Daily feeding periodicity of the intertidal goby *Caffrogobius caffer*

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The daily feeding periodicity of *Caffrogobius caffer* was investigated at three sites in the eastern Cape. Two 24-h collections were taken at each collection site. Three methods were used to examine stomach contents. Relative stomach fullness was assessed for all six collections, while back-calculated time of ingestion and dry mass of the stomach contents as a percentage of dry somatic mass were applied to two collections each. The results from the three methods were similar. Feeding activity of *C. caffer* was not influenced by tide phase; peaks of feeding occurred during both high and low tide. Feeding occurred throughout the day with a tendency for slight crepuscular peaks of feeding activity.
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Die daaglikse periodisiteit van voedselinname vir *Caffrogobius caffer* is by drie plekke in die Ooskaap ondersoek. By elke versamelpunt is twee 24 h-versamelings gemaak. Die maaginhoud is ondersoek deur die toepassing van drie metodes. Vir al ses versamelings is die relatiewe maagvolheid bepaal terwyl die tyd van inname terugbereken is en dit, asook die droë massa van die maaginhoud wat as 'n persentasie van die droë liggaamsmassa uitgedruk is, is toegepas op twee versamelings elk. Die resultate van die drie metodes het ooreengekom. Voedselinname deur *C. caffer* word nie deur die gety-fase beïnvloed nie. Daar was hoogtepunte van voedselinname gedurende beide hoogwater en laagwater. Voedsel is dwarsdeur die dag ingeneem en daar is 'n effense neiging tot hoogtepunte in die voedingsaktiwiteit gedurende skemertye.
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Caffrogobius caffer (Günther) is a common intertidal goby found between False Bay (18°30'S/34°10'E) (Pitt-Kennedy 1968) and Umgazi (31°41'S/29°27'E) (Winterbottom 1976) on the southern African coast. Feeding studies showed that *C. caffer* was opportunistic in its choice of food items, ingesting a wide variety of algae and invertebrate fauna (Pitt-Kennedy 1968; Butler in prep. a). *C. caffer* moved between pools in its home range during the initial stages of high tide and was thus able to utilize food types which were not found in all habitat pools (Butler in prep. b). In order to determine whether *C. caffer* was opportunistic in the utilization of its food resources on a diel basis or showed rhythmic feeding activity (possibly linked with tide cycles) the feeding periodicity of this species was studied at three sites in the eastern Cape.

Other studies have shown that two major factors influence the feeding activity of marine fish. Gibson (1967) reported that *Blennius pholis* L. showed an endogenous feeding activity rhythm that corresponded to the tidal cycle of the fish's habitat. Peaks of feeding activity occurred over high tide, even if the fish were kept in an aquarium away from the effect of the tide. A similar rhythm was shown for *Coryphoblennius galerita* (L.) (Gibson 1970). Hobson (1965) noted that some species of inshore fish in the Gulf of California were nocturnal, while others were diurnal or crepuscular in habits. Domm & Domm (1973) found that light intensity affected the activity of tropical reef fish. These latter authors examined the dawn and dusk behaviour of reef fish and their results suggested that the fish studied were capable of monitoring light intensity levels accurately. These two phenomena, tide and light intensity, might be expected to have an effect on the feeding periodicity of *C. caffer*.

Twenty-four-hour collections were taken from three sites in the eastern Cape; Sea View (34°01'S/23°21'E), Clayton's Rocks (33°32'S/27°04'E) and West Bank (33°02'S/27°54'E). Three methods were used to analyse stomach contents for the 24-h collections. Two methods, points and stomach content dried mass *vs* dried somatic mass, allowed the relative volume or mass of the stomach contents at the time of collection to be compared with tide height and time of day (indirectly light intensity). In the third method the time of ingestion of various food items was back-calculated and examined relative to time and tide.

Methods

Fish collections

Two 24-h collections were taken from each of the three collection sites. Collections were made over spring and neap tides so that any change in feeding periodicity due to tidal influence could be monitored. Fish were captured using three methods: hand nets, multiprong spears and baited hooks. Randall (1967) commented that baited hooks can bias collections towards fish with empty stomachs. Investigation of gut contents of *C. caffer* caught with baited hooks revealed that only 5% of such fish had empty stomachs (Butler in prep. a) and thus this method was used during 24-h collections. For the two West Bank collections fish were caught throughout the day, while at Sea View approximately 10 fish were caught every 4h. At Clayton's Rocks 10 fish were captured at 3-h intervals. The time of capture of each fish was recorded and the specimens immediately preserved in 10% formalin in sea water.

Laboratory techniques

Three methods were used to analyse stomach contents from 24-h collections. One method was applied to all six collections while each of the other two techniques was applied to the collections from one site only.

All six collections were analysed by the points method. This method of diet analysis gives maximum points to a distended stomach (in this case 30 points) and zero points to an empty stomach. Stomachs of intermediate fullness are awarded intermediate points values (Hynes 1950; Christensen 1978; Butler in prep. a). Points awarded to fish from the 24-h collections were combined for each 3-h period.

The second method used was applied only to the two Clayton's Rocks collections. The fish and stomach contents were dried separately to constant mass in a drying oven at 90° C. The dried mass of the stomach contents was expressed as a percentage of the dry somatic mass of the fish (hereafter called '% mass'). Once again data was combined for 3-h periods.

The third method of analysis involved the back-calculation of the ingestion time for the various food items found in the stomachs of the fish from the two 24-h collections taken at Sea View. To allow back-calculation of ingestion time for food items from 24-h collections a digestion rate experiment was conducted.

Seven groups of approximately 10 fish were caught and placed into food-free cages in the fish's habitat at Sea View. Clean, food-free, rocks were placed in each cage to afford cover. This was done for two reasons; firstly to keep the cages securely in position, and, secondly by giving the fish cover, it was hoped to minimize the effect of capture on their digestion rates. After the fish had been caged they were not disturbed until they were killed and preserved in 10% formalin.

The stomach contents of the fish, killed at hourly intervals, were examined in the laboratory and the state of digestion of food items was assessed following the standard food item method of Darnell & Meierotto (1962). By examining the condition of a standard food item's exoskeleton and musculature these authors were able to recognize three stages of digestion and the length of time taken for each of these stages to be reached. By applying these findings to the standard food item in the natural diet, Darnell & Meierotto (1962) were able to back-calculate the time of ingestion of the standard food item.

The choice of a standard food item for omnivorous *C. caffer* would have been difficult and the collection of sufficient quantities of such a food item for laboratory digestion rate experiments complicated. Thus although Darnell & Meierotto's (1962) method of identifying the state of digestion was used, it was applied to a modification of the technique used by Seaburg & Moyle (1964).

Seaburg & Moyle (1964) placed freshly caught fish in food-free live boxes in the natural habitat. Fish were killed at hourly intervals and the number of hours required for the stomach contents to become 25, 50, 75 and 100% depleted were recorded. In the present study the length of time each food type took to disappear as well as the state of digestion was noted.

Several assumptions were made in the present study. Firstly, it was assumed that most fish had fed prior to capture, and secondly that capture and handling had only a minimal effect on digestion rate. The advantage of the method used in the present study over that of Darnell & Meierotto (1962) was that the time of ingestion of a variety of food types could be estimated directly. As the fish used in this study were freshly caught, laboratory acclimation could not affect the results.

The results of the digestion rate experiment are presented in Table 1. The example of adult insects can be used to show how time of ingestion was back-calculated. Adult insects were found to be virtually unaffected after 1h in the stomach, while after 3h the body had become broken up with no trace of musculature or viscera visible. No insects were found in the fourth hour sample and all estimates of the residence time of adult insects would have to have been less than 4h, with shorter periods being assigned according

Table 1 The presence or absence of various food items in the stomachs of fish caught at Sea View and killed after different periods in food-free cages

	Hours after capture						
Food item	1	2	3	4	5	6	7
Ulva spp.	+	+	+	+	+	+	+
Enteromorpha spp.	+	+	+	+	+	–	–
Codium spp.	+	+	+	+	+	–	–
Amphipoda	+	–	–	–	–	–	–
Isopoda	+	–	–	–	–	–	–
Copepoda	+	–	–	–	–	–	–
Ostracoda	+	–	–	–	–	–	–
Palaemon pacificus	+	+	+	+	+	–	–
Anomura	+	+	+	+	+	+	–
Brachyura	+	+	+	+	+	+	–
Insecta	+	+	+	–	–	–	–
Mollusca	+	+	+	+	+	+	+
Polychaeta	+	+	+	–	–	–	–

+ = present; – = absent

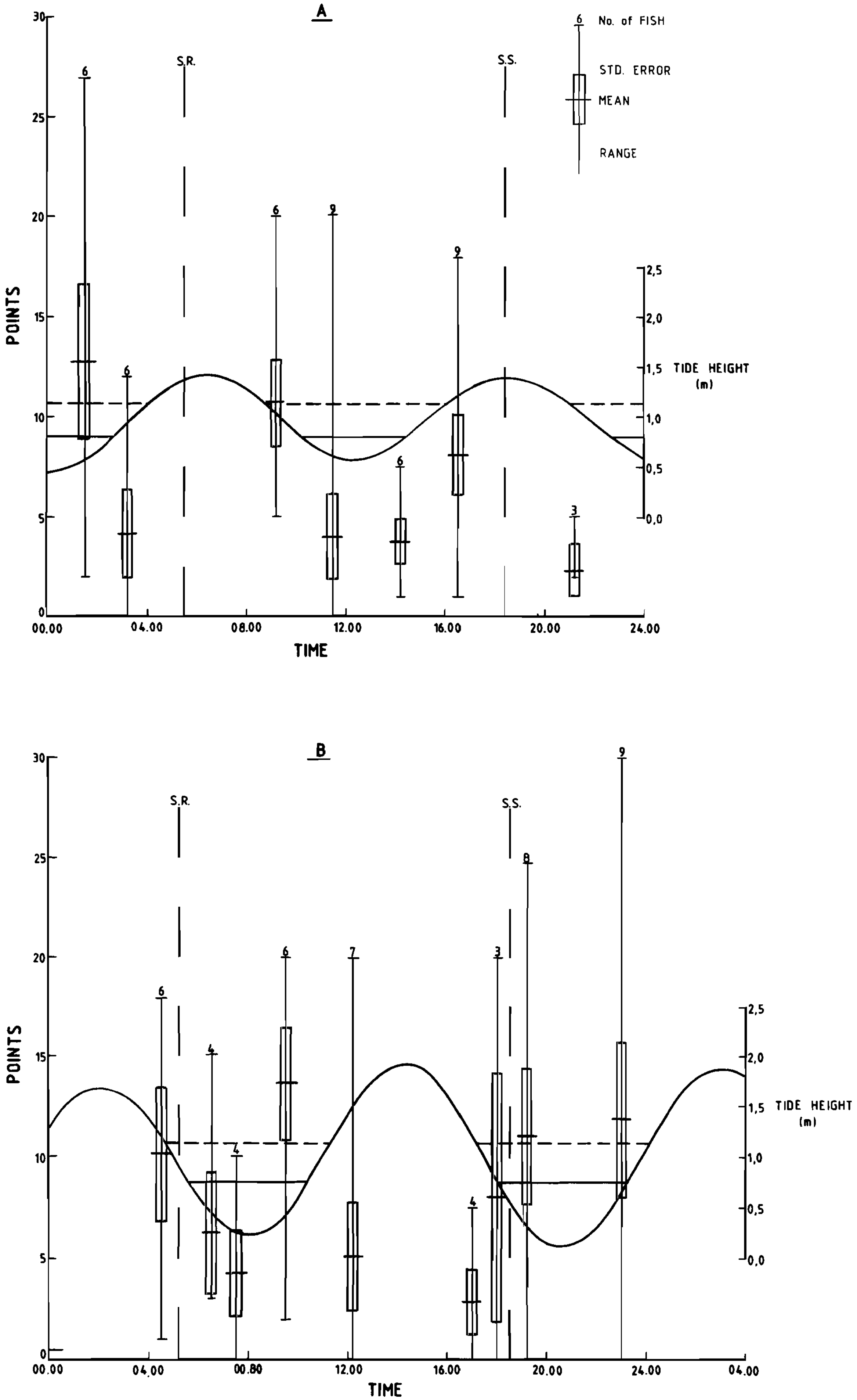

Figure 1 Results from the two 24 h diet collections made at West Bank analysed for points (A, 14/10/76; B, 21/10/76). The sinusoidal curve represents the predicted tide height, while the dashed and solid horizontal lines represent the upper and lower pool heights (relative to MSL) of the pools from which *C. caffer* were collected. During periods spanned by these lines the fish were experiencing no water movement.

to the state of digestion. Although fish were killed at hourly intervals, interpolations for digestion times were made to the nearest half hour.

Each food item from the Sea View 24-h collections had been awarded a number of points on the basis of the volume that the food item represented of the total volume of the stomach contents. Thus a food item constituting 25% by volume of the total stomach contents would be awarded 25% of the total number of points awarded to that stomach. The points assigned to various food items were combined for hourly periods according to their estimated time of ingestion.

Not all food items could have their ingestion time estimated. Although algae were found in all hourly digestion rate experiment samples, including the fish from the seventh hour, algae had to be ignored when estimating ingestion times for food items from the 24-h collections. This was because no discernible change in the state of digestion could be determined for algae. Mollusca did show a change in the state of digestion but the change was so slow that no accurate assessment of ingestion time could be made for this food type (their slow digestion rate may have been owing to the protection afforded by their shells). Thus, although points were allocated to all food items found in 24-h collections from Sea View, only those food items which could be aged were used in the construction of feeding periodicity curves. The points assigned these ageable food items were combined as 'aged points' and the number of aged points occurring in each 1-h period was expressed as a percentage of the total number of points for the entire collection.

Results

Analysis of points *vs* time and tide height

Points vs *time of day*

When the means for each 3-h period were examined relative to time of day a general trend could be seen. There was a tendency for two feeding peaks to occur each day, one in the morning and one in the evening. The morning peak was usually higher than the evening peak. Figure 1 shows the results from the two West Bank 24-h collections. Gaps of longer than 3h between data points were caused by high tide making the collection of specimens impossible.

The time of the actual feeding peaks varied from collection to collection. This may have been owing to different light intensities at the same time on different days. The possibility that light intensity may have played a role in determining feeding times was illustrated by the fact that on clear days morning peaks tended to occur earlier than was the case on overcast days. It must be borne in mind that these are possible trends and not proven facts and that the graphs represent means for 3-h periods and thus only indicate approximate feeding times. This approximation is owing to the fact that collection of large samples of *C. caffer* at hourly intervals would have had a marked effect on population densities and was thus avoided.

The points data for all six collections were combined into a single graph (Figure 2) to determine whether the crepuscular tendency evinced in the individual collections could be considered a general trend. The means (Figure 2) showed the same pattern of feeding found in individual collections, but the relative heights of the peaks were lower owing to the variability of peak feeding time on different

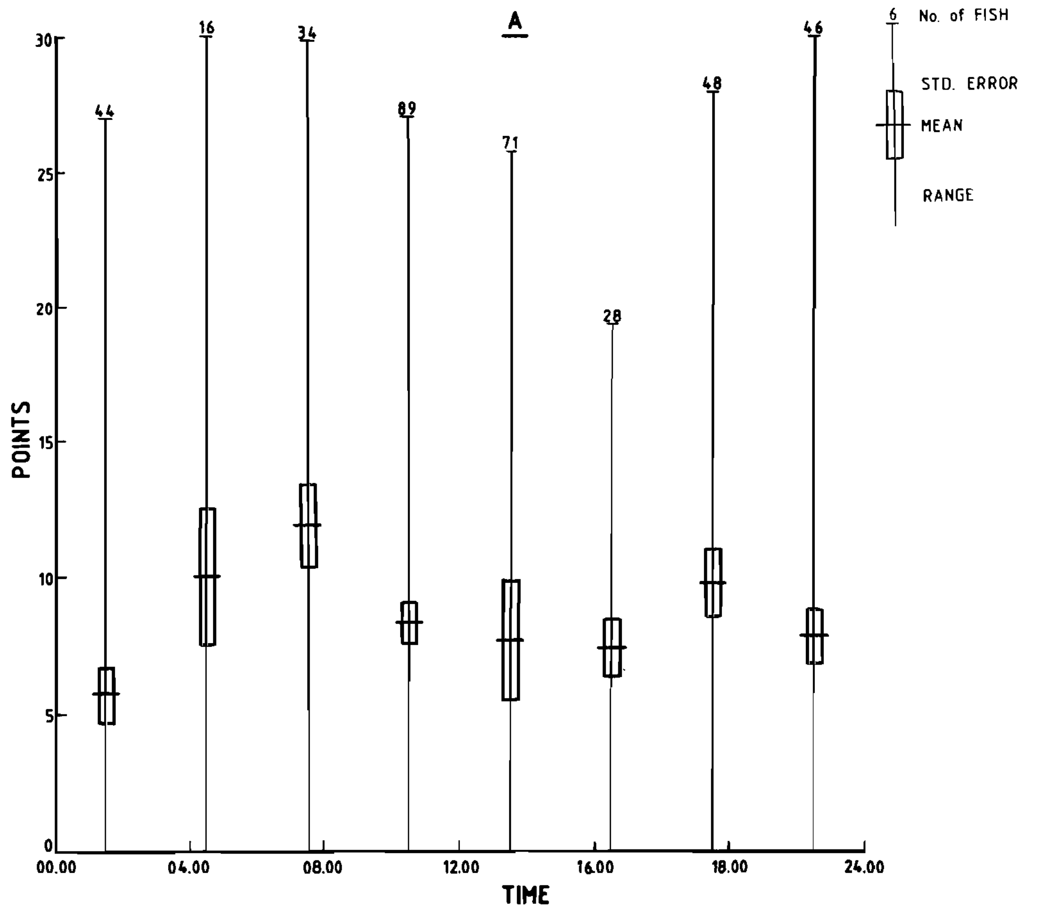

Figure 2 Results of all 24 h diet collections from the three collection sites combined and analysed for points *vs* time of day.

days. Due to overlap at the double, or even single, standard error level there was no significant difference between concurrent datum points.

Thus on the basis of the above results it can be said that *C. caffer* feeds throughout the day with the possibility of a slight increase in feeding activity at dawn and dusk.

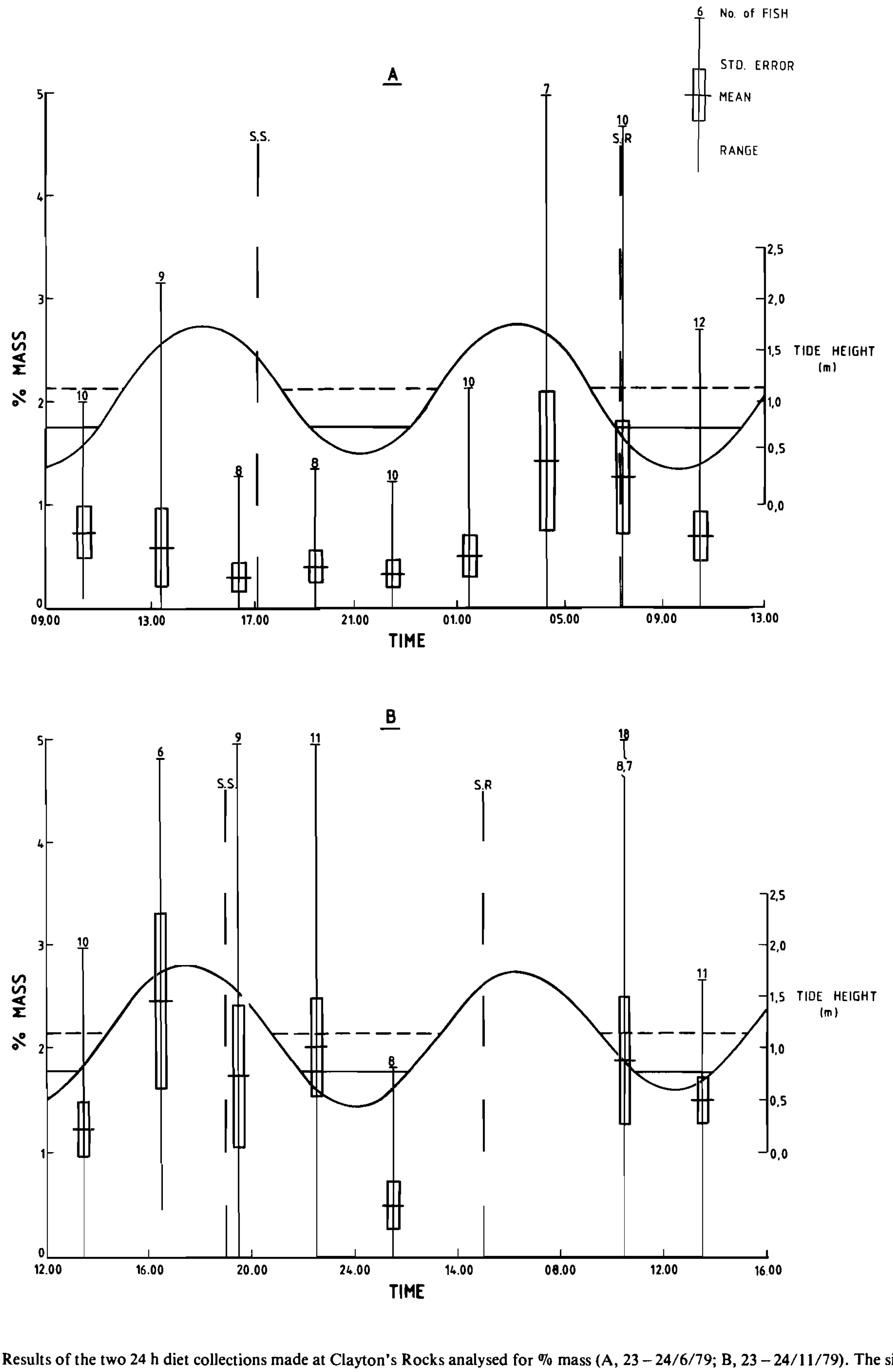

Figure 3 Results of the two 24 h diet collections made at Clayton's Rocks analysed for % mass (A, 23 – 24/6/79; B, 23 – 24/11/79). The sinusoidal curve represents the predicted tide height, while the dashed and solid horizontal lines represent the upper and lower pool heights (relative to MSL) of the pools from which *C. caffer* were collected. During the periods spanned by these lines the gobies were experiencing no water movement. The term % mass is explained in the text.

Points vs *tide height*

Feeding was found to occur at any stage of the tidal cycle, with peaks of feeding activity occurring in both still and moving water (Figure 1). It is pertinent at this point to remember that *C. caffer* is an intertidal animal. This means that the predicted tide height is only relevant to this species during those periods when the tide is high enough to reach the habitat pools. Thus a large part of the tide cycle is experienced by *C. caffer* as periods of zero, or very minimal, water movement. All specimens used for 24-h analysis were caught in pools lying between 0,78 m and 1,13 m above mean sea level. No note was made of the individual pool of capture so these lower and upper height limits were indicated on all relevant 24-h graphs by a solid and hatched line respectively. During the time periods spanned by these height limit lines the fish were experiencing minimal current, if any at all.

Percentage mass *vs* time and tide height

Time of day vs *% mass*

The results from the two Clayton's Rocks 24-h collections (Figure 3) show a trend similar to that found for the time of day *vs* points graphs. Figures 3a & b show morning and evening peaks in % mass with troughs occurring overnight and over midday.

The data from the two collections were combined (Figure 4) and the resultant graph showed a trend very similar to that shown by the combined data graph for points data (Figure 2). The morning peak occurred earlier than was the case for the points combined graph. This difference was probably owing to the fact that Figure 4 was based on data from only two collections as compared to six for the points graph (Figure 2).

The large magnitude of the standard errors in the % mass graphs was owing to the presence of such divergent food types as polychaetes and crabs in the stomach contents. The dried mass of a crab is obviously higher than that of a polychaete of similar volume. Despite this reservation and overall trend similar to that found for points data was shown, i.e. a tendency for a crepuscular increase in feeding activity.

Tide height vs *% mass*

As with the points method no correlation between tide height (or water movement) and % mass was found. In both collections (Figures 3a & b) feeding took place over both high and low tide with no preference being shown for either tide phase.

Back-calculated ingestion time *vs* time and tide height

Time of ingestion vs *time of day*

The results obtained by back-calculation of food ingestion times proved to be inconclusive. One graph (Figure 5) showed major feeding peaks occurring throughout the day with no discernible trend. In the second graph (Figure 6)

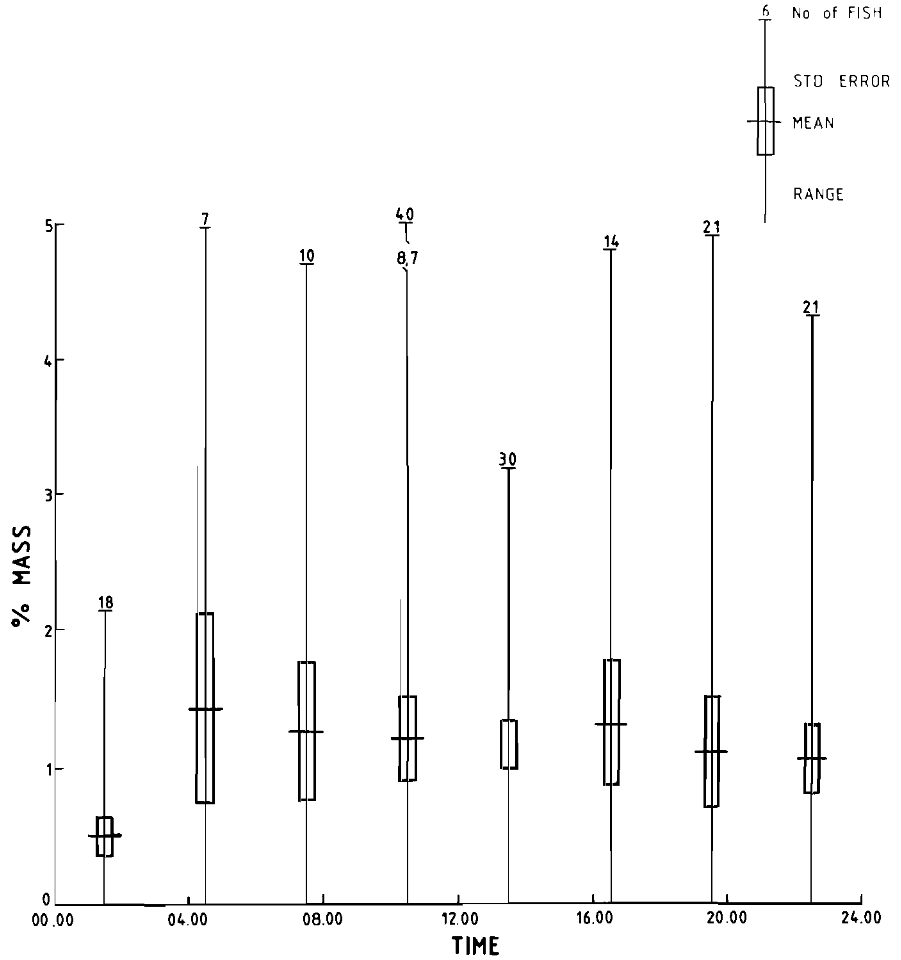

Figure 4 Results of the two 24 h diet collections from Clayton's Rocks combined and analysed for % mass. The term % mass is explained in the text.

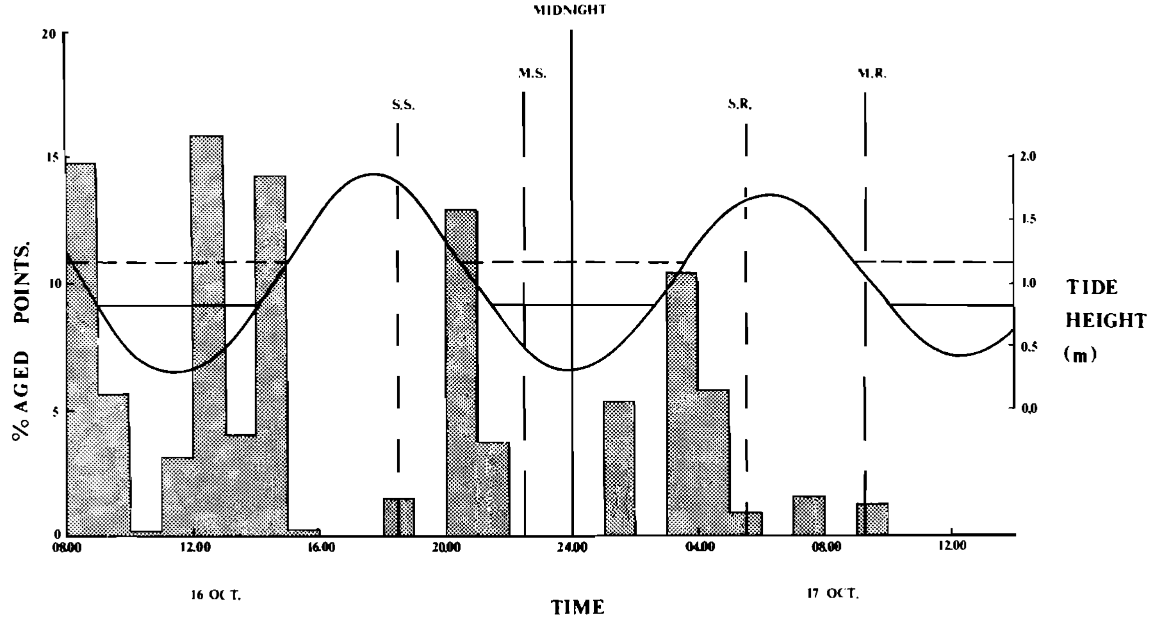

Figure 5 Results of a 24-h collection at Sea View taken on 16/17 October, 1977, to examine daily feeding peaks in *C. caffer.* (Aged points are explained in the text. S.S. = sunset, S.R. = sunrise, M.S. = moonset, M.R. = moonrise.) The sinusoidal curve represents the predicted tide height. The dashed and solid horizontal lines represent the upper and lower pool heights (relative to MSL) of the pools from which *C. caffer* were collected.

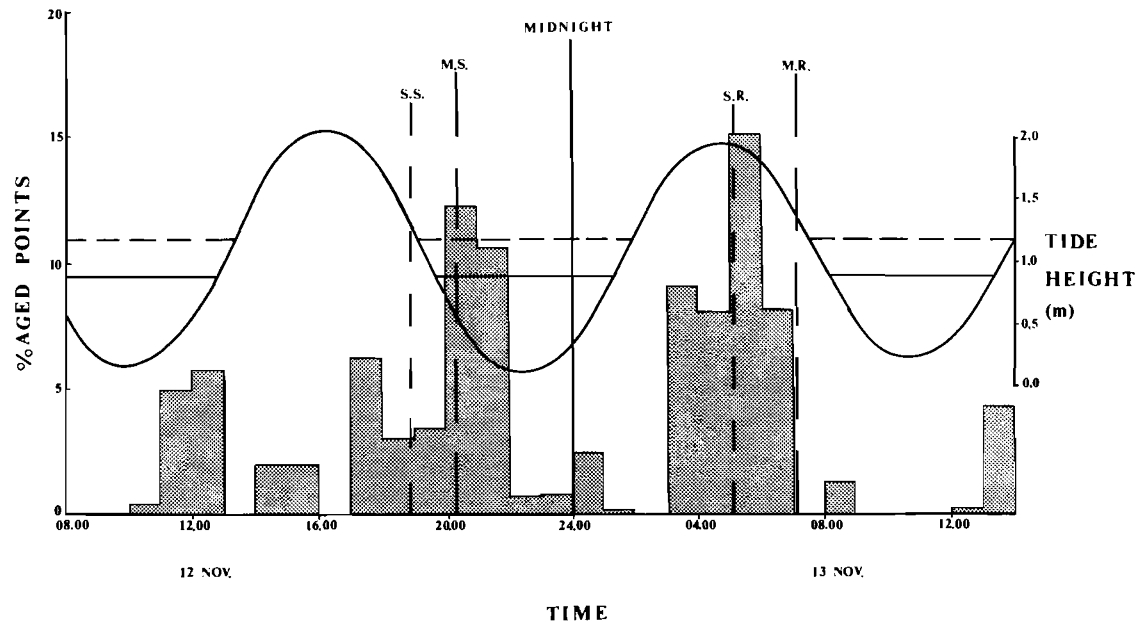

Figure 6 Results of a 24-h collection at Sea View on 12/13 November, 1977, to examine daily feeding peaks in *C. caffer.* (Aged points are explained in the text. S.S. = sunset, S.R. = sunrise, M.S. = moonset, M.R. = moonrise.) The sinusoidal curve represents the predicted tide height. The dashed and solid horizontal lines represent the upper and lower pool heights (relative to MSL) of the pools from which *C. caffer* were collected.

a crepuscular pattern of feeding peaks was shown.

In the first of the two collections, the largest feeding peak occurred at midday, while in the second collection the most important feeding peak occurred in the early morning. In both collections there were marked feeding peaks in the morning and evening, indicating the possibility of a crepuscular pattern of feeding. Both graphs show that feeding activity took place throughout the day, and one graph (Figure 5), with a major peak over midday, indicated that a definite crepuscular rhythm could not be postulated for that collection.

Time of ingestion vs *tide height*

Feeding occurred at all stages of the tidal cycle with peaks during both still and moving water.

Discussion

Pitt-Kennedy (1968) conducted no 24-h collections of *C. caffer;* all specimens he examined had been caught at low tide or in the very early stages of a rising tide during daytime. He found that 70,2% of the fish he examined had empty stomachs, a finding that differed from the 5% empty stomach found during the present study. On the basis of his information, Pitt-Kennedy (1968) concluded that most feeding took place over high tide, with feeding probably continuing after dark under the appropriate tidal conditions. The results from the present study showed that Pitt-Kennedy's (1968) conclusions are correct only in part. *C. caffer* was found to feed both during the day and night. No preference, however, was found for high-tide feeding, and feeding occurred during both extremes of the tidal cycle and during the intervening period.

The data from the three methods used to analyse feeding periodicity gave substantially the same answer — feeding throughout the day with a tendency towards a crepuscular increase in feeding activity. Only one graph (Figure 5) showed any significant deviation from this trend with a major feeding peak occurring over midday. The reason for this deviation could be one of two factors, firstly that the graph does not accurately represent the feeding activity of *C. caffer* during this collection period, or, secondly, that some unusual factor had caused the feeding activity pattern on this day to change. Every attempt was made to minimize the effect of capture stress on the fish in the digestion rate experiment in that they were placed in cages with cover and left undisturbed until they were killed. It is possible that despite these precautions the fish in these experiments suffered sufficient stress to affect their digestion rates significantly and thus adversely affect the back-calculated data from the two Sea View 24-h experiments.

There are several factors pointing to the conclusion that Figure 5 does in fact represent the true situation for this collection. Figure 6 shows results derived by the same technique and the resultant pattern is in agreement with the data from the two other methods used to establish feeding periodicity. This similarity indicates that the back-calculated data was based on reliable digestion rate estimates. Over midday of the day on which the high noon feeding peak was recorded, the sky was heavily overcast. Although other collections were taken on overcast days, this day, 16 October 1977, was the only day on which a totally overcast sky occurred only over noon. The other collections were taken on days that were clear or had overcast conditions all day or only in the morning or evening. All feeding periodicity graphs, including Figure 5, indicate a rise in feeding activity during the intermediate light intensities of dawn and dusk and it is possible that the lowered light intensity caused by the heavily overcast sky over noon of the collection on 16 October, could have led to a rise in feeding activity at this time.

Studies of interpool movement of *C. caffer* (Butler in prep. b) showed that this species undertook limited movement between pools over high tide. The diel opportunism in this species's feeding habits enabled the fish to utilize food from pools to which they had access only over high tide. Certain major food items in the diet of *C. caffer*, for example *Ulva* spp. (Butler in prep. a), were patchily distributed in the fish's habitat and this temporal opportunism in feeding allowed all members of the population access to these sparse food types, at least over high tide.

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