

The Activity Rhythm of *Blennius sanguinolentus* PALLAS*, an Adaptation to its Food Source?

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With 3 figures

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Abstract. In the field, feeding activity of the algivorous *Blennius sanguinolentus* increased remarkably from morning to late afternoon. Swimming is evenly distributed; other behaviour does not fall into regular daily patterns. No association was found, save in extreme values, between the distribution of any activity and environmental factors measured simultaneously. We suggest that the feeding cycle is an adaptation to the metabolic properties of green algae, the staple diet of *B. sanguinolentus*. Activity distributions following predictable short-term fluctuations in food quality are expected to be found in other animals.

Problem

The marine littoral and upper sublittoral zones are extremely fluctuating habitats. Organisms living there must adjust their activity to environmental conditions varying not only periodically with the independent phases of light and tide, but also more or less irregularly with water turbulence, temperature, food availability, predation, pressure, etc.

Short-term activity cycles of animals from these habitats have been studied for the most part in the laboratory, concentrating mainly on circadian or tidal rhythms and their exogenous or endogenous nature (GIBSON, 1967, 1970, PALMER, 1973; earlier literature reviewed by HARKER, 1958, and FINGERMAN, 1960). However, field studies are particularly suited to give information on the ecological variables which, singly or together may influence behaviour, thereby providing insight into the probable adaptive bases to such influences (see ENRIGHT, 1970, for a lively discussion of the different interests of ecologists and physiologists in research on activity rhythms).

* Taxonomy of the blennies and the correct generic name of the species "*sanguinolentus*" is not yet clear (NORMAN, 1943; BATH, 1977; ZANDER, 1978).

The present field study deals with the daily activities of *Blennius sanguinolentus*, a benthic fish inhabiting the upper sublittoral zone. Special attention was given to possible correlations between these activities and certain environmental variables.

Adults are 9–16 cm in length, irregularly patterned and sexually monomorphic. They are abundant down to 4 m depth and they often hide under stones and boulders or in clefts.

Approximately 550 hours were spent on behavioural observation and data collection during the non-reproductive season (June 1975 and from June–Sept. 1976). The territorial system of the species will be described in a subsequent publication.

Methods

Location

The field work was done in Rovinj (Yugoslavia, 44° 04' N, 13° 38' E), on the Adriatic coast. Data were collected on the southern mainland coast opposite Figarola Island and on the north coast of the Isle of Rossa. The substrate there is rocky and covered with cobble-sized stones and boulders, with intermediate sandy stretches, especially in the mainland study area. All rock was densely covered with algae, mostly *Chlorophyceae*.

General Methods

Observations: All data were collected by snorkeling, using PVC sheets, pencil and stop watch, mostly at a distance of 2–3 m from the fish. The observer remained 5–15 mins quietly in position before actually recording. Fish did not appear to be disturbed by the observer. An analysis of the first and last mins of observation sessions showed no consistent differences in fish abundance and performance. It can be assumed that the observer's influence on behaviour was constant and rather low.

Marking: Over 100 fish were individually marked with coloured glass beads attached by a plastic thread passed through the base of the fin behind the first ray (see WALKER & HASLER, 1949, REINBOTH, 1954). The fish did not seem to be disturbed by the tags.

Collection of activity data

Preliminary recordings. A square with 1.8 m sides (a size allowing competent surveillance) was defined at 4 different sites. On three successive days, the number of fish in a square and their forms of activity were recorded at 10.00, 12.30, 15.00 and 17.30 h. Each session included eight single observation mins which were separated by 2-min breaks. As the bout length of all the activities performed was much shorter than these breaks, autocorrelations are unlikely.

The behaviour of each fish in a square for each observation min was assigned to one of the following categories:

resting: stay in the square without any activity

swimming, passing by: locomotory activity of any duration (but not balancing movements to offset currents and turbulence)

feeding: feeding activity of any duration, either while stationary or combined with locomotion.

Agonistic behaviour was so rare it was disregarded, but very occasional chasing was recorded under "swimming".

Recordings were made 0.5–1 m distant from one corner of the square during half a session; another corner was chosen for the second half.

Single monitored fish and ecological measurements. Six marked fish were observed continuously from pre-dawn to after dusk for one day each by 3–5 successive observers. Many additional observations were made around dawn and dusk, and during the night. All activities were recorded continuously and assigned to four behavioural categories:

swimming: active position-change without direct substrate contact

feeding: all feeding movements, including intake and chewing (mostly algae were plucked off rocks); intervals between successive food intakes were included when not exceeding 5 s without chewing.

chafing: rubbing against substrate, with body tilted to one side; it occurred singly, or in series of up to 15 times in rapid succession (= "chafe swimming").

attack: chasing conspecifics by rapid approach, sometimes with repeated thrusts with the mouth against the opponent's flank.

Flight was not treated as a distinct behavioural class as it is indirectly included in "attack". Occasionally other agonistic behaviour patterns occurred at obviously irregular intervals; these are not included in the recordings.

Swimming and feeding times were measured in sec, whereas chafing and attack frequencies (not thrusts) were counted. Locomotion accompanying chafing, attack or other agonistic behaviour was recorded as swimming.

The behavioural repertoire of *B. sanguinolentus* was small, especially in regard to social interactions, presumably because observations were made outside the reproductive season.

Four ecological factors were assessed at roughly regular intervals while monitoring each fish:

a) tide level, measured from ground with a surveyors' pole

b) Water motion, estimated continuously from the shifting and from compensatory movements of the recorded fish resulting from current or turbulence. The rating scale was from quiet water (0) to high wave action (5) (when even 20–30 cm diameter stones were occasionally displaced). Estimates do not represent surface motion.

c) Temperature, recorded at various times each day and at the same site – 10 cm below the surface. Results showed that recordings made at depths where fish were observed differed less than 1°C from surface values and that variations throughout the day at such depths were even smaller than at the surface.

d) Light intensity, measured with an exposure meter in the same way as water temperature. For all measurements during any given day the meter was pointed in the same direction, and the sensitized coating was vertical.

Analyses

The continuous activity data for each fish were summed and plotted for blocks of 10, 30, 60, 70, 80 and 90 min. As all distributions proved to be similar, one was taken as representative (the 60-min-block, Fig. 2). The significance of activity increase or decline was tested by a sign test for trend (Cox and STUART, 1955). These tests were run with the 10-min-block data. Peaks and depressions of all activity parameters were considered in relation to the environmental factors pertaining before, during and after the recorded activity.

Results

General observations

Our dawn and dusk recordings showed a very slow activity increase towards and after sunrise, whereas activity seemed to drop abruptly from a relatively high level to zero around sunset. Before dark, we occasionally observed *B. sanguinolentus* disappearing under a stone or into a hole, where they remained. No activity was ever seen during all night observations, and members of this species

could be found only beneath stones. There is little doubt that *B. sanguinolentus* is diurnal. Nocturnal inactivity was also noted by ABEL (1959) in various Mediterranean blennies.

During extreme turbulence, little or no activity was seen. Fish emerging from cover at level 5 (see rating scale p. 145) were dashed against rocks and had difficulty in regaining their shelters.

Activity rhythm

Preliminary recordings. Results are summarized in Fig. 1. Of the fish present in the squares, the percentage feeding more than doubled between the morning and the 15.00 h observation time, remaining at a high level for the last observation period. Swimming and resting values were lower at 15.00 h than in the early morning, however after 15.00 h, resting remained at this low level but swimming increased again for the last value. The swimming curve is certainly influenced by the recording method: if locomotion and feeding occurred together in the same observation minute, only feeding was registered (locomotory feeding). When this category is added to "swimming and passing by" the swimming curve is completely flattened.

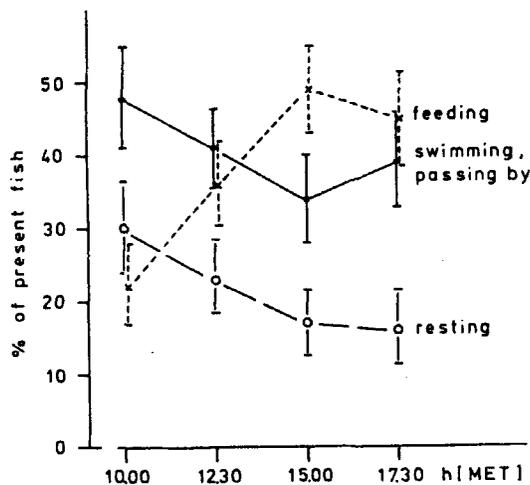


Fig. 1. % of fish in a square performing particular activities, with 95 % confidence intervals. Data are lumped from 4 obs. squares (a total of 96 obs. min for each point of time, with a mean no. of 258 recordings; range: 226-299). A total of 49 individuals were recorded, 17 of these regularly, the others up to 25 % of obs. time per square. For definition of behavioural categories see p. 144.

Single monitored fish and ecological measurements. To determine whether possible fluctuations in activity were ignored by directly connecting the 4 measured values in Fig. 1, we recorded the activity of 6 single fish continuously for the whole daylight period. Results are graphed in Fig. 2.

The distribution of total activity (swimming plus feeding) shows a distinct increase from early morning until late afternoon. This increase is less obvious in fish 6, probably due to starting observations later in the day and consequent omission of earlier low activity.

If swimming and feeding data are separately graphed it becomes evident that swimming is evenly distributed, apart from a smooth increase around sunrise and a smooth decrease around sunset. Feeding activity, starting later than swimming, increased until about 15.00–17.00 h and stayed at this highest level till 19.00 or 20.00 h. This increase was more pronounced than in total activity, and was significant ($p < 0.002$) for both categories from 09.00 h (when data of all fish had been recorded) to 16.00 h. Feeding and total activity remained constant between 16.00 and 20.00 h.

Frequencies of agonistic behaviour and chafing did not show any consistent daily periodicity.

All activities dropped more or less rapidly at the onset of darkness.

A close look at the distribution of swimming shows about 3 peaks for all fish (a peak is arbitrarily defined as activity lasting more than 200 s/h in excess of the preceding and subsequent periods). Such peaks are also evident in feeding and total activity, at least when data blocks of 70 or 80 min are used. The second and third feeding and total activity peaks coincide in 4 fish, whereas peaks for fish 1 and 2 (recorded at the mainland coast 7 to 14 days later) were 1 and 2 h earlier respectively.

The lapse of time between the first and last outburst of activity (mean 8 h 48 min, range 8 h 30 min – 9 h) was fairly constant for all fish.

Of the 4 environmental variables recorded, 3 are shown in Fig. 2. Water temperature has been disregarded, as daily change was minimal and without obvious regularity.

As with water temperature, there is no evident relationship between any of the ecological factors measured and any particular activity. A close inspection of activity peaks and troughs (original 10-min-block data) and of the corresponding sections of each environmental factor did not indicate any relationship apart from a slight one between low and declining water levels and the reduction of feeding activity, and between high turbulence and decline in total activity; therefore the data were not analysed further. No activity at all occurred at light intensities below ~ 50 lux.

Discussion

Some animals of the littoral and upper sublittoral zones are known to have short-term rhythms following the tides rather than the light cycle. Most organisms known to have an activity cycle of 24.8 h are invertebrates (for a survey see PALMER, 1973). Tidal rhythmicity can be assumed for some fish subject to extreme tide fluctuation, and in two cases such rhythms were demonstrated to be endogenous (WILLIAMS, 1957, GIBSON, 1967, 1970).

There are many examples of diurnal activity rhythms in fish; some of the more subtle ones are reported by DAVIS (1963), KRUK (1963) and KOVALSKII *et al.* (1966) and in THORPE (Ed., 1978). In the littoral zone, diurnal periodicity, suggested as endogenous, has been described for *Blennius gattorugine* and *B. sanguinolentus* by GIBSON (1969). Referring to the Mediterranean, where tide changes are very small, he thinks that "... littoral fish in such a habitat would exhibit rhythms, if present, of circadian rather than tidal frequency." But

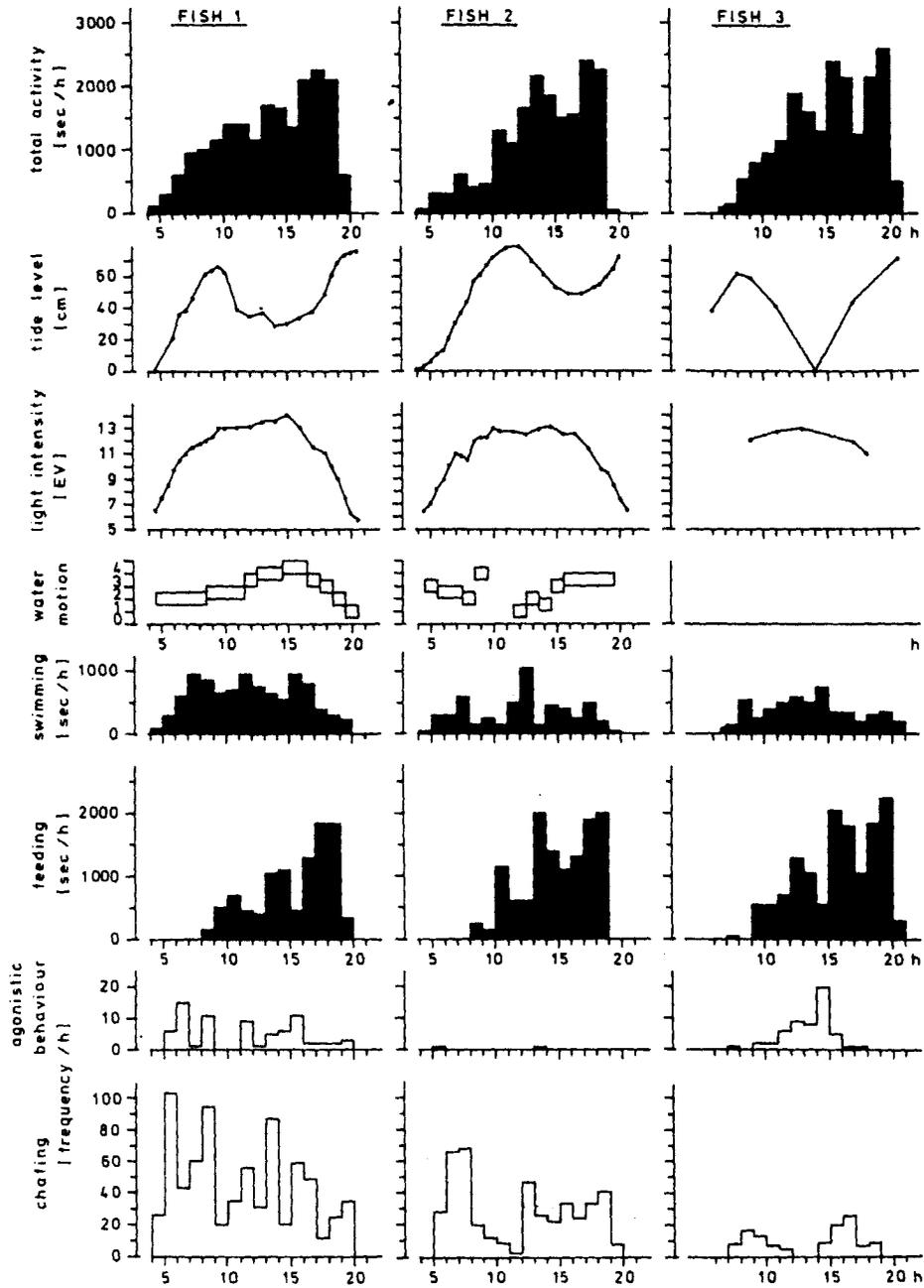
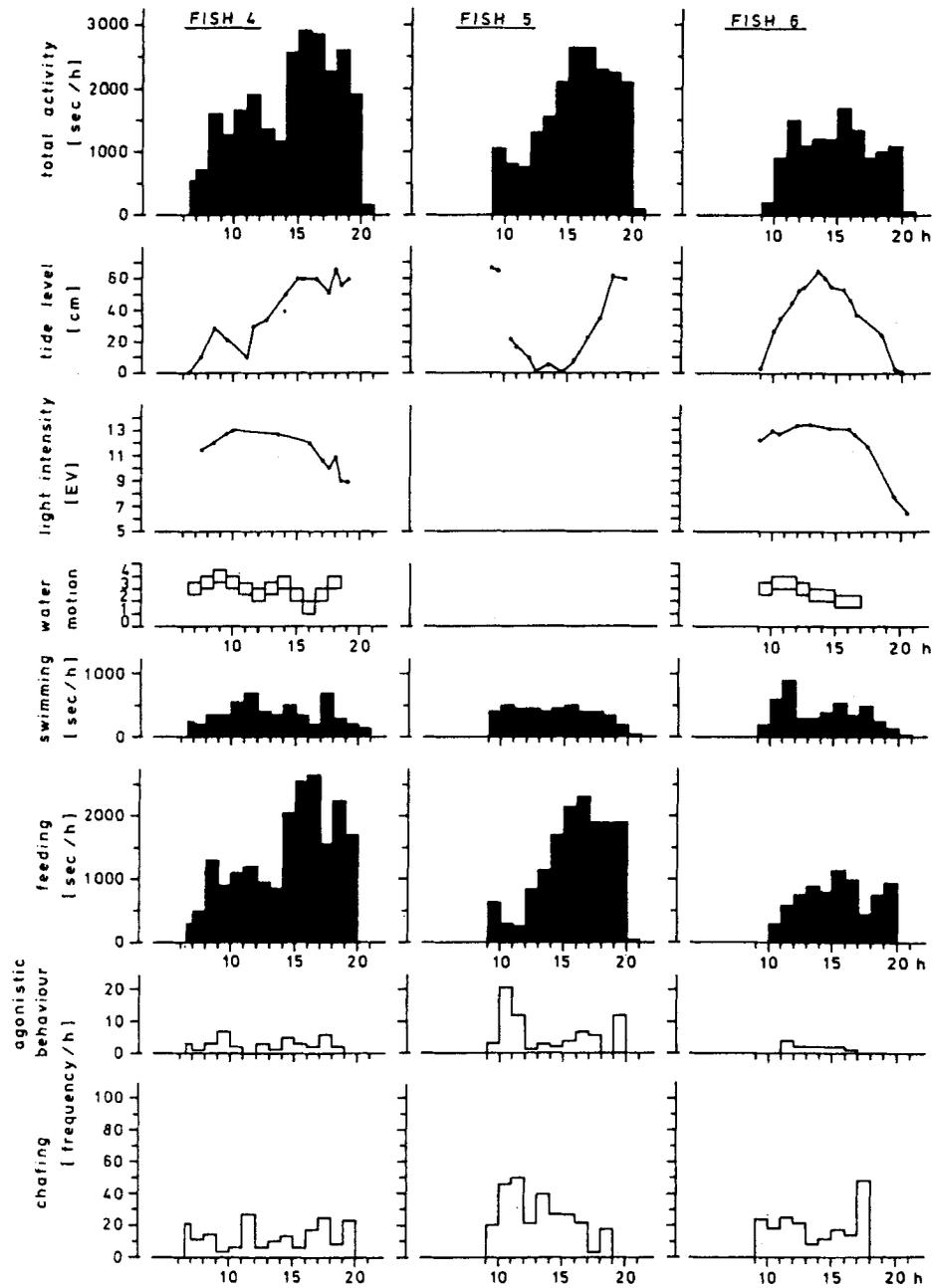


Fig. 2. Several activities of 6 continuously measured environmental variables plotted for the daylight period. Abscissa: time of day (MET). Start of obs. time at first graduation mark. All recordings continued until complete darkness (21.00). Sunrise: 04.30, sunset: 19.45 h (LD 15.15:8.45). Civil twilight: 03.50 a.m.; 20.30 p.m. Lowest tide level was taken as zero. Light intensity is scaled in EV



[Exposure Value; with EV, lux values increase logarithmically. The highest light intensity measured (14 EV) equals ~ 10000 lux, the lowest at which activity occurred was ~ 50 lux]. Water motion is calibrated in 5 arbitrary classes. At times where no environmental factors are graphed but activity continues, data are lacking.

the activity pattern of *B. sanguinolentus*, as described by GIBSON in the laboratory, was unlike our field results. He measured for three days the total activity of three fish each in a 30 x 15 cm plastic mesh cage connected to an actograph. Under natural daylight conditions, the fish showed a diurnal activity rhythm with peaks at sunrise and sunset. The pattern vanished however with continuous illumination while in continuous darkness a nocturnal activity pattern occurred.

It cannot be ruled out that the difference between GIBSON's findings and our results is due to a difference in populations as his fish came from Banyuls on the French Mediterranean. But it appears likely that his subjects were disturbed by the highly unnatural situation, without space, shelter or, especially, grazing facilities. As we have shown, the specific activity pattern of *B. sanguinolentus* in the field is based mainly on the daily distribution of feeding activity. GIBSON's fish were not fed during his experiments, let alone having no access to their natural food source.

To our knowledge, no other accounts exist of an activity distribution resembling that of *B. sanguinolentus* in the field. As the diurnal activity pattern centres mainly on feeding, the function of this rhythm may be explained by examining the natural food resource.

Although *B. sanguinolentus* was once thought to be carnivorous on account of its tooth structure (THIELE, 1963), histological and morphological studies of its mouth and digestive tract, and several analyses of gut content, showed that it feeds predominantly on green algae (IMHOF, 1935, ANDRIASHEV, 1946, GIBSON, 1968, MAYER, 1971, 1972). This agrees with observations of NIKOLSKY (1954), ABEL (pers. comm) and our own, from which this species can be characterized as a typical „Aufwuchsfresser“. The metabolic properties of green algae differ from those of most other autotrophic organisms. The daytime accumulation of various substances, brought about by assimilation, is not stored in special organs as in plants of a higher complexity, but is spent each night in metabolic processes and cell division. This means that animals utilizing such a resource meet with the same low nutritive value every morning, which increases during the light period and reaches a maximum in the late afternoon. Nor can these animals exploit any storage organs independent of metabolic short-term fluctuations.

Several authors have studied and described the protein content and storage products of green algae (e. g. LEEDALE, 1959, COOK, 1961, EDMUNDS, 1965). We could not find any similar literature on those marine green algae (*Enteromorpha* sp., *Cladophora* sp. and *Chaetomorpha* sp.) known to form part of the diet of *B. sanguinolentus* (IMHOF, 1935, MAYER, 1971, and own observations). To gain a general assimilation pattern of green algae we therefore chose the by far best-investigated subject in this respect, the unicellular photoautotrophic *Euglena gracilis* (Fig. 3). The graph for microalgae is considered to be a reliable substitute, as it seems highly probable from many studies that macroalgae, including those consumed by *B. sanguinolentus*, show a roughly equivalent pattern of productivity (BRUCE, 1964, KUSEL-FETZMANN, pers. comm., references in discussions of LEEDALE, 1959, and BERNSTEIN, 1964).

It can be seen in Fig. 3 that maximum feeding activity parallels both the maximum content of algae storage products and protein. Some fish were then feeding 80 % or more of their time.

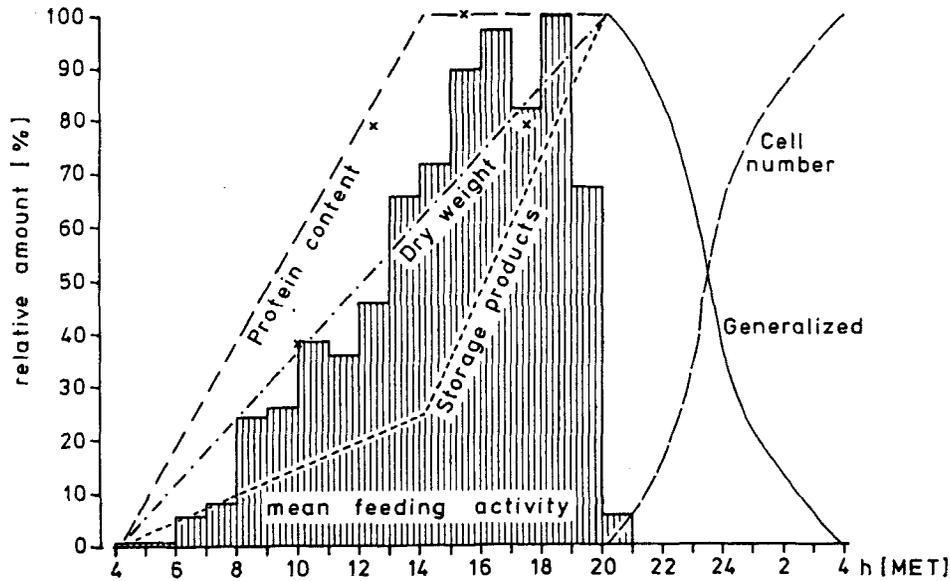


Fig. 3. Diurnal distribution of feeding activity in *B. sanguinolentus* in relation to the assimilation cycle of green algae. Graphs of day values of algal substances taken from COOK (1961), night values from EDMUNDS (1965; *Euglena gracilis*, see text). The levels for a given h are relative to total daily production. The mean feeding activity is averaged for 60 mins and 6 single monitored fish. x = values of feeding activity from prelim. obs. The max. feeding activity registered per h (interval) was taken as 100 %.

We therefore hypothesize that the activity rhythm of *B. sanguinolentus*, arising mainly from the specific diurnal distribution of feeding, is probably an example of an animal's adaptation to its feeding source. It remains unanswered whether the periodic change in the nutritive value of the algae is measured directly, or whether an endogenous rhythm has evolved in which perhaps photoperiod is used as „Zeitgeber“. But the differences between GIBSON's and our results make it unlikely that the rhythm is endogenous.

The bursts of activity within the diurnal rhythm are similar to those in many rodents and other herbivorous mammals (for references see ASCHOFF, 1962). A causal correlation may be found between plant-eating and the occurrence of short-term activity oscillations.

When turbulence and activity were compared, it was evident that high levels of water motion hinders activity in *B. sanguinolentus*.

The correspondence between declining water levels and reduced feeding activity is understandable, as much of the algae is above water when tides are very low. The lack of activity below a certain level of light intensity is to be expected if *B. sanguinolentus* is regarded as a highly visual animal. This may be why feeding activity does not continue to follow the nutritive value of algae after the onset of darkness: protein and storage products are spent gradually throughout the night (Fig. 3), and do not of course decrease as abruptly as feeding.

Time-dependent feeding economy appears to be another form of optimal foraging, occurring where food quality fluctuates diurnally. If our hypotheses

applies, other animals should exist whose feeding activity conforms similarly to short-term fluctuations in the nutritive or other values of their natural food resources. For example topi (*Damaliscus korrigum*) feed most intensively at those hours when grasses have the highest moisture content (JARMAN, 1977). ENRIGHT (1977) hypothesized that the timing of the diurnal vertical migration in planktonic crustaceans feeding on algae might depend on the daily increase in phytoplankton density (in terms of caloric content, not necessarily cell numbers!).

Summary

At Rovinj, Yugoslavia, *B. sanguinolentus*, an algivorous fish of the upper sublittoral zone, was observed for a total of 4 months. Activity was recorded 4 times daily with a few night probes, and 6 marked fish were observed from pre-dawn to after dusk for one day each. During observations light intensity, water level, water temperature and turbulence were registered.

Total activity showed a remarkable increase from early morning to late afternoon, wholly attributable to the specific distribution of feeding activity. Swimming was evenly distributed during daylight, whereas agonistic behaviour and chafing showed no regular daily patterns. No activity occurred at night. Detailed analyses revealed about three bursts of activity within the distribution of swimming, feeding and total activity. No correlation was obvious between any measured environmental factor and any form of activity, except for a slight influence exerted by extreme values.

The biological significance of this activity cycle is discussed. It is interpreted as an adaptation to the metabolic properties of green algae, the staple diet of *B. sanguinolentus*. The timing of feeding activity to exploit a resource having periodic short-term fluctuations in nutritive or other values is considered to be another form of optimal foraging, which can be expected to prove a common phenomenon, at least in algae feeders.

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