk periods ($400 \text{ m} \cdot \text{h}^{-1}$).

Discussion

Under the natural conditions of this study, juvenile seabass appeared to switch from being nocturnal to diurnal in response to social interactions. The adaptive significance of such a pattern inversion may be found in the adaptive advantages of

shoaling. The group effect defined by Welty (1934) as social facilitation that arises owing to the presence of conspecifics, group stimulation, and weaker reactions in stressful situations has been proven to facilitate feeding behavior (Pitcher 1986; Ryer and Olla 1992); to maintain shoal organization, which is dependent on sensory contact (Pitcher 1979, 1986); and in seabass, to lower metabolism and stress (Stirling 1977) and to cause a pattern inversion associated with reduced swimming activity. Similar results were observed in seabream, *Sparus aurata*, also a serranid fish (Bégout and Lagardère 1994). However, in Helfman's reviews (1978, 1986) serranids can appear to be diurnal, nocturnal, active at twilight, or even arrhythmic depending on the study in question, suggesting that study conditions greatly influence the swimming behavior of serranids.

In the context of this study, nocturnal behavior could be explained by avoidance of avian predators. Solitary fish may choose cryptic or refuging in deeper zones of the pond during daylight as they are more vulnerable to predation, more timid than fish in a shoal (Pitcher 1986), and also more sensitive to stress (Parker 1973; Ross et al. 1992). While diurnal behavior was observed for a member of a group at a density of $65 \text{ g} \cdot \text{m}^{-3}$, this level, below which swimming pattern, swimming level, and schooling behavior are impaired, is certainly species specific (Kavaliers 1980). This group feeding species mainly preyed on patchy distributions of shrimp in salt marshes, where they could be observed hunting in shoals moving around the pond. Feeding only took place during subdued light at dawn or dusk whether hunting or activating a self-feeder (Bégout Anras 1995).

It must be remembered that fish behavior is influenced not only by social interactions but also by the combined action of meteorological factors and the hydrological conditions they affect. While we recognize that meteorological and hydrological factors have certain determinant influences on swimming activity of this species, we first demonstrated the importance of social interactions on activity patterns and swimming amplitudes. The switch from nocturnal to diurnal activity in seabass can be explained by the fact that activity rhythms are under the control of an external overriding biotic factor: group effect linked to fish density. A similar strong effect of density on circadian activity was demonstrated in killifish, *Fundulus heteroclitus*, by Kavaliers (1980), though Müller (1978b) found that whitefish, *Coregonus lavaretus*, displayed the same activity pattern whether alone or in shoals. At the same time, juvenile seabass showed a clear constancy in the swimming activity rhythm over each study condition whether diurnal in a group or nocturnal alone.

However, seasonal rhythm inversions are common (Eriksson 1978; Müller 1978c; Kavaliers 1979): a change to nocturnal activity in winter was observed in Atlantic salmon, *Salmo salar* (Fraser et al. 1993), brown trout, *Salmo trutta* (Heggenes et al. 1993), and medaka, *Oryzias latipes* (Yokota and Oishi 1992). As light and temperature vary greatly with season they partly explain the plasticity of the pattern of fish swimming activity. The more that light and temperature levels fluctuate, the more activity rhythms are modified. Thus, seasonal effects are observed in fish living at circumpolar latitudes (Andreasson 1973; Müller 1978b, 1978c). In this experiment conducted at latitude 46°N , photophase variations are more moderate, thus contributing to the constancy of seabass activity rhythm over the year.

Fig. 3. Swimming speeds of fish within a group of 60 recorded between June and November 1993. Panel coding is as follows: H to M denote individual fish; numbers indicate repeated recordings for the same individual. Grey block in M1 indicates technical interruptions for re-attachment of the tag.

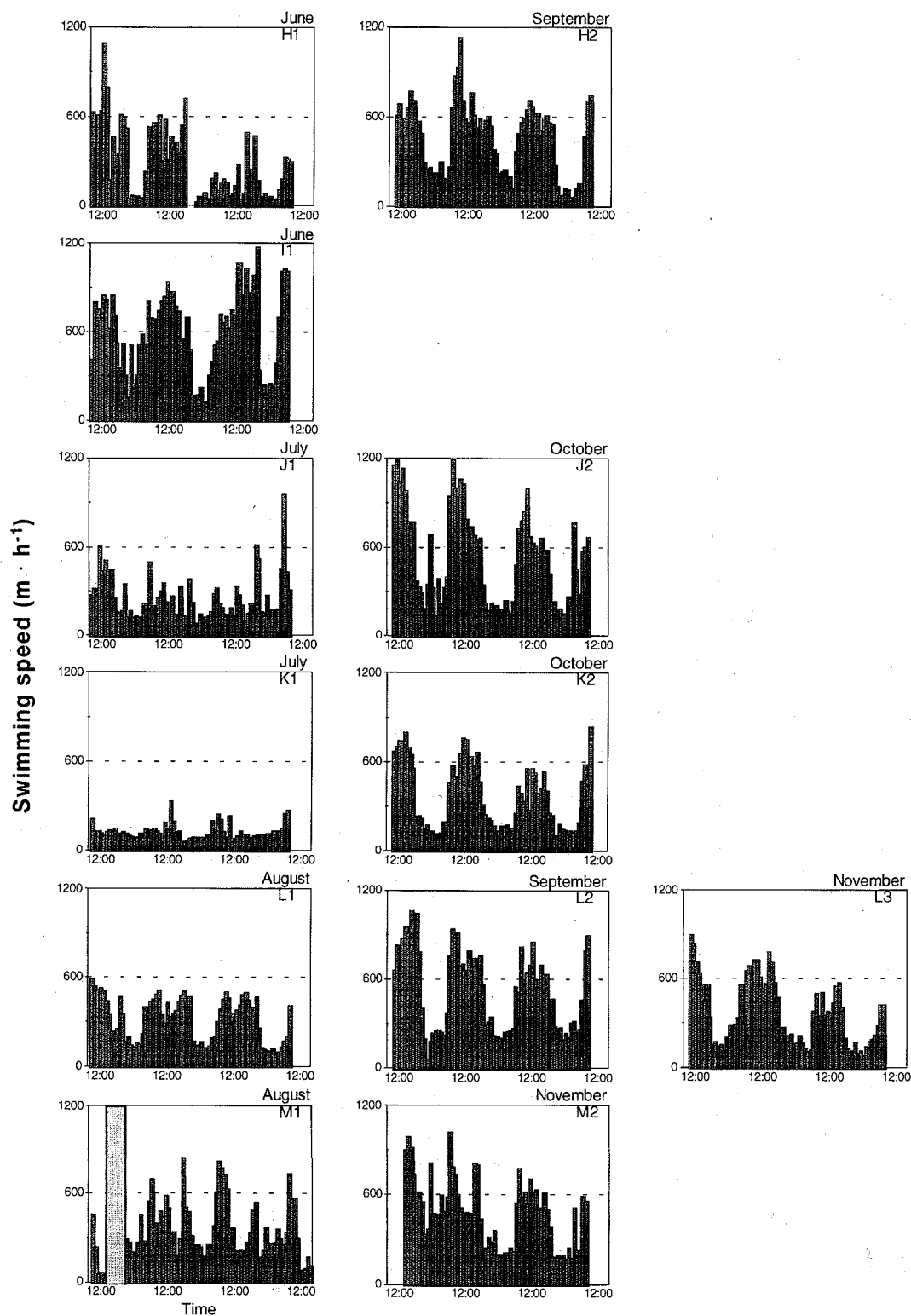
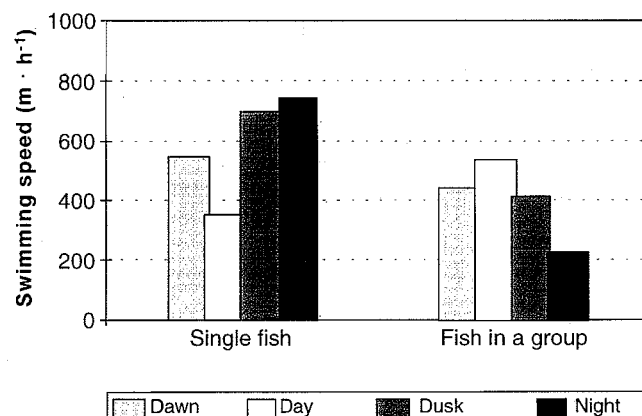


Fig. 4. Mean swimming speeds observed for each component of the daily activity budget and for each study condition: single fish in a 250-m² pond and fish in a group of 60 in a 250-m² pond.



The group effect modifies both the patterns and the amplitudes of swimming activity. Fitzsimmons and Warburton (1992) reported similar results for mullet, *Mugil cephalus*, which displayed reduced swimming speed and turning angle frequency with increasing group size. Attempts to integrate swimming activity into bioenergetics models must account for such effects. Indeed, basic metabolism varies with fish density (Lucas and Priede 1992); the activity coefficient value, which is part of any bioenergetic model (Boisclair and Sirois 1993), is variable with light conditions and fish density (Hartman and Brandt 1993), and the net swimming energetic cost differs depending on the type of swimming activity performed (Boisclair and Tang 1993). Thus, we reached the same conclusions as Kavaliers (1980) and Tang and Boisclair (1993) that it is almost impossible to extrapolate data obtained with single individuals to bioenergetics models applied to a group or a population moving about a large volume or especially in the field.

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