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ACTIVITY RYTHMS IN TWO SPECIES OF *BLENNIUS* FROM THE MEDITERRANEAN

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On shores which experience a large tidal range, certain littoral fish have been shown to possess rhythms of locomotory activity, the peaks of which coincide with the times of high water (GIBSON, 1965, 1967). These tidal rhythms are endogenous because they persist for varying lengths of time under constant laboratory conditions.

It is of interest therefore, to compare the activity patterns of littoral fish living in the almost non-tidal conditions of the Mediterranean with those that experience a much greater tidal range. It would be expected that littoral fish in such a habitat would exhibit rhythms, if present, of circadian rather than tidal frequency. Indeed it has already been shown that one fish, *Blennius pavo* Risso, has a nocturnal rhythm of activity (FISHELSON, 1963).

NAYLOR (1961) in a similar comparison of British and Mediterranean *Carcinus* found that although *C. maenas* in Britain exhibited a locomotor rhythm of predominantly tidal frequency, the closely related *C. mediterraneus* at Naples showed a nocturnal rhythm of 24 hour period.

MATERIALS AND METHODS

The experiments described below were carried out in April and May 1967 at the Laboratoire Arago, Banyuls-sur-Mer, where the tidal range is of the order of 0.6 ft. on spring tides (Admiralty Tide Tables, 1967).

The fish used in the experiments were *Blennius gattorugine* L., and *Blennius sanguinolentus* Pall. *B. gattorugine* was caught in wickerwork creels baited with crushed *Paracentrotus* and *Mytilus* and placed in 1-2 m of water. The *B. sanguinolentus* were mostly caught in shallow rock-pools on the shore near Banyuls, although some were also taken in the creels. All fish were placed in the activity recording apparatus no more than 2-3 hours after their capture.

The activity of these fish was recorded in an undisturbed N facing room for up to three days under the following conditions :

- i) In natural daylight and darkness
- ii) In constant darkness
- iii) In constant illumination of 60 ft. candles intensity.

The temperature of the water in all experiments was kept between 15-16 °C, and the fish were not fed while their activity as being recorded.

The apparatus employed to record the activity of the fish consisted of a plastic meshwork cage 30 cm long and 15 cm square. The cage was suspended in a large tank of aerated sea-water from a brass rod 3 mm in diameter which passed through a 4 mm diameter hole in a copper plate. The upper end of the brass rod and the copper plate were connected to a "Moduprint" printing counter. As the fish swam about in the cage, the brass rod was displaced and touched the sides of the hole in the copper plate, completing a circuit which triggered the counter. The number of contacts thus made was printed out every hour onto a sheet of paper, thereby providing a continuous hourly record of the fishes activity.

Clearly the amount of activity in each case is dependent to a certain amount upon the size of the fish used, the larger the fish the easier it is for the apparatus to record its activity. To rule out any discrepancy of this sort, activity is plotted in Figures 1-4 as the percentage of the total activity occurring each hour.

RESULTS

Blennius gattorugine

Under conditions of natural daylight and darkness *B. gattorugine* exhibited an activity pattern in which large peaks of activity occurred in the early morning from 0200-0600 h. (Fig. 1a and 2a). These peaks of activity corresponded closely with the times of sunrise (SR). Smaller peaks also occurred between 1900 and 2100 h., i.e., just after sunset (SS).

In conditions of constant darkness a similar activity pattern was shown, peaks occurring at or near the times of SR and SS (Fig. 1b and 2b), although the "SS peaks" rapidly declined in amplitude.

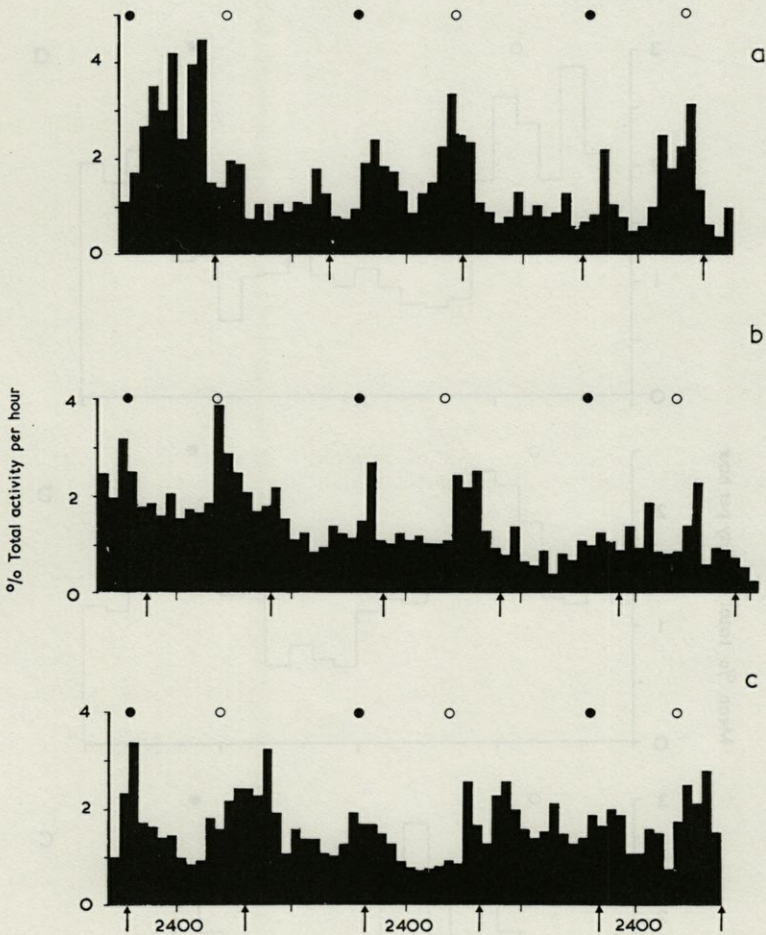


FIG. 1. — Activity patterns of *Blennius gattorugine*.

- a) In natural daylight and darkness, mean value for three fish.
 - b) In constant darkness, mean values for three fish.
 - c) In continuous illumination, mean values for six fish.
- Sunrise ○ Sunset ● Predicted time of high water shown by arrows.

When the fish were kept constantly illuminated, the peaks of activity were less sharply defined (Fig. 1c and 2c). However, peaks could still be recognised at, or just after, the time of SR and SS, but here again the SS peaks soon declined. Also the SR peaks occurred later than in the previous experiments.

These results differ from those of BAUDIN (1933) who found that the oxygen capacity and degree of saturation of the blood

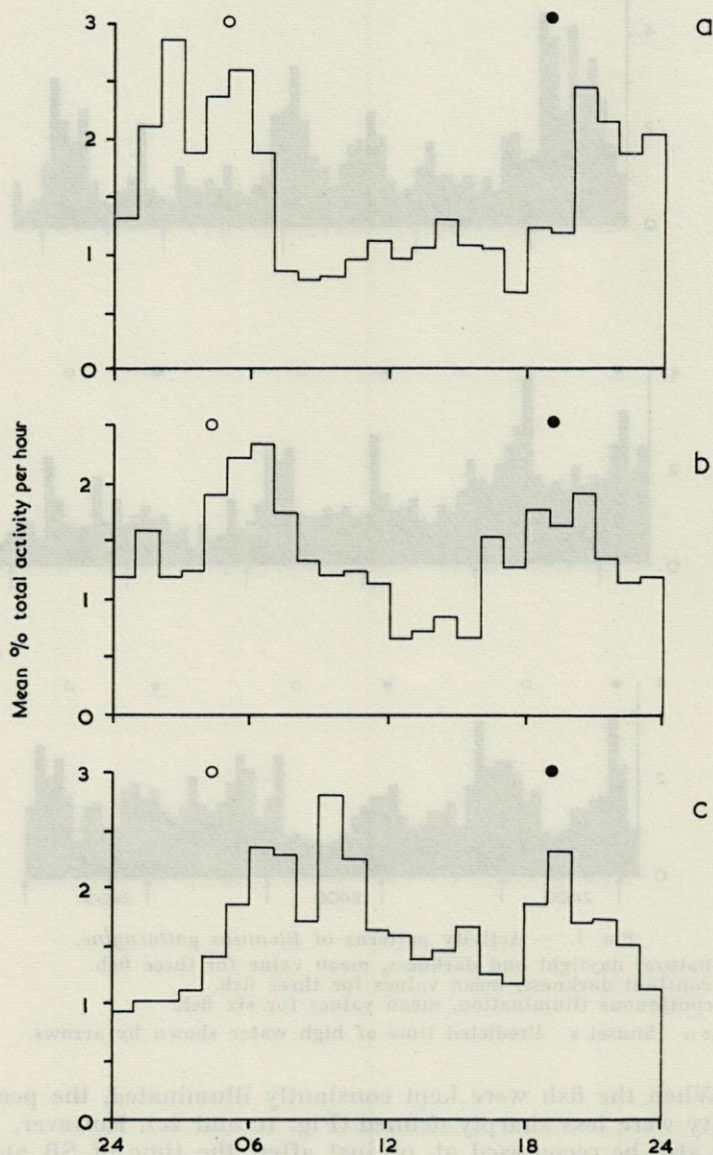


FIG. 2. — 24 hour 'form estimates' (Enright, 1965) for *Blennius gatto-rugine* calculated from the results plotted in Fig. 1. The histograms show that the SR and SS peaks are still evident in constant darkness and continuous illumination. a, b, c, and symbols as in Fig. 1.

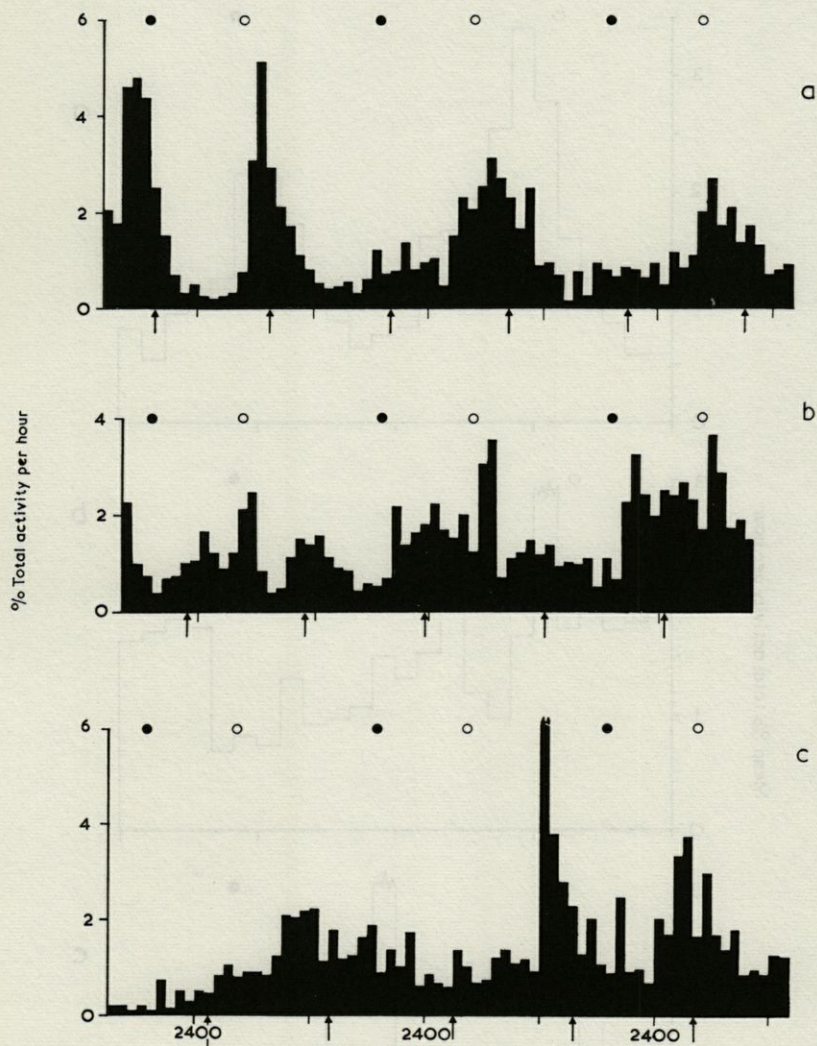


FIG. 3. — Activity patterns of *Blennius sanguinolentus*. The records in each case are the mean values for three fish. a, b, c, and symbols as in Fig. 1.

of *B. gattorugine* from the Atlantic coast of France showed a diurnal rhythm, oxygen capacity and saturation being highest from 1000-1200 h., and suggested that these changes in blood composition were correlated with a diurnal rhythm of respiration and swimming activity.

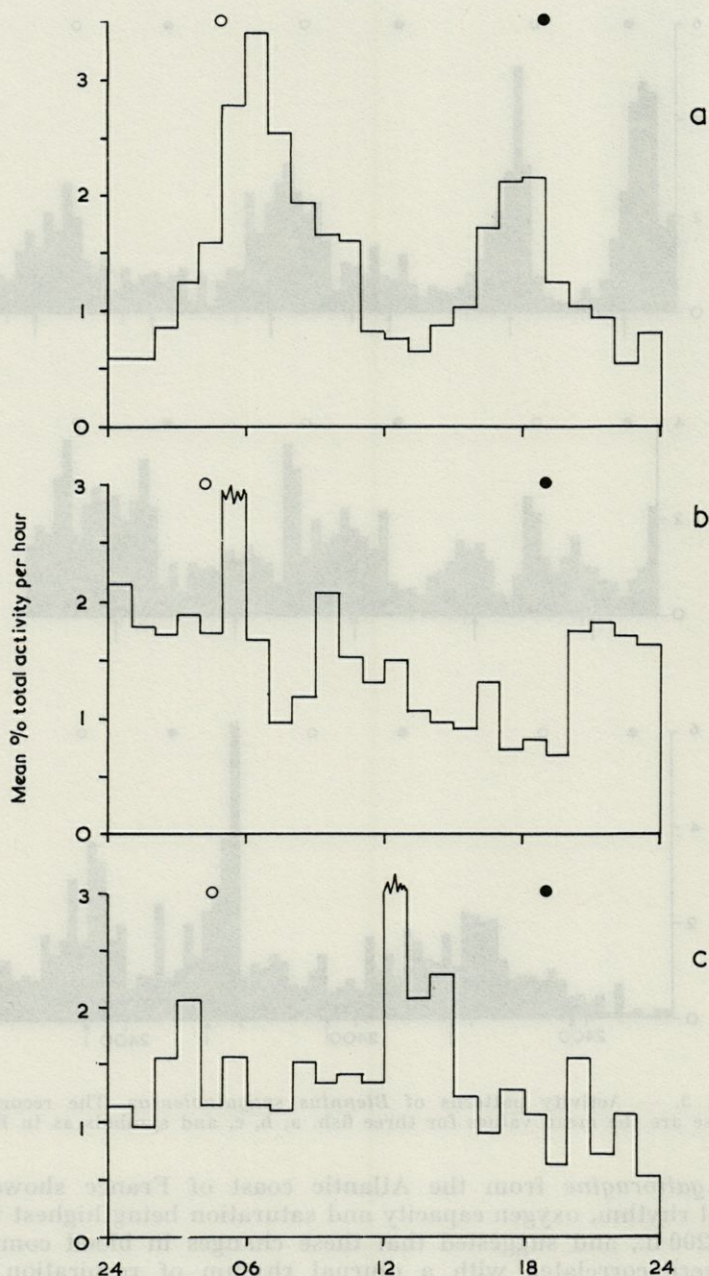


FIG. 4. — 24 hour 'form estimates' for *Blennius sanguinolentus* calculated from the results plotted in Fig. 3. Symbols, a, b and c as in Fig. 1. The SR and SS peaks are clearly evident in a). In b) these peaks can still be recognised, but nocturnal activity i.e., that occurring between SS and SR is enhanced. Fig. 4c shows the estimate in continuous light when no clear rhythm was evident.

Blennius sanguinolentus

In natural daylight and darkness *B. sanguinolentus* showed a similar activity pattern to *B. gattorugine*, the major peaks of activity occurring at or just after SR, with smaller ones at SS (Fig. 3a and 4a). The first SS peak was large, but the height of the other peaks at this time quickly declined.

In darkness, peaks of activity still occurred at or near SR and SS, but a clearer nocturnal rhythm was shown, activity between the times of SS and SR being greater than that between SR and SS (Fig 3b and 4b).

When the activity of *B. sanguinolentus* was recorded in continuous illumination, no clear rhythm could be seen, although if anything, the times of highest activity seemed to be reversed, occurring now at around midday (Fig. 3c and 4c). The large peak of activity at midday on the third day was the result of a particularly large outburst of activity by one of the three fish.

DISCUSSION

The rhythms exhibited by *B. gattorugine* and *B. sanguinolentus* correspond to the "bigeminus" activity pattern described by ASCHOFF (1966) in which two activity peaks occur each day, the first (here called the SR peak) is larger than the second (the SS peak). Similar rhythms in which activity is greatest at dawn and dusk or SR and SS have been described for several fish, notably the burbot *Lota vulgaris* (WIKGREN, 1954), the eel *Anguilla rostrata* (BOHUN and WINN, 1966), and SCHNEIDER (1964) demonstrated that the tiger fish *Therapon* has a rhythm of sound production in which maxima occur at dawn and dusk. WOODHEAD (1966) has recently reviewed the whole subject of the behaviour of fish in relation to light in the sea.

The rhythmic activity described for both species appears to be related to light intensity rather than to the tides as is the case with littoral fish from shores with a large tidal range (GIBSON, 1965, 1967). The loose correspondence found between the time of the activity peaks and the predicted time of high water seems to be coincidental, mainly because high water occurred at approximately the same time as SS and SR for the duration of the experiments. This is borne out by the facts that the peaks do not regul-

arly occur an hour later each day to keep in step with the tides, and that there is a much closer correspondence of the peaks with the times of SR and SS than with the times of high water. Also the time between successive activity peaks is not approximately 12 and 12 hours as would be expected if the rhythm was tidal, but closer to 10 and 14 hours, the times between SS and SR and SR and SS respectively.

The persistence of the rhythms in constant conditions shows that they are endogenous. Furthermore, this persistence demonstrates that the two peaks of activity, in *B. gattorugine* at least, are not a direct response to the dim or changing light intensity at SR and SS. If they were, these peaks would be expected to disappear in continuous light or darkness.

B. sanguinolentus still produces peaks of activity in constant darkness and continuous illumination, but these conditions alter the nature of the rhythm from that seen in natural daylight and darkness. In constant darkness the rhythm is more truly nocturnal as darkness appears to enhance activity during the night hours. Continuous light seems to have the opposite effect, enhancing activity during the daylight hours so that the greatest activity occurs around midday, as well as reducing rhythmicity as a whole.

The reasons for these differences are unknown, but presumably they are caused by the experimental conditions (see HARKER, 1964), the natural rhythm being that shown by the fish when they are kept in natural daylight and darkness. However, it may be that as *B. sanguinolentus* is a shallower water species than *B. gattorugine* (ABEL, 1962), it is subjected to greater light intensity fluctuations and may therefore be more sensitive to drastic changes in the light : dark regime.

Both species investigated therefore show patterns of activity which are phased according to the time of day rather than to the time of the tides. In the area where the fish live the tidal range is very small and much greater fluctuations in water level are caused by wind and changes in atmospheric pressure. Any rhythm which was related to these would necessarily be irregular and consequently of little advantage to the fish. Changes in light intensity on the other hand are more consistent and regular and it is to these that the fish appear to relate their activity. In general, it seems that *B. gattorugine* and *B. sanguinolentus* are capable of exhibiting a rhythm in which two peaks occur every 24 hours, as is shown by the peaks at approximately 14 and 10 hour intervals corresponding with the periods of daylight and darkness. It is conceivable that under strongly tidal conditions this rhythm could become entrained to have a 12.4 hour period coincident with that of the tides.

It would clearly be of interest to investigate the activity pattern of *B. gattorugine*, the only one of these two species which occurs outside the Mediterranean, in waters with a greater tidal range to determine whether in such a habitat the fish still regulates its activity with respect to light and darkness or to the tides.

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SUMMARY

The swimming activity of specimens of *Blennius gattorugine* L. and *Blennius sanguinolentus* Pall. was recorded in natural periods of daylight and darkness, in constant darkness, and in continuous illumination. Both species showed marked locomotory rhythms in daylight and darkness, with peaks of activity occurring at or near sunrise and sunset. This rhythm was still shown in constant darkness, but continuous light suppressed rhythmicity, particularly in *Blennius sanguinolentus*.

RÉSUMÉ

L'activité natatoire de *Blennius gattorugine* L. et de *Blennius sanguinolentus* Pall. était enregistrée pendant le jour et la nuit, en obscurité continue, et en illumination continue. Les deux espèces montraient les rythmes de locomotion de jour et de nuit, avec des sommets d'activité qui arrivaient près du coucher et du lever du soleil. Ce rythme était conservé en obscurité constante, mais l'illumination continue supprimait le rythme, spécialement chez *Blennius sanguinolentus*.

ZUSAMMENFASSUNG

Die Schwimmaktivität von Individuen der Arten *Blennius gattorugine* L. und *Blennius sanguinolentus* Pall. wurde bei natürlichem Wechsel von Tageslicht und Dunkelheit, in ständiger Verdunkelung und unter ununterbrochener Beleuchtung aufgezeichnet. Beide Arten zeigten ausgeprägte Rhythmen der Schwimmaktivität bei Tageslicht und Dunkelheit, mit Höhepunkten um Sonnenaufgang und Sonnenuntergang. Dieser Rhythmus zeigte sich noch bei ständiger Verdunkelung, wurde jedoch durch ununterbrochene Beleuchtung unterdrückt, besonders bei *Blennius sanguinolentus*.

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