ASPECTS OF THE BIOLOGY OF
CAFFROGOBIUS CAFFER (GÜNTHER) (PISCES : TELEOSTEI : GOBIIDAE)
IN THE EASTERN CAPE.

by

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A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science of Rhodes University. September 1980.

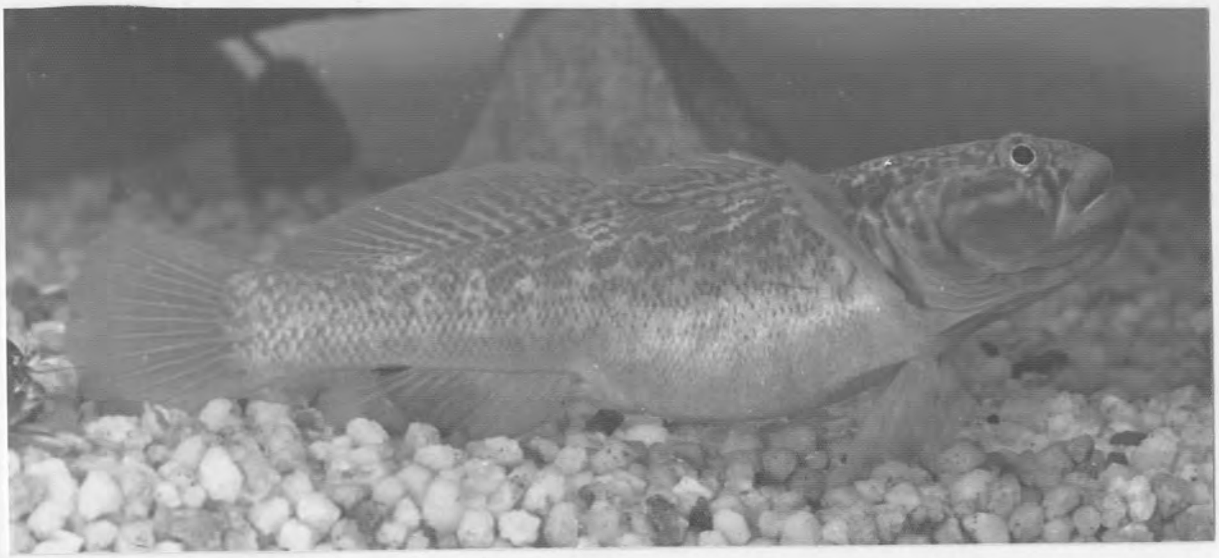

Plate 1. *Caffrogobius caffer*.

Plate 2. The collection site at Clayton's Rocks.

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ABSTRACT

Several strategies used by the gobiid fish *Caffrogobius caffer* enabling it to colonise the harsh intertidal environment in the eastern Cape were studied. *C. caffer* is opportunistic in its use of available food resources and feeds throughout the day with a slight tendency towards crepuscular peaks of feeding activity. The system of space utilisation used by *C. caffer* is so organised that all individuals of the population have access to patchily distributed food resources. Current velocities occurring over high tide limit the movements of *C. caffer* and interpool movements occur only during the initial stages of a rising tide and in the final stages of an ebbing tide when the current velocities are below the tolerance limit of *C. caffer*. The epifauna associated with the alga *Ulva rigida*, which forms an important constituent of the diet of the intermediate size classes of *C. caffer*, was examined and it appears that this epifauna is an important source of food to *C. caffer*. This report presents the results of the first detailed study of the biology of an intertidal fish in southern Africa.

INTRODUCTION

The intertidal zone represents the ecotone between marine and terrestrial environments and the plants and animals inhabiting this ecotone have to be capable of dealing with constantly varying conditions, such as the change in relative water movement between high and low tide. That there are a variety of solutions to the problems posed by these fluctuations is witnessed by the great diversity of animals and plants found in the intertidal zone. Most of the reasearch on South African intertidal animals has been of a taxonomic nature with relatively less attention having been paid to ecological studies. The reason for the lesser emphasis on ecological studies has largely been due to the difficulties of such studies in the intertidal zone. The vagaries of weather and its effects on the tides makes predictions of conditions unreliable, while wave action makes observation of animals over high tide difficult, even hazardous. Even during low tide a slight breeze can so ruffle the water surface that observation of subjects is difficult. The eastern Cape intertidal areas examined during the present study were no exception to this general rule. 'Typical' conditions were difficult to define and nearly all work was conducted during calm conditions, which probably do not represent truly typical conditions in the eastern Cape.

Despite the difficulties facing ecological research, several studies of intertidal fish have been conducted in South African waters. Jackson (1950) initiated ecological intertidal studies when he examined the distribution and diet of several fish species in the western Cape and provided a list of species present in the intertidal zone of this area. Penrith (1965) studied in detail the diet of six western Cape clinids and commented on the diets of five other species. Pitt-Kennedy (1968) examined the diet of two gobies, Coryphopterus nudiceps (C. & V.) and Coryphopterus caffer (Günther) in the western Cape (both of these species are now placed in the genus *Caffrogobius* (Hoese & Winterbottom, 1979)). Hutchings (1968) conducted a preliminary investigation into the diets two sparids, *Sarpa salpa* (L.) and *Pachymetopon blochii* (Val.). Two cheilodactylids, *Cheilodactylus fasciatus* Lacepede and *Chirodactylus brachydactylus* (Cuv.), juveniles of which are found in the intertidal zone, were the subject of a preliminary investigation by Butler (1975). The feeding habits of three sparids, *Sarpa salpa*, *Diplodus sargus* L. and *D. cervinus* (Val.), were studied in detail by Christensen (1976, 1978b) in the eastern Cape, and Christensen also extended Jackson's (1950) checklist of intertidal fish and their distribution within the intertidal zone to include the eastern Cape. Marsh *et al.* (1978) studied the behaviour of intertidal clinids in the western Cape, paying particular attention to movements within their habitats. Stobbs (1980) studied the diet and feeding behaviour of *Chorisochismus dentex* (Pallas) which feeds on limpets in the surf zone.

The gobiid, *Caffrogobius caffer* (Günther), was chosen as the subject for the present study for several reasons. Intertidal collections of the J.L.B. Smith Institute of Ichthyology (RUSI) indicated that *C. caffer* is the most numerous permanent resident of the intertidal zone in the eastern Cape. Pitt-Kennedy (1968) studied the diet of *C. caffer* in the western Cape and thus comparisons between the results of the two studies would be possible. A secondary consideration was that, due to its abundance, no difficulty was foreseen in obtaining specimens of *C. caffer*.

None of the studies of intertidal fish conducted in South Africa have dealt with more than a single facet of the species' survival strategy. Most of the studies have dealt with diet, distribution or behaviour but there have been few attempts to relate these factors to the overall strategy of the fish. In the present study the aim was to investigate several aspects of the biology of C. caffer so that some understanding of the mechanisms used by this fish to overcome the harsh conditions of the intertidal zone could be reached.

Diet was studied as food represents the most important resource available to an animal and as such the feeding strategy can be considered as the central strategy around which other survival mechanisms revolve. Many marine and intertidal fish have either a circadian or tidal rhythm of activity (Gibson, 1967b; Domm & Domm, 1973; Collette & Talbot, 1972). The way in which an intertidal fish utilises time and tide phase, in relation to diet, has a direct bearing on its success in colonising a habitat. For this reason six 24h collections were made at three different sites and at different times in the spring-neap tidal cycle. From the results from these collections it was possible to examine the feeding activity of C. caffer in relation to time of day and tide phase.

In addition to the study of temporal utilisation of food resources, the spatial organisation of C. caffer was investigated. The single largest hazard facing an intertidal animal is water movement (Jones & Demetropoulos, 1968). The possibility that C. caffer might be limited in its movements by current velocity was investigated in the laboratory and current readings were taken in the field to allow comparison between the laboratory results and habitat conditions. This study of current tolerance proved invaluable in interpreting the results obtained from tagging experiments undertaken to analyse the system of space utilisation employed by C. caffer. C. caffer was known to ingest algae and that fish from algae-free pools also included algae in their diet (Pitt-Kennedy, 1968). The understanding of the movements of C. caffer in the intertidal region was of assistance in providing an understanding of the apparent anomaly of fish from algae-free pools eating algae. The distribution of C. caffer in the intertidal zone was investigated as a facet of the study of intertidal movements. Salinity and temperature in the field were also investigated to determine whether this species distribution was limited by these parameters.

Not all aspects of the biology of C. caffer were investigated. Age and growth studies were not conducted, nor were breeding behaviour or fecundity examined. The effects of predation were not examined as the collections that such a study would have required would have been beyond the scope of this project.

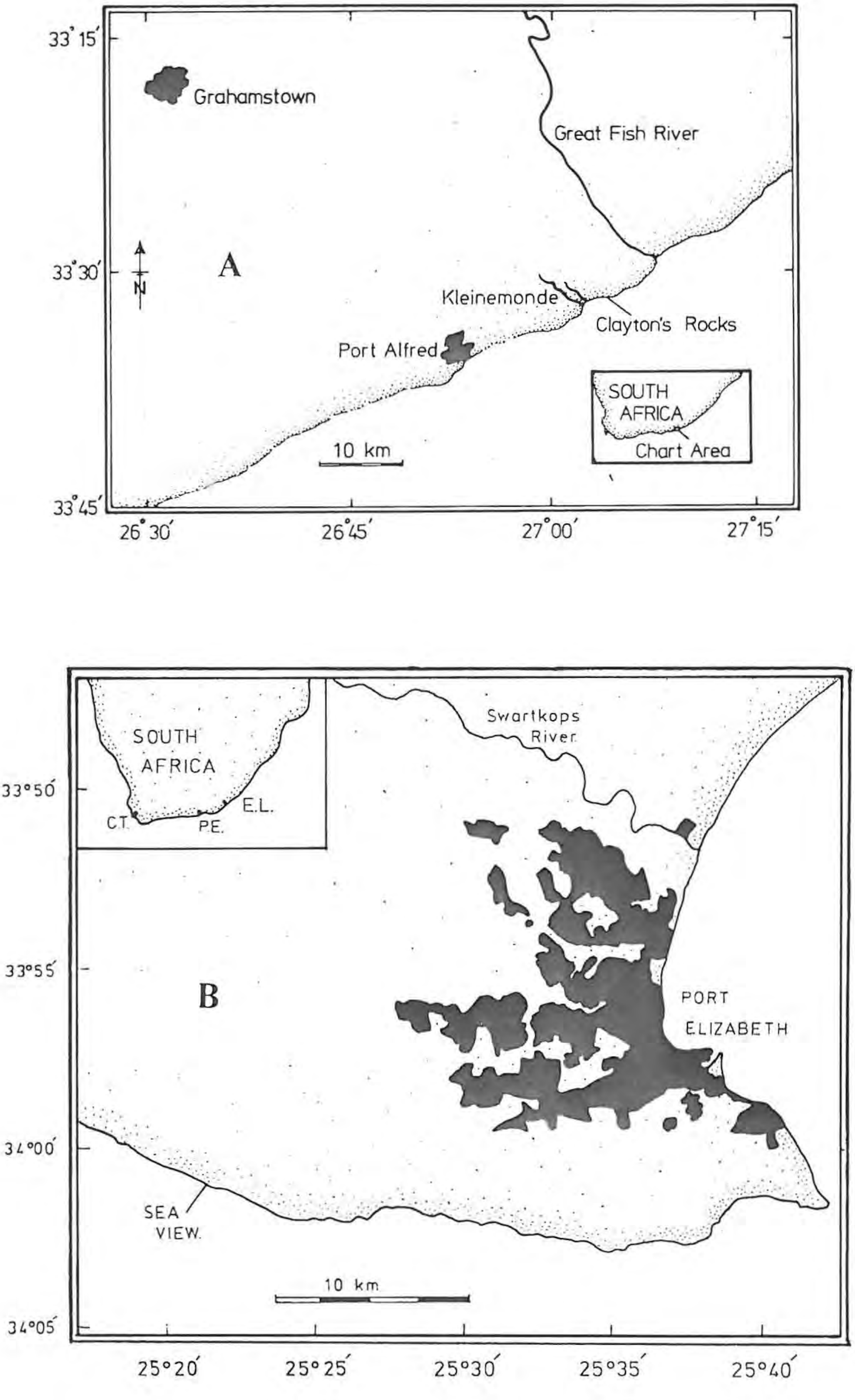
This report thus details the findings of investigations into some of the strategies utilised by the common intertidal goby, Caffrogobius caffer, which allow this species to survive the harsh conditions of the intertidal zone.

TAXONOMIC STATUS

As it is imperative that the identity of any species that is the subject of ecological study be accurately known, a short note on the taxonomic status of *Caffrogobius caffer* is given here.

Gobius caffer was first described by Günther (1874) on the basis of two 'purchased' specimens from Port Elizabeth. Steindachner (1881) and Thompson (1918) used the name *Gobius caffer* in their respective lists, but Barnard (1927) included all the naked headed gobies, *Gobius caffer*, *G. natalensis* and *G. gilchristi*, in the synonomy of *Gobius nudiceps*. Smith (1960) placed *G. nudiceps* and *G. caffer* into the genus *Coryphopterus*. Smith's key, description and illustrations enabled subsequent workers to separate *caffer* from the true *nudiceps*. Hence only those publications and records subsequent to 1960 have been consulted for distribution records and biological data.

C.R. Robins of Miami pointed out to M.M. Smith (pers. comm.) that the American genus *Coryphopterus* cannot be used for South African gobies, so Smith (1975) and Winterbottom (1976) placed *caffer* (along with several other species of gobies) temporarily into the genus *Gobius*, stating that these species would probably be divided between two or more genera by subsequent workers. Hoese & Winterbottom (1979) placed *caffer* into the genus *Caffrogobius* and thus the combination *Caffrogobius caffer* has been used in this study.



<u>Fig. 1</u>. Location of collection sites at Clayton's Rocks (A) and Sea View (B). (A, After Christensen, 1976).

STUDY AREAS

Three collection areas were used. The intertidal pools at Clayton's Rocks ($33^{\circ}32'$S, $27^{\circ}04'$E), which are situated 3,2km west of the two blind Kleinemonde estuaries in the eastern Cape, were used for diet studies and tagging experiments (Fig. 1a). The rock pools at this location were described by Christensen (1976) who divided the pools into three categories: 1) upper intertidal pools, 2) shallow pools in the mid-intertidal zone and 3) deep pools in the mid-intertidal zone. C. caffer was found in all three pool types, but occurred only in the shallow periphery of the deep pools. Their main distribution extends over the upper and mid-intertidal pools. The upper pools were situated at or above 1,55m above mean sea level (MSL) while the mid-intertidal pools lay between 0,7 and 1,3m above MSL. The upper intertidal and the mid-intertidal pools are referred to in this account as the high and low level pools respectively.

The topography of the high level pools was found to vary due to windblown sand. Sand deposits are built up during the neap tide periods (especially after strong winds) and are scoured out by spring tides (neap tides do not reach these pools). The low level pools were very constant in their topography as normal weather and heavy storms have little effect on sand distribution in these pools. A map of the pools used in the tagging studies at Clayton's Rocks is given in Fig 2. These pools were mapped by triangulation using a dumpy level. No attempt was made to map the detailed outline of the pools due to their irregular periphery. Thus the accurately plotted points obtained by triangulation were simply joined by straight lines.

For tagging and feeding studies, fish were captured at Sea View ($34^{\circ}01'$S, $25^{\circ}21'$E) which is situated 14km west of Port Elizabeth (Fig. 1b). Fig. 3 is a sketch map of the pools used during experiments conducted at this location. Sea View's intertidal area differed from that at Clayton's Rocks

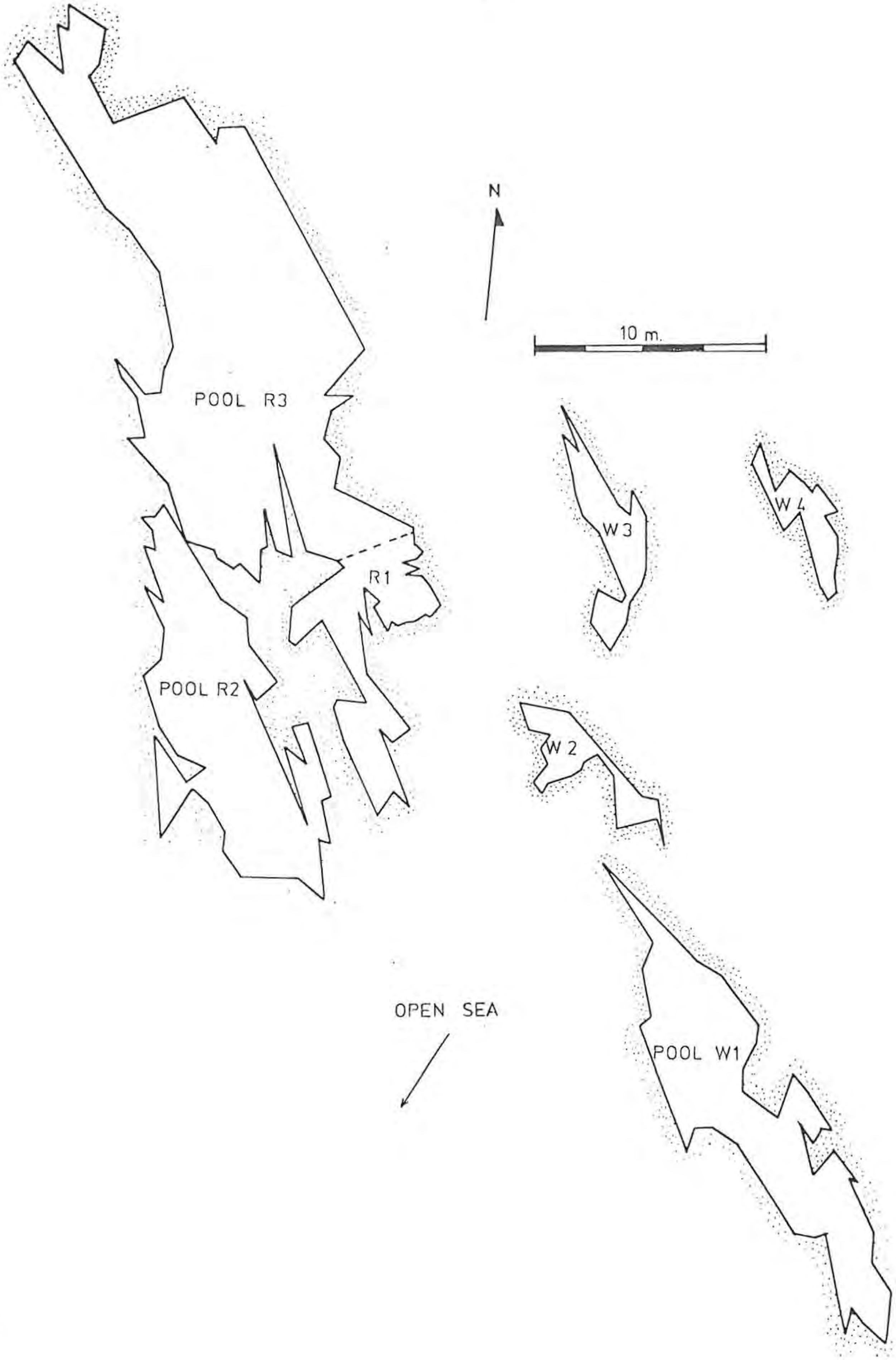


Fig. 2. Map of some of the pools used for feeding study collections and tagging experiments at Clayton's Rocks. Mapped during low tide,

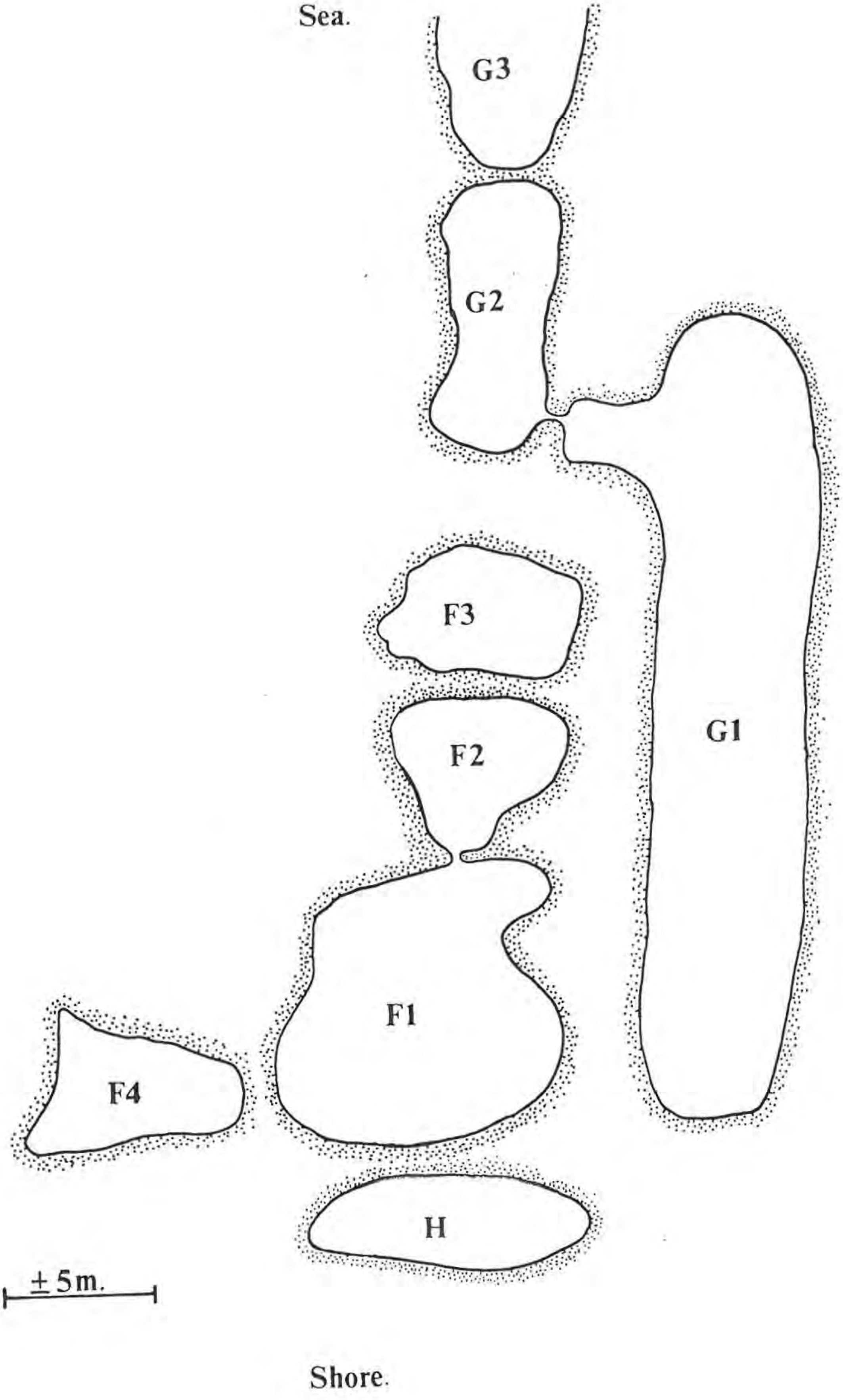


Fig. 3. Sketch map of pools used in tagging experiments at Sea View. Drawn during low tide.

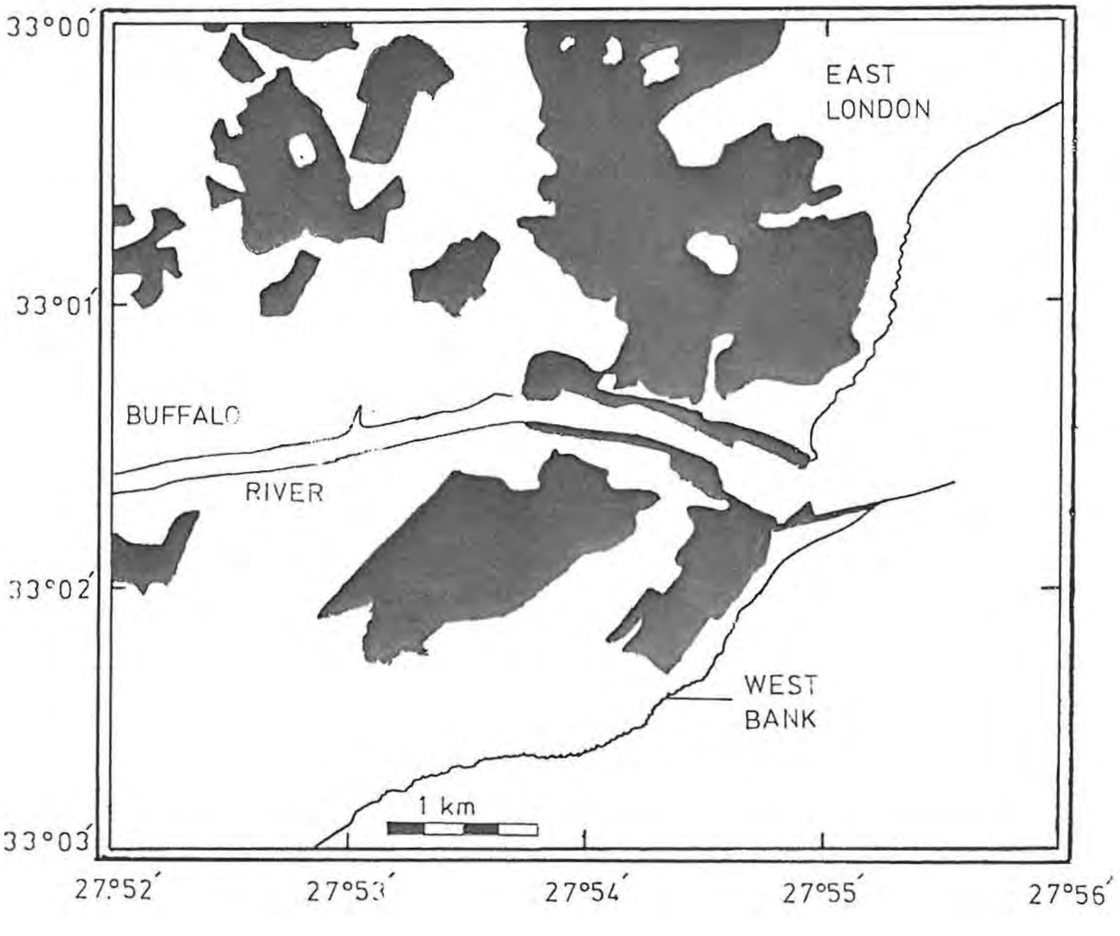


Fig. 4. Location of collection site at West Bank.

in that the latter is backed to landward by unconsolidated sand dunes, while at Sea View the coast is backed by low-lying, well-vegetated land inshore. Thus the high level pools at Sea View were not subjected to the rapid changes experienced by their counterparts at Clayton's Rocks due to sand deposition. Due to the strike of the rock strata at Sea View erosion has occurred in such a manner that the pools have a lineation running almost perpendicular to the coast. This contrasts with Clayton's Rocks where erosion has caused the pools to be protected by low ridges running at approximately 30° to the coast.

Several mid-intertidal pools and a single high level pool at West Bank (33°02'23"S, 27°54'20"E) (Fig. 4), situated 2km west of East London harbour, were used for two experiments (a tagging experiment and a test of a regurgitant for diet studies). The intertidal zone was narrower at West Bank than at the other sites. The mid-intertidal pools had the same characteristics as those at the other two locations, but the high level pools were similar to those at Sea View and were not filled by sand at any time. The pools at West Bank had no consistent lineation as at Sea View and Clayton's Rocks.

The high level pools at all three sites were devoid of algal cover. The low level pools could be subdivided into two broad categories on the basis of their algal cover. Those pools nearest to the open sea (below 0,85m above MSL at Clayton's Rocks) contained copious growths of corallines, while in the pools above this height, but below 1,5m above MSL, Ulva rigida J. Ag. dominated although no sharp interface between the two algal types existed (Fig. 5).

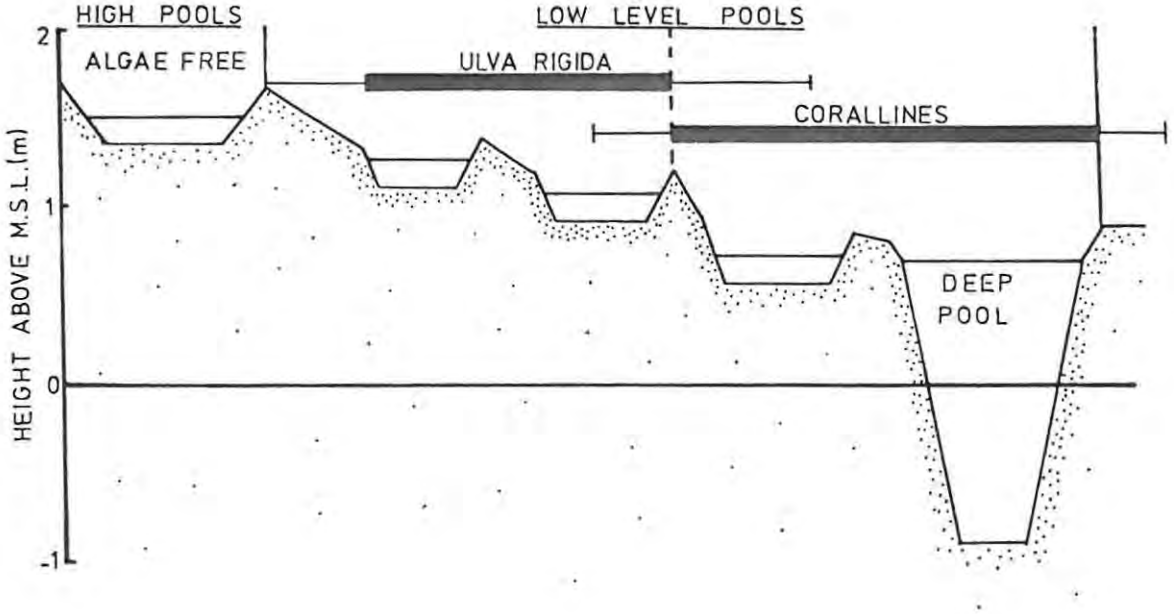


Fig. 5. Diagrammatic cross-section of the pools at the three collection sites, showing relative heights of high and low level pools and distribution of two major algal types. Vertical scale is accurate, horizontal scale compressed.

DISTRIBUTION OF CAFFROGOBIUS CAFFER

According to Smith (1960), C. caffer ranges from the Cape to Natal. Winterbottom (1976) established the northerly record at Umgazi (31°41'30"S, 29°27'24"E), while Pitt-Kennedy (1968) found this species in False Bay (18°30'S, 34°10'E) in the south. C. caffer is thus found along at least 1200km of the eastern seaboard of South Africa. The collection records of RUSI and personal observations showed that C. caffer is restricted to the intertidal zone in its distribution on the shore, and is found from the upper limits of the intertidal zone to a maximum depth of 1,5m in deep protected pools.

Gibson (1970a) reported that the distribution on the shore of the goby, Gobius cobitis Pallas, was not even with respect to size, as juveniles were more common in the higher pools of the intertidal region than in the lower pools. Branch (1975a) found that some Patella (Gastropoda) species were unevenly distributed on the shore in the western Cape. The juveniles remained in the surf zone while the adults moved up the shore as they grew. The possibility that C. caffer might also show a size dependent zonation up the shore was investigated by direct observation and by means of three poison collections. Two collections of C. caffer were made using the ichthyocide Pro-Noxfish from pools R1-3 and W4 at Clayton's Rocks (Fig. 2). After the poison had been placed in the water the pools were continuously monitored for dead fish over a four hour period. Dead fish were preserved in 10% formalin. A single poison collection was taken from a high level pool at West Bank. (Fish from the poison collections were not used for diet analysis, as poisoned fish may feed on other poisoned organisms, which they would not normally eat, prior to succumbing (Randall, 1967).)
The two collections from Clayton's Rocks were deposited as voucher specimens in the collection of RUSI (RUSI 77.1, RUSI 77.6).

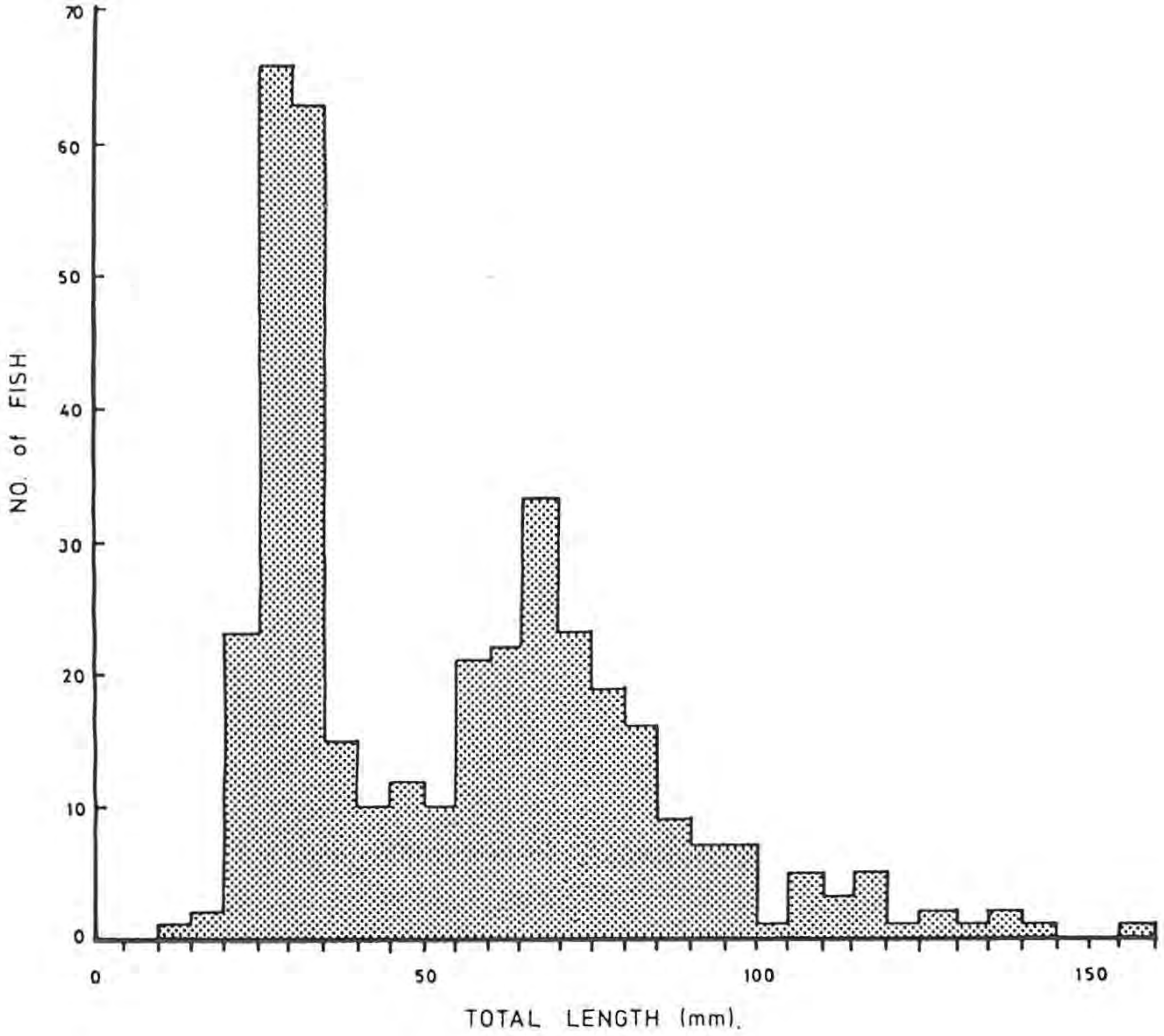


Fig 6. Length frequency histogram for 381 C. caffer collected from two adjacent low level pools at Clayton's Rocks (RUSI 77-1, RUSI 77-6, February 1977).

The two Clayton's Rocks poison collections showed that all size classes were present in this area (Fig. 6). The collection made at West Bank, primarily for movement studies (see below), showed that all size classes were present in the high level pools. The three poison collections confirmed visual observation and diet study collections that C. caffer did not exhibit any size dependent zonation on the shore, and thus that the population was evenly distributed on the shore relative to size.

Temperature and salinity were examined to determine their effect on the intertidal distribution of C. caffer. A Goldberg temperature-corrected refractometer, which gave immediate readings of total dissolved solids in parts per thousand, was used to measure salinity on each occasion that the collection sites were visited. Temperature was measured to the nearest 0,5°C at the same time as salinities were measured. A hand held mercury thermometer was used for temperature measurements.

The lowest salinity recorded from the habitat of C. caffer was 1°/oo. This reading was obtained from a pool into which there was freshwater seepage. The highest salinity recorded in the field was 45°/oo, while in the laboratory fish were unaffected by a salinity of 55°/oo.

Water temperatures recorded from the tide pools inhabited by C. caffer ranged from 14°C (winter) to 30°C in small isolated high pools in summer. The majority of the pools utilised by C. caffer were found to be within 1-2°C of the open sea temperature throughout the year. Those pools in which higher temperatures were recorded represented only a small proportion of the pools utilised by C. caffer.

No cases of mortality that could be attributed to either salinity or temperature were recorded. In most cases the temperature changes during a rising tide were in the order of 1-2°C (the difference between the open sea temperature and pool temperature). In those pools for which a high temperature was recorded the greatest temperature drop recorded was from 30°C to 18,5°C. The greatest recorded change in salinity was 34°/oo. Despite these extremes, C. caffer was found to inhabit the affected pools both before and after the change.

Discussion

Although temperature and salinity were found to vary over wide ranges within the intertidal zone,there was no indication that the environmental extremes recorded had an effect on the distribution of C. caffer. All permanent pools in the intertidal zones of all three collection sites, with the exception of very small pools devoid of cover, were inhabited by C. caffer. The evidence obtained indicated that C. caffer was able to tolerate the extremes of temperature and salinity in its environment. The tolerance shown by this species is not unique among intertidal fish. Beebe (1931) found that Bathygobius soporator (C. & V.) was able to survive salinities ranging from 0°/oo to ± 83°/oo in the laboratory with no apparent ill effects. Gibson (1969a), in his review of the biology of intertidal fish, reports similarly wide tolerances in several other intertidal fish species. Day et al. (1952) found that in the Knysna estuary many marine animals which inhabited the upper levels of the shore penetrated further up the estuary than those which lived in the lower levels of the intertidal region. These upper level animals were exposed to long periods of low salinity. Hill (in press) states that, 'Animals do not live in estuaries because of salinity, they live there despite it.' The same is probably true of intertidal animals. Gibson (1969a) cited various examples of tolerance of high temperatures by intertidal fish; for example, two Hawaiian tide pool fish species, a bleniid and a gobiid, survived a temperature of 41,2°C.

As the extremes of salinity and temperature found to occur in the habitat of C. caffer did not have a limiting effect on the intertidal distribution of this species in the eastern Cape, no detailed examination of the tolerance limits of C. caffer for these factors was necessary.

FOOD AND FEEDING

Introduction

Prior to this study the diet of C. caffer had been investigated by Pitt-Kennedy (1968) who studied two species, Caffrogobius nudiceps and C. caffer. He showed that C. caffer was omnivorous.

Several aspects of the diet of C. caffer were investigated during the present study. Many authors have reported a change in diet as fish increase in size (Hynes, 1950; Gibson, 1970a; Christensen, 1978b). Pitt-Kennedy (1968) reported that the diet of C. caffer changed as the fish increased in size, but his sample did not include any fish below 51mm in length. The change in diet associated with growth was investigated again in this study but in this case the smaller size classes were examined so that a more complete picture of the pattern could be obtained.

Pitt-Kennedy (1968) found that the green alga, Ulva spp., made up a large proportion of the diet of the size classes which he studied. He speculated about the value of such a food item in the diet of C. caffer as it appeared the Ulva underwent no change due to digestion. Pitt-Kennedy suggested two reasons why C. caffer might have ingested Ulva : C. caffer might have benefitted from the epifauna on the Ulva, or Ulva was ingested as, '...the fish, finding insufficient animal food available, eat the algae for its bulk in order to still their hunger, without deriving any nourishment from it' (p. 22). The first of these possibilities appeared to be the more plausible explanation and for this reason the epifauna of Ulva was examined in some detail in the present study.

Blaber (1974) found that juvenile Rhabdosargus holubi (Steindachner) in the West Kleinemond estuary utilised the epiphytic diatoms on Ruppia spiralis L.

Christensen (1978b) found that Sarpa salpa utilised epiphytic diatoms on Ulva at Clayton's Rocks. In the present study Ulva from Clayton's Rocks and also from the stomachs and intestines of C. caffer were examined under both the light and scanning electron microscope (SEM) to ascertain whether epiphytic diatoms were used by C. caffer. Beckley (1977) studied the epifauna associated with various algal species on St Croix Island, Algoa Bay (approximately midway between the Sea View and Clayton's Rocks collection sites), and found that many different types of animals were associated with the algae. Collections of Ulva from Clayton's Rocks were made during the present study and examined for epiphytic animals to determine whether the epifauna associated with this alga might be a source of nutrient for C. caffer.

The goby population at Clayton's Rocks was divided between two distinct pool types. The high level pools were reached by high spring tides only and were almost devoid of algal cover, while the low level pools were covered each high tide and had a well developed algal cover (Fig. 5). In view of the differences between the two pool types at Clayton's Rocks it was anticipated that dietary differences could have occurred between specimens from the different areas. Collections of C. caffer were made at monthly intervals for 12 months from both pool types. Monitoring the diet for a year allowed an examination of seasonal variation in diet, an aspect not covered by Pitt-Kennedy (1968). To further assist with this latter aspect, two of the 24h collections made for feeding periodicity studies (see below), one taken in winter and the other in summer, were examined to determine seasonal dietary variation.

Materials and Methods

Field methods

At least 10 fish per month were collected from both the high and low level pools at Clayton's Rocks. Collections were made over spring tides during the period March 1976 through February 1977. The high level pools were subject to periodic filling with sand and there were five months during which no collections could be made from these pools.

The same technique used by Jackson (1950) for the capture of *G. nudiceps*, (which probably included *C. caffer*) was used in this study. Jackson used both hand nets and baited hooks, and commented that larger specimens were most easily caught with baited hooks. In the present study the foot of *Oxystele* spp. was used as bait so that it could later be recognised and removed from the stomach.

There are two objections to these capture methods. The first, and probably the most important, is that the fish so caught do not necessarily represent a random sample of the population, as each fish has to be caught individually. This problem could not be avoided, but every attempt was made to capture fish from all size classes present in the pools. Secondly, there is the possibility that fish caught on baited hooks might not be representative for feeding studies (Randall, 1967), as their stomachs are either empty or contain only chum (digested, unidentifiable food remains). *C. caffer* of all size classes took baited hooks on all occasions. This fact, coupled with the low incidence of empty stomachs (5%), indicates that the fish caught had been feeding prior to capture. Windell & Bowen (1978) comment that fish should be placed into fixative as soon as possible after capture, and state that the use of a hook and line, which allows immediate preservation, has been shown to be a successful technique for catching fish for diet studies.

The use of anaesthetics and poisons is usually precluded in feeding studies for several reasons. Randall (1967) comments that the stomach contents of poisoned fish may not be reliable indicators of diet as small fish and invertebrates succumb to the poison first and may be eaten by more tolerant fish. Zweiacker & Summerfelt (1973) reviewed feeding data from six collections of largemouth bass (Micropterus salmoides (Lacepede)). They found that fewer fish taken by poison had empty stomachs than in collections made using electrofishing gear. No C. caffer could be caught in traps, and drag and throw nets could not be used due to the uneven nature of the topography of their habitat.

Attempts to cause regurgitation of stomach contents using tartar emetic (Jernejcic, 1969) proved unsuccessful. A laboratory test on fish fed artificial foods gave encouraging results which indicated that the technique might be usable for diet studies on C. caffer. In the field it was found that the percentage volume of the stomach contents actually regurgitated varied between 0% and 100%. Due to the fact that the fish sometimes regurgitated food when placed in formalin, each fish was placed in a separate bottle of preservative. The regurgitated portion of the food could then be reclaimed for analysis.

Laboratory methods

Wet mass and total length of the fish were determined and the fish were transferred to 40% propyl alcohol. For diet analysis the stomach contents only were examined. Food in the intestine was not identifiable as digestion of animal matter had proceeded too far. Stomach contents were identified using the following keys:

Invertebrates - Sars (1895), Barnard (1940), Barnard (1969), Griffiths (1974), Branch (1975b) and Day (1967 & 1969);

Algae - Taylor (1928), Seagrief (1967) and Day (1969);

Fish - Smith (1953).

Table 1.

Points allotment for stomach contents. The fullness was estimated by eye, after removing the stomach from the body cavity, and a number of points (0 - 30) was allotted. Captive fish fed to saturation with beef heart would have given a reading of 20 - 24 points. Wild caught fish sometimes contained a single large food item (e.g. Brachyura) which would greatly distend the stomach, giving a reading of 24 - 30 points.

Fullness Index	Points
Very distended	30
Distended	28
Very full	24
Full	20
$\frac{3}{4}$ Full	15
$\frac{1}{2}$ Full	10
$\frac{1}{4}$ Full	5
Empty	0

(After Christensen, 1976)

The techniques chosen for diet analysis were the points and occurrence methods (Hynes, 1950; Windell, 1971; Christensen, 1976). These two methods were chosen for their simplicity and speed (Hynes, 1950; Christensen, 1976). After excision from the body cavity the fullness of the stomach was estimated and then given the appropriate number of points (Table 1).

Food items were identified and the percentage volume which each food type contributed to the total was estimated using the chart presented by Christensen (1976)(Fig. 7). When this procedure had been conducted for all food types the number of points allocated to the stomach contents as a whole was divided between all food types in proportion to their volume. Any food that had been regurgitated was collected by centrifugation and its volume compared with that obtained from the stomach, which had already had points allocated to it. The regurgitated food was then added to the total, and the number of points was corrected accordingly.

For example, if a stomach had been awarded five points, but 50% of the total food volume had been regurgitated, then the number of points awarded was corrected to 10. The number of points awarded to a particular food item in each collection was expressed as a percentage of the total number of points awarded to all food items in that collection. The number of fish in which a particular food item occurred was expressed as a percentage of the total number of fish in that collection.

Recently, criticism has been leveled against the points method of diet analysis, and it is relevant here to defend my use of this method. The points method of diet analysis has been used for many years since Swynnerton & Worthington (1940) first used it. In their analysis they listed the food items in each stomach as very common, common or rare. They awarded points to these categories by scoring very common as 3 points, common as 2 points and

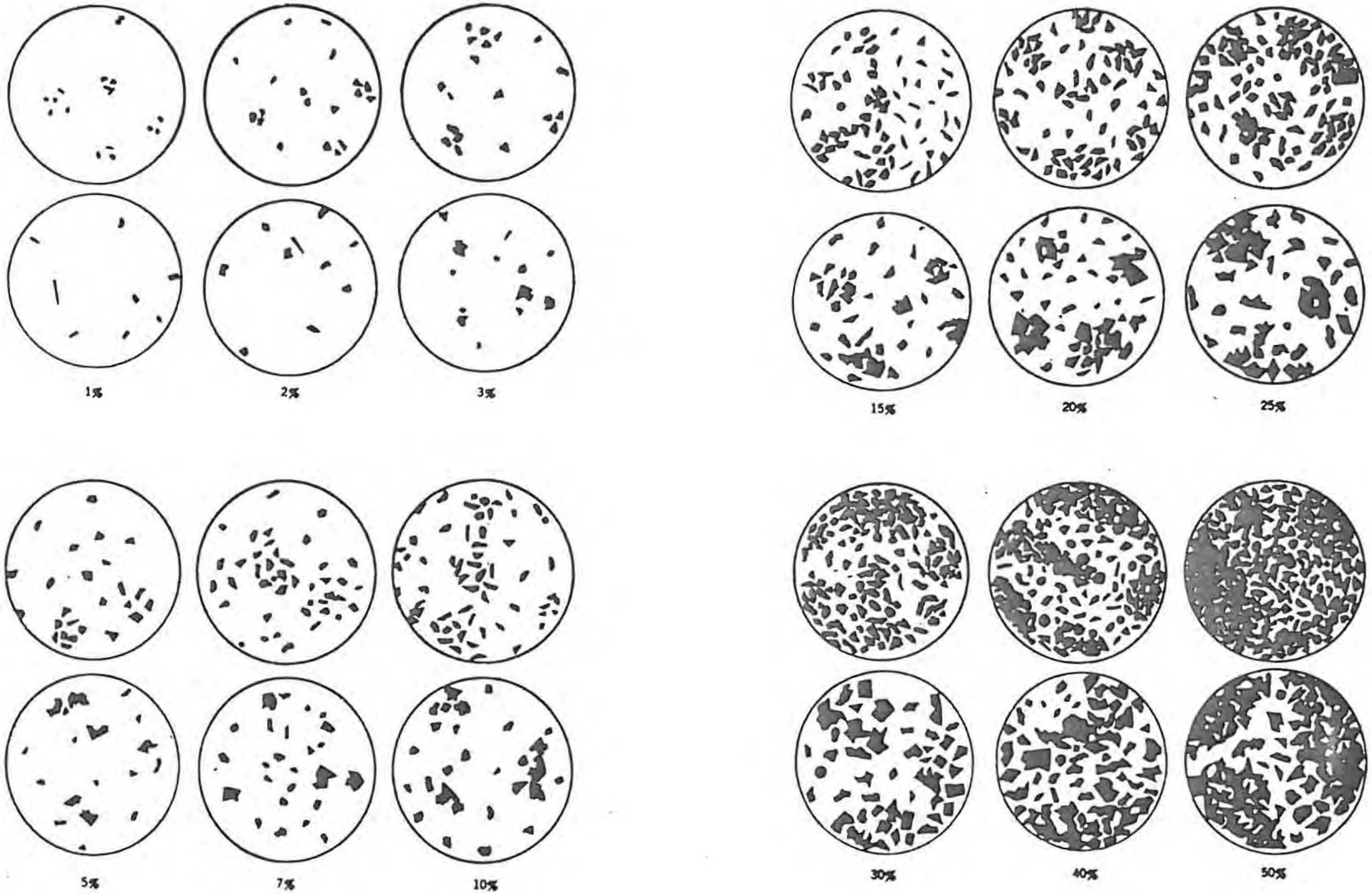


Fig. 7. Chart for estimating percentage composition of stomach contents. Stomach contents were spread evenly in a petri dish and the relative density of each food item compared under the microscope with densities in this chart. (After Christensen 1976).

rare as a single point. The reason that Swynnerton & Worthington (1940) gave for their choice of the points method was that they doubted whether the results from volumetric and gravimetric analysis justified the labour involved in producing these results. Frost (1943) adopted the points method but also took into consideration the fullness of the stomach when assigning points to food items. Hynes (1950) modified the method still further and increased to 30 the number of points that could be assigned to the stomach contents. He described his method of assigning points as follows: 'Food species present were identified as far as possible, and then each food item was allotted 1,2,4,8 or 16 points according to the volume of it present in the stomach. In this way one large organism counted as much as several small ones. in allotting the points the size of the fish and the fullness of the stomach were also taken into account, a full stomach, irrespective of the size of the fish receiving a total of about 20 points, and a distended stomach receiving about 30.' Hynes, 1950, 38).

Hynes (1950) found that his method of allotting points led to difficulties with a stomach distended with a single food item as such a stomach could only be given a total of 16 points instead of the 30 normally given to a distended stomach. He suggested that it might be better to award the stomach contents as a whole a number of points depending on stomach fullness and then to sub-divide this total amongst the various food items according to their different volumes. Christensen (1978a, b) followed this latter suggestion but did not use the discrete points values of 1,2,4, etc., allowing intermediate values to exist up to a total of 30 points for a distended stomach. All estimates were made with the food items spread out to an even depth throughout the microscope field. The relative volumes were then estimated with the aid of Data Sheet No. 6 of Geotimes (Fig. 7).

Arguments for and against the use of the points method have appeared in the literature. Hynes (1950), while recognising the limitations of the method, was strongly in favour of the points method. He felt that it was a rapid method requiring no special apparatus for its measurement, that it was not affected by frequent occurrence of small organisms or by large items and that it did not give the spurious impression of accuracy given by some other methods. Hynes realised that the method was subjective but felt that when large samples were used experience would be gained and the allotment of points would become uniform. (See Appendix 1 for a full quote of Hynes' arguments.)

Windell & Bowen (1978) severely criticised the points method and considered it of little use in solving any clearly defined question and that it therefore did not meet modern requirements for a method in critical scientific investigation. This criticism is based on several arguments, which are of interest because they are inaccurate in their reporting of the literature. Windell & Bowen's criticism is based on Hynes' (1950) paper. They incorrectly state that his allotment of points to food item was (1),'based on the number of items present and (2) the size of the items in the category'. (Windell & Bowen, 1978, p. 223). It is correct that these factors were taken into account by Hynes, but Windell & Bowen make no mention of the fact that Hynes also took the fullness of the stomach into consideration, thus ignoring an important part of the technique proposed by Hynes.

Windell & Bowen (1978) went on to state: 'Workers who have used the points method in conjunction with the numerical and volumetric methods (Fagade, 1971; Munro, 1967) have generally drawn their conclusions from the latter and found points to be of little use. ' (p. 224). Munro (1967) did not in fact use the points method at all, rejecting it with the following comment: 'Hynes (1950) reviewed the methods used in the studies of the food of fishes, and concluded that the "points method" is the most satisfactory. He was, however, dealing with small fishes (Gasterosteus and Pygosteus), and it would appear that this method might not be the best when dealing with larger fish' (p. 391) and : 'The "points method" described by Hynes (1950) assesses only the relative importance'(of food items in the stomach)(p. 391). Munro offered no explanation as to why the points method should not be applied to fish larger than the sticklebacks studied by Hynes. Fagade (1971) did, in fact, use the points method, but he offered no criticism of it. He based his modification (up to 100 points, no fish with less than half filled stomachs used) on Swynnerton & Worthington's (1940) method, but he did not give reasons why he modified their method. Fagade's (1971) discussion of his results included both the points and occurrence methods that he had used, thus: 'The tables show that although qualitatively the food is alike in the 2 species there are significant quantitative differences' (p. 155). In this quote 'qualitative' refers to the occurrence method, while 'quantitative' refers to the points method.

Windell & Bowen (1978) state that the points method of diet analysis is a numerical-volumetric hybrid. This is true of the method in its earliest form (Swynnerton & Worthington, 1940; Frost, 1943), but it does not hold true for the method with the modifications suggested by Hynes (1950) and applied by Christensen (1978a, b) and in the present study. In these three latter studies the points method provided an estimated volumetric index independent of fish size. This particular misunderstanding on the part of Windell & Bowen appears to be due to these authors ignoring the inherent potential of the modifications to the method which Hynes suggested.

Windell & Bowen (1978) also claim that statistics can not be applied to results obtained by the points method. While it is true that parametric statistics should not be applied to indices (Sokal & Rohlf, 1969), the same is not true of non-parametric statistics (Siegel, 1956). In this study the non-parametric statistic, Spearman's rank correlation coefficient, was applied to points data (Siegel, 1956). This test was also used by Christensen (1978a, c) for comparisons involving points data.

The outright condemnation of the points method by Windell & Bowen (1978) is therefore open to question. This is especially true when these authors' interpretation of the evidence in the literature is taken into consideration. The points method appears to be as valid a method as any other for analysing diet if relative information only is required.

Examination of *Ulva rigida*

Samples of *Ulva rigida* were collected from the field and from the stomach and intestine of freshly killed *C. caffer* and preserved in either gluteraldehyde or 10% formalin. These samples were then examined under both light microscope and SEM to establish whether *C. caffer* was utilising epiphytic diatoms and bacteria. Samples of *Ulva rigida* were also examined for the number of animals (e.g. Crustacea and Polychaeta) per gm dried mass of alga. All alga and fish samples used in these investigations were collected at Clayton's Rocks.

Statistical treatment of the feeding data

To compare the total diet of those fish caught in the high level pools with those from the low level pools, the non-parametric statistic, Spearman's rank correlation coefficient, was used. This statistic allows comparison of the relative importance of data pairs from two separate sets of data. The statistic can be applied to data used to calculate relative abundance (e.g. points and occurrence data). Ranks are given serially to data, the highest rank, N, (where N is equal to the total number of data pairs) is given to the numerically largest datum points in the samples.

Ranks are affected by relative numerical values only and no difference results if ranks are applied to derived data (e.g. percentages) or to original results. Samples to be compared can be of unequal size, but the number of ranks given to each sample must be equal. If two or more items have the same value within one sample they are referred to as ties. The rank assigned to tied values is the mean of the ranks that would have been assigned had no ties occurred.

After each food item had been ranked for each sample to be compared, for both points and occurrence data, Spearman's rank correlation coefficient was calculated for each comparison by applying the following formulae;

$$\text{where} \quad rs = \frac{\Sigma x^2 + \Sigma y^2 - \Sigma d^2}{2\sqrt{\Sigma x^2 \, \Sigma y^2}}$$

$$\text{and} \quad \Sigma x^2 = \frac{N^3 - N}{12} - \Sigma Tx$$

$$\text{and} \quad \Sigma y^2 = \frac{N^3 - N}{12} - \Sigma Ty$$

$$\text{and} \quad T = \frac{m^3 - m}{12}$$

where rs = Spearman's rank correlation coefficient, N = number of ranks, d = difference between ranks for the same food item, T = correction factor for tied data, and m = number of observations tied at a given rank.

rs can be converted to a Student's t value, allowing the probabilities to be read off the appropriate tables (Rohlf & Sokal, 1969) for a one tailed test, by applying the formula;

$$t = rs\sqrt{\frac{N - 2}{1 - rs^2}}$$

where t = Student's t, rs and N as defined above. The degrees of freedom are equal to N - 2. (Siegel, 1956; Sokal & Rohlf, 1969).

Table 2.

Results from the application of Spearman's rank correlation coefficient, testing for correlation between the diets of fish from the low and high level pools on a monthly basis. The % points data from the low level pools was tested against the % points data from the high level pools and the process repeated for the % occurrence data. The null hypothesis states that the two variables are unrelated. $p < 0,05$ is considered significant. rs = Spearman's rank correlation coefficient, t = Student's t for a one tailed test and df = degrees of freedom.

	% points				% occurrence			
Date	rs	t	p	df	rs	t	p	df
March	0,1352	0,5106	>0,1	14	0,2858	1,1159	>0,1	14
April	0,1658	0,5317	>0,1	10	0,3662	1,2445	>0,1	10
July	-0,2109	-0,7474	>0,1	12	-0,0099	-0,0343	>0,1	12
Sept.	0,1135	1,3613	>0,1	10	0,0419	0,1326	>0,1	10
Nov.	-0,5026	-2,1753	<0,025	14	-0,1152	-0,4339	>0,1	14
Jan.	0,4772	2,1031	<0,05	15	0,5662	2,6604	<0,01	15
Feb.	-0,0927	-0,3088	>0,1	11	0,0549	0,1824	>0,1	11
Meaned data for entire year;								
	0,8218	6,7651	<0,0005	22	0,8144	6,5825	<0,0005	22

This technique was used by Fritz (1974) to compare the diets of fish of the same species from similar but widely separated areas. Christensen (1978a) used Spearman's test to compare the diets of two species of clinids when trying to establish ecological separation between the two species. In the present study diets of high level pool fish were compared with the diet of low level pool fish on a monthly basis. To allow comparison of the diets from the two areas for the entire year of study the monthly data was combined for each area, ranked serially, and compared by using Spearman's test. The two 24h collections made at Clayton's Rocks (see Daily Feeding Periodicity, below, for a description of the methods used for these collections) were compared by this test to help establish whether C. caffer displayed any seasonal variation of diet.

Results

Comparison of high and low pool feeding data

The diet of C. caffer was different in the two pool types on a monthly basis as shown by the various graphs (Figs. 8-14). For example, Ulva spp. were less important in the high level pools than in low pools. This difference was no doubt due to the algae-free nature of the high level pools. Amphipods were relatively more important in the high level pools than was the case in the low level pools (this latter trend can best be seen in the size class diet graphs, Figs. 8-11).

For those months in which collections were taken from both pool types the diets were statistically compared by Spearman's test (Table 2). Significant correlation between the diets from the two areas was found for only three comparisons ($p < 0,05$ was used as the critical level of significance). When the results of the points method were compared positive correlation occurred in November ($p < 0,025$) and in January ($p < 0,05$). Positive correlation between data from the two areas existed in January ($p < 0,01$) for the

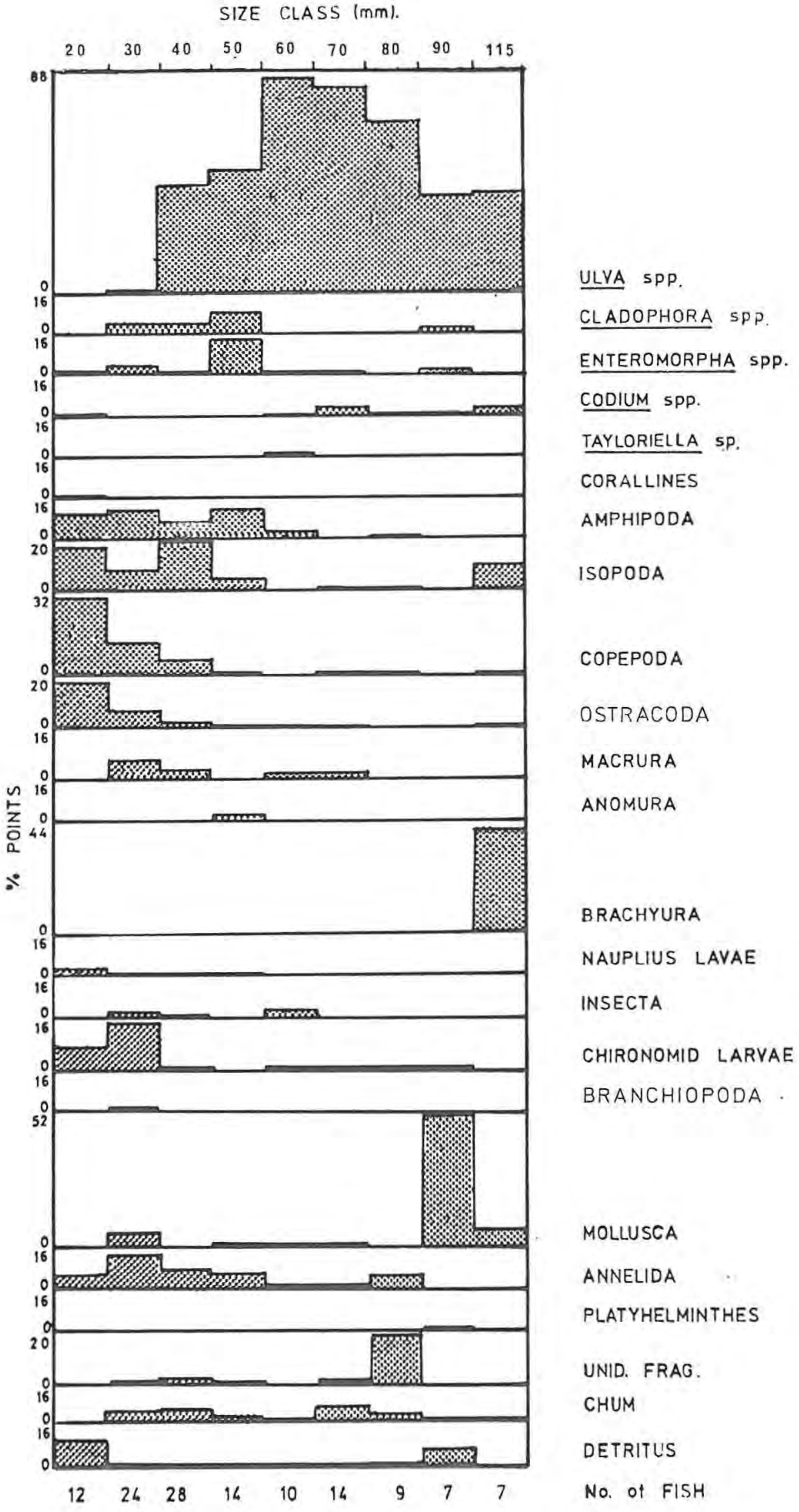


Fig. 8. Results of stomach content analysis using the points method for different size classes of *C. caffer* caught in low level pools at Clayton's Rocks.

occurrence data. All other monthly comparisons showed that the diet of C. caffer was significantly different in the high and low level pools.

When the feeding data for the whole year from the high level pools were combined and compared statistically with the combined low level pool data for the year, a different result was obtained. In this case the dietary data from the two areas were found to be significantly correlated for both diet analysis methods ($p < 0,0005$ in both cases).

There was thus a difference in the diet of C. caffer from the different pool types on a monthly basis, but this difference was not significant over a year.

Size class diet analysis

a. Low level pools (Figs. 8,9 & 12b)

Some food types were rarely ingested and showed no discernible trend in relation to fish size. These included Cladophora spp., Enteromorpha spp., Tayloriella spp., corallines, Macrura, Anomura, adult Insecta, Branchiopoda and Platyhelminthes.

Three trends were discernible among the remaining food types. Ulva spp. were absent from the smallest size class and, after appearing in the second, increased in importance to become the most important single food item in the middle size classes. This importance then decreased in the largest size classes. The second trend was shown by some of the prey (Amphipoda, Copepoda, Ostracoda, nauplius and chironomid larvae and, to a lesser degree, Annelida). These organisms were found more frequently (Fig. 9) and in relatively greater volume (Fig. 8) in the smaller size classes and decreased in importance as the importance of Ulva increased. The third trend was less obvious and less well substantiated than the previous two.

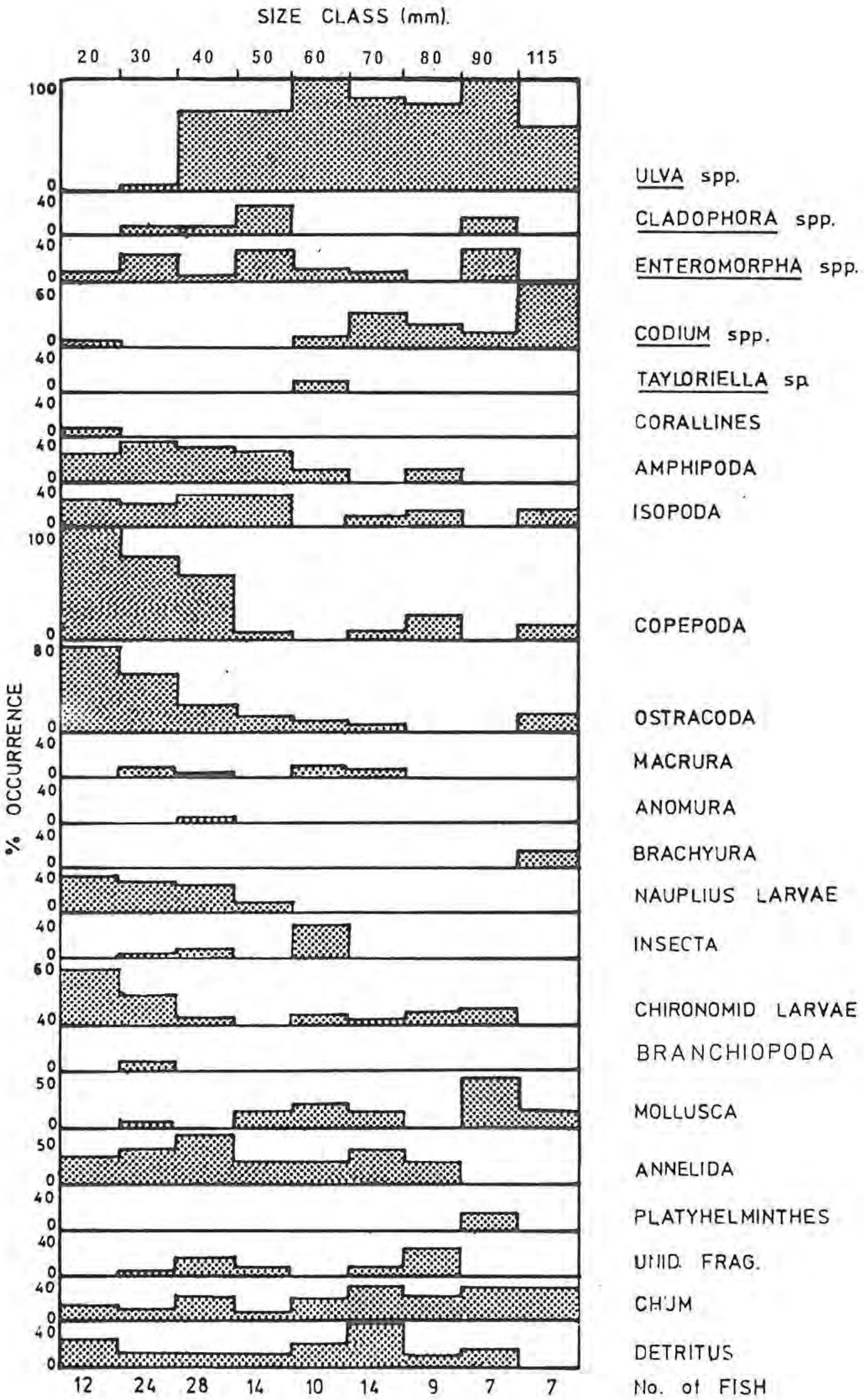


Fig. 9. Results of stomach content analysis using the occurrence method for different size classes of *C. caffer* caught in low level pools at Clayton's Rocks.

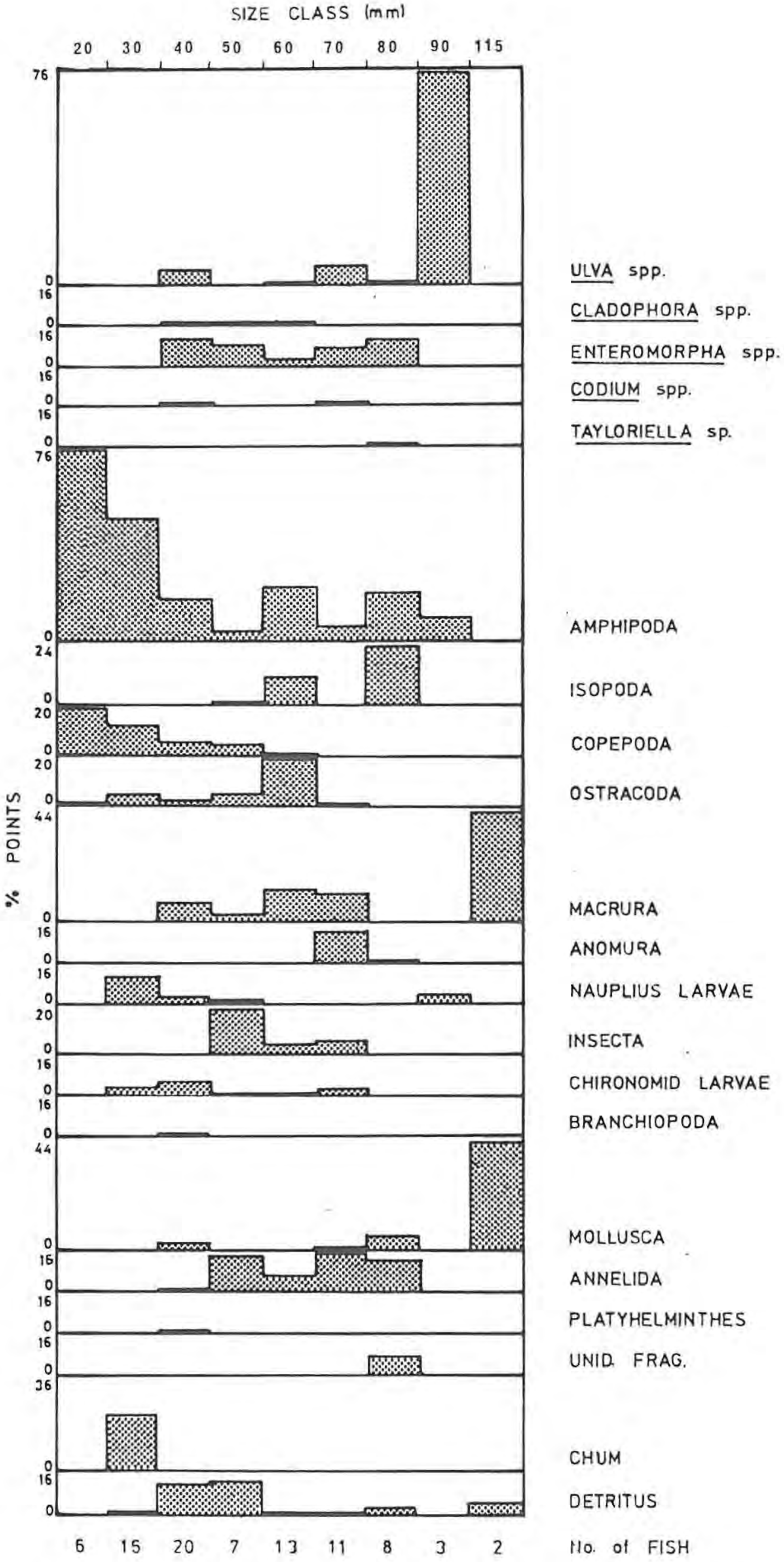


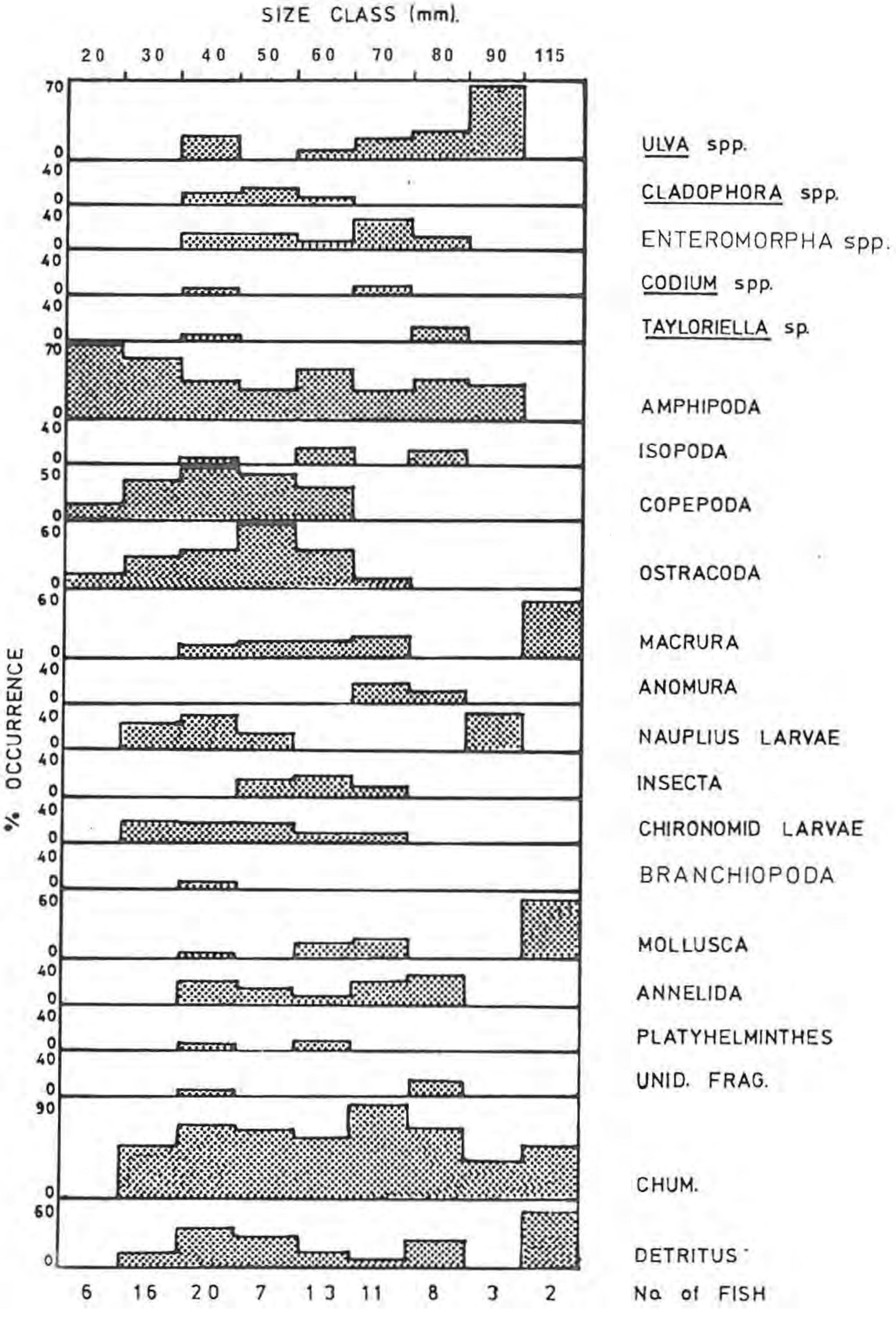
Fig. 10. Results of stomach content analysis using the points method for different size classes of C. caffer caught in the high level pools at Clayton's Rocks.

Codium, Brachyura and Mollusca were most important in the diet of larger fish but were absent in smaller specimens.

The overall trend, therefore, appeared to be for the smaller fish to feed predominantly on smaller food items (<3mm), changing to a more herbivorous diet in the intermediate size classes. The larger fish fed on larger prey organisms such as molluscs and crabs. The change in diet is summarised in Fig. 12b.

b. High level pools (Figs. 10,11 & 12a)

The trends exhibited by fish from the low level pools were not clearly seen in high level pool fish. In these latter fish Ulva first occurred in the second size class, which compared well with the data from the low level pools. Ulva did not, however, attain the importance or uniformity of occurrence that was found in the low level pool diet. Amphipoda were the most important food type volumetrically and were most important in the smallest size classes. The occurrence data for Amphipoda remained relatively constant for all size classes in which they occurred, indicating that an approximately constant percentage of fish in each size class ate Amphipoda. Copepoda showed the same trend as Amphipoda for volume - a decrease in importance as fish size increased, but this trend was reversed for the occurrence data. Ostracoda gained in importance volumetrically with increasing fish size, reaching a peak in the 60mm size class, while a trend similar to that exhibited by Copepoda was shown by the occurrence data - an increase in importance with increasing fish size. Ostracods and copepods were not ingested by fish of the 70mm size class and above. Mollusca and Brachyura reached maximum importance in the largest size classes, the same situation found for these food types in the low level pool diet.



<u>Fig. 11</u>. Results of stomach content analysis using the occurrence method for different size classes of <u>C. caffer</u> caught in high level pools at Clayton's Rocks.

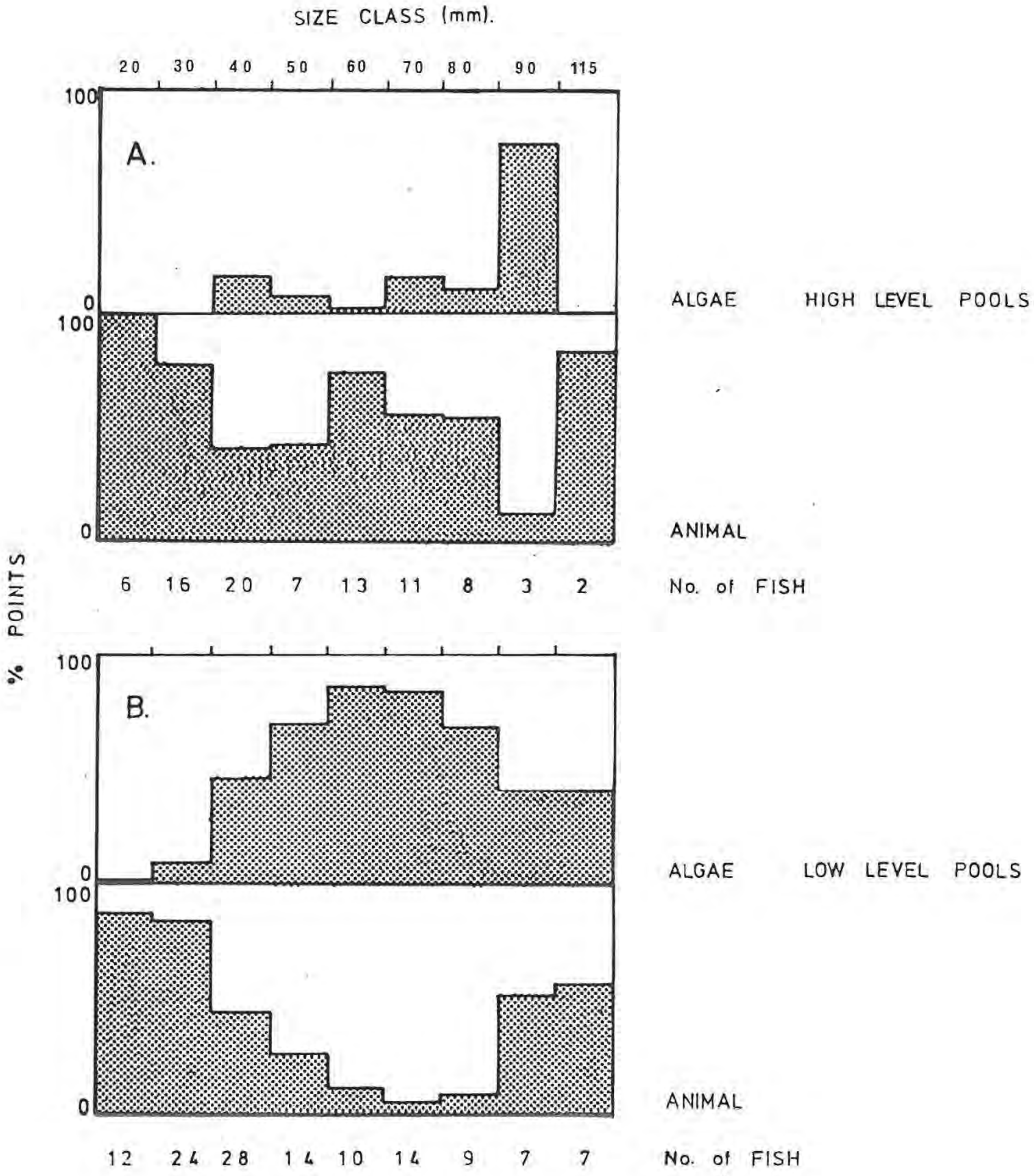


Fig. 12. Results of stomach content analysis using the points method for different size classes of *C. caffer* caught in (A) high and (B) low level pools at Clayton's Rocks. Data from all algal food types are combined to form the category 'Algae', while data from all animal food types are represented by the category 'Animal'. Unidentified Fragments, Chum and Detritus have not been included in either category.

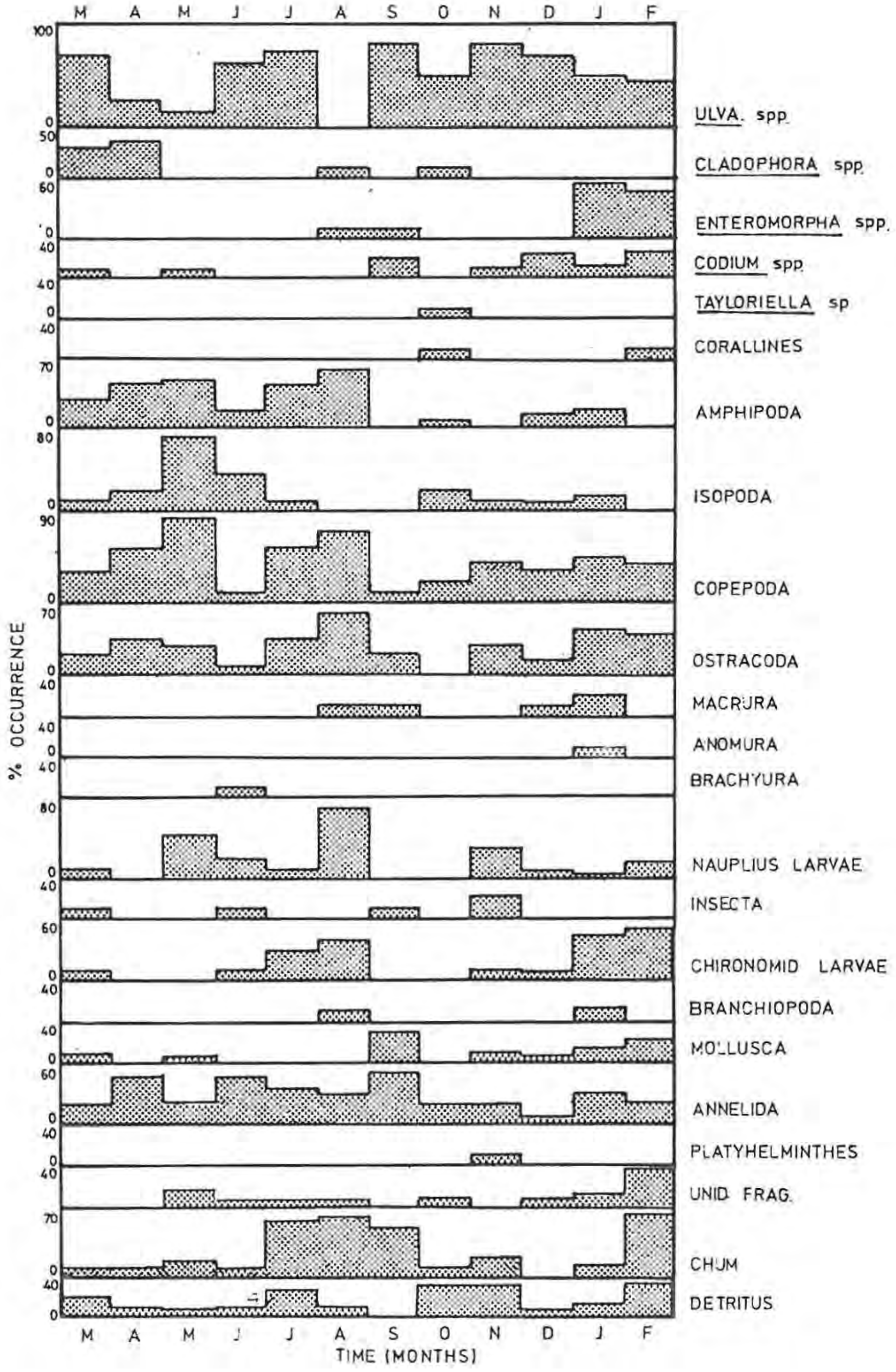


Fig. 13. Results of stomach content analysis using the occurence method for collections of C. caffer taken during different months from the low level pools at Clayton's Rocks.

Seasonal diet analysis (Figs. 13, 14 & 15)

When the 12 months data from the low level pools were examined it was found that no discernible trends due to seasonal influence were evident. Determination of seasonal trends in the diet of the high level pool fish was complicated by the fact that collections were only taken during seven months. The lack of collections during the remaining five months was due to the pools being full of silt.

Food items that had been found to have size dependent trends of ingestion had scattered or continuous occurrence throughout the year, e.g. Copepoda. Even though in some months these food items were not present in the diet, these absences appeared rather to be due to chance than to any seasonal rhythms in diet. The absence of Ulva from the diet of low level pool fish in August (a month for which no high level pool data was available) was considered as being due to chance and not to seasonal variation. Were this absence due to a seasonal variation it would have been flanked by low or zero values for Ulva in other months. Observation in the field during August showed that Ulva was present in the habitat of C. caffer.

The two 24h collections made at Clayton's Rocks (Fig. 15) from the low level pools were compared by Spearman's test for both points and occurrence data. These tests showed that there was no significant difference between the summer and winter diets of C. caffer. For the points data the t value (4,618) gave $p < 0,0005$ (df = 18), while for the occurrence data the t of 3,452 gave $p < 0,0005$ (df = 18). It would thus appear that the diet of C. caffer was not dependent upon the time of year during the sampling period 1976 to 1979.

An interesting difference between the two 24h collections and the diet

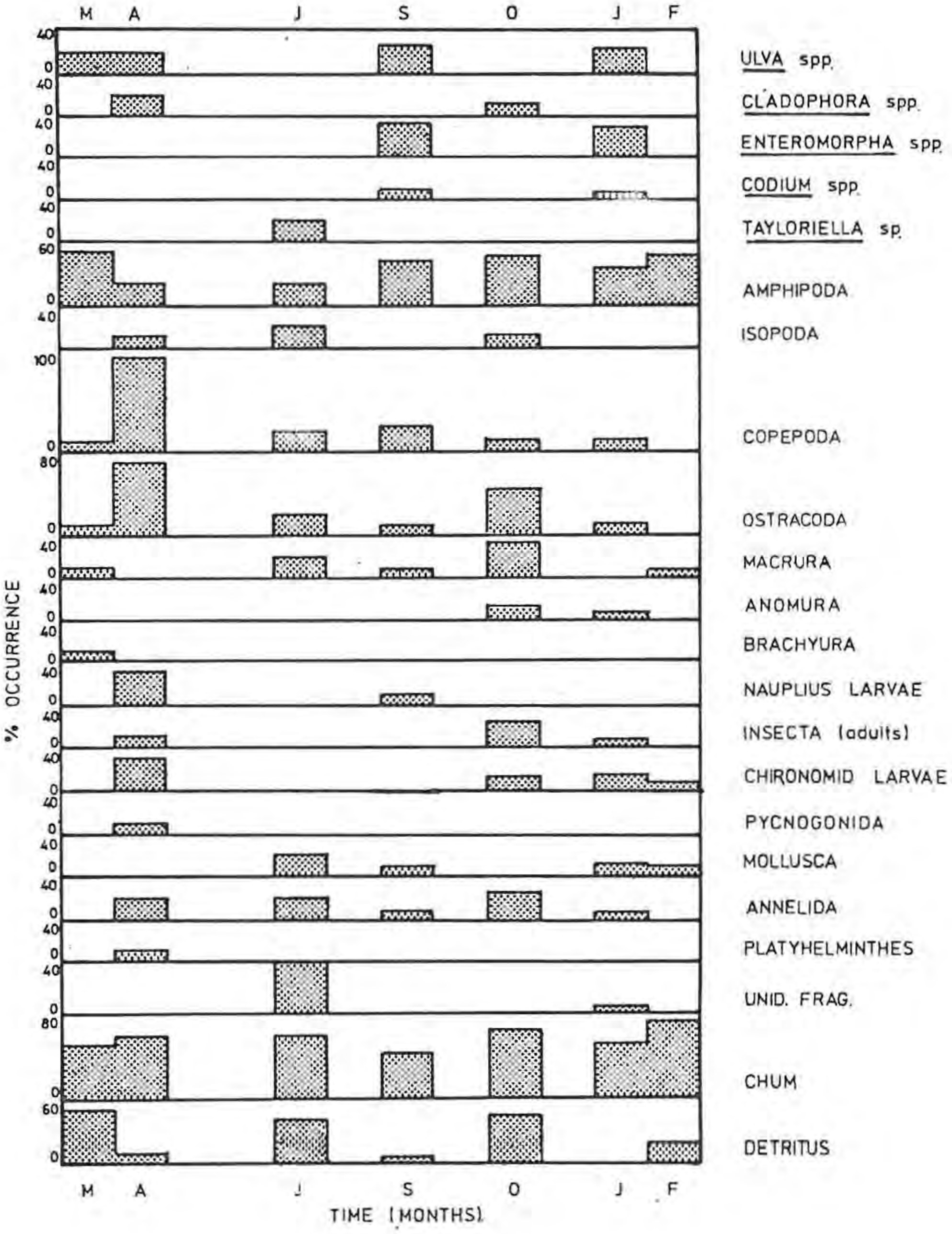


Fig. 14. Results of stomach content analysis using the occurrence method for collections of C. caffer taken during different months from high level pools at Clayton's Rocks.

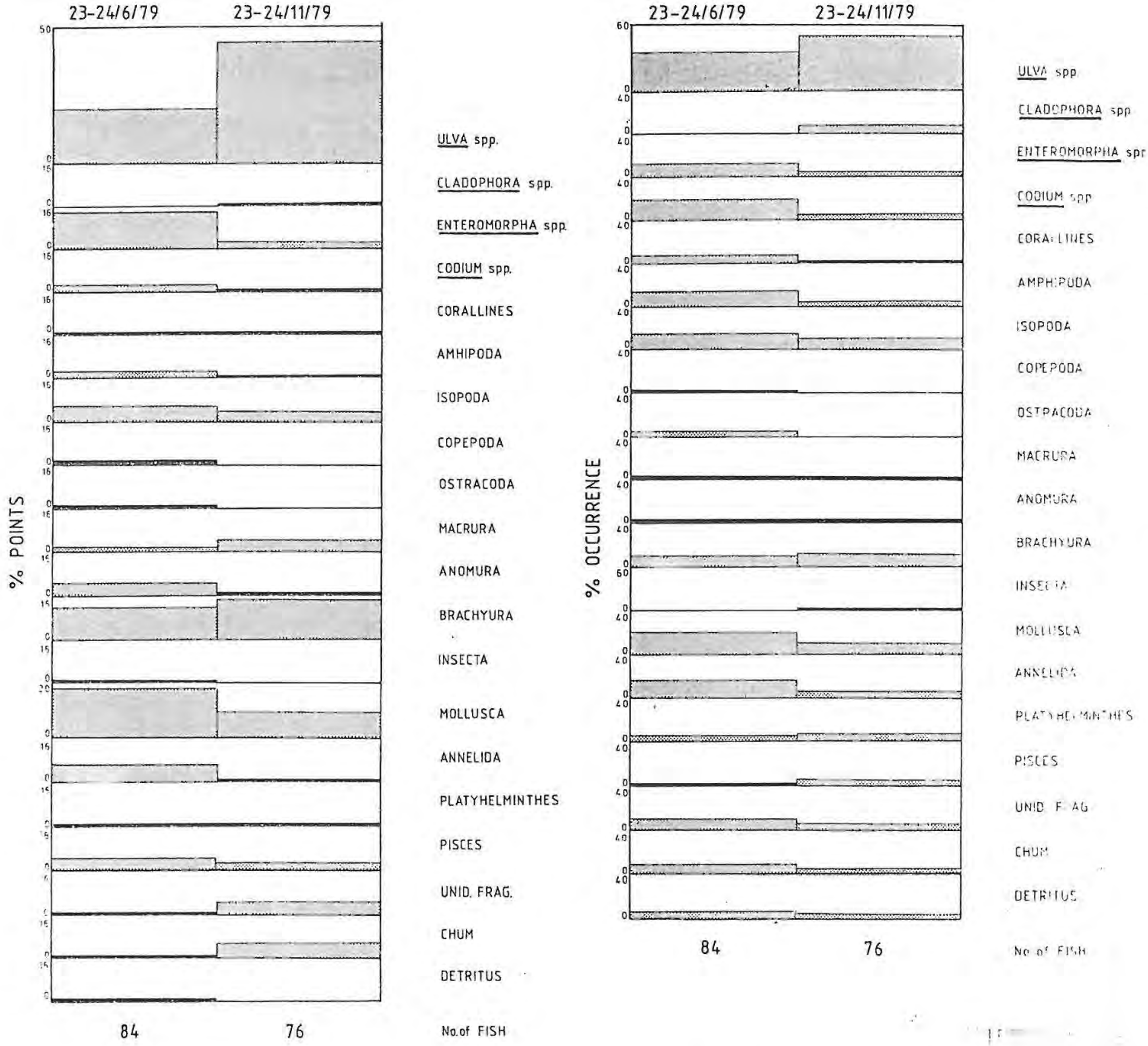


Fig. 15. Results of the two 24h diet collections made at Clayton's Rocks analysed for points and occurrence presented together to allow comparison of winter (23-23/6/79) and summer (23-24/11/79) collections for seasonal variation in diet.

study collections was that fish were found to form part of the diet of *C. caffer*. The ingested fish were found to be *C. caffer*, illustrating the fact that *C. caffer* is sometimes cannabalistic under normal conditions. Cannabalism had been seen in the field on two other occasions. When fish were being freeze branded for movement studies a small fish that had just been branded was eaten by a larger conspecific before it had time to recover from the anaesthetic used. During a later stage of the movement studies a large specimen of *C. caffer* was captured at night in a hand net and was found to contain a smaller conspecific.

Microscopic examination of *Ulva rigida*

Under the light microscope no change to *Ulva*, after passage through the alimentary canal, that could be ascribed to digestive action was recorded. No difference was noted between alga from the field and that taken from the guts of *C. caffer*. The same findings were true for examination under the SEM.

The SEM revealed the presence of epiphytic bacteria and diatoms on *Ulva rigida* in low numbers. This finding was true for specimens of alga taken from the field and from *C. caffer* guts. If diatoms were utilised by *C. caffer* it was expected that gut samples of *Ulva* would have fewer diatoms than found on field samples, with the number of diatoms on the alga decreasing progressively along the gut. No such progressive decrease in diatom numbers was seen under either light or scanning electron microscopes. *Ulva* was taken from the stomachs, middle of the intestine and the end of the intestine near the anus. It thus appeared that *C. caffer* did not ingest *Ulva* for the nutritional benefit that could be obtained from the diatoms and bacteria.

Ulva rigida samples taken from the field were examined for epifauna and

Table 3.

Mean number of epifaunal animals found per gram of dried mass on algal samples from St Croix Island by Beckley (1977)(first three columns) and mean number of epifaunal animals per gram of dried mass of *Ulva rigida* at Clayton's Rocks (fourth column).

	St Croix Island After Beckley (1977)			Clayton's Rocks present study
	Ulva rigida	*Enteromorpha* spp.	*Corallina* spp.	*Ulva rigida*
Foraminifera	7	4	10	0
Nemertea	5	0	1	3
Nematoda	996	37	51	851
Annelida	74	1	15	150
Echiura	39	110	0	0
Ostracoda	9	9	75	81
Copepoda	1742	339	83	598
Isopoda	3	62	6	20
Amphipoda	50	9	11	34
Nauplius larvae	4	196	9	96
Insect larvae	1	0	0	6
Arachnida acari	12	1	7	0
Gastropoda	17	2	18	130
Pelecypoda	20	0	3	1
Echinoidea	0	0	1	0
Number of samples	8	4	4	14

results are presented in Table 3. The first three columns of Table 3 are based on data presented by Beckley (1977) and represent the means of data she collected from three different transects on St Croix Island, Algoa Bay, for three different algal types. The fourth column represents the mean of 14 different collections of Ulva rigida collected by the writer during 1978 and 1979 at Clayton's Rocks. Table 3 shows that several of the food types ingested by C. caffer were associated with algae. Notable among these organisms are Copepoda, Mollusca and Annelida which are important in the diet of C. caffer (see Figs. 8 - 14). Although C. caffer probably does not only obtain food items off algae, it would appear that algae is an important source of animal food to this species.

Discussion

The pools used in this study were chosen as they represent two extremes of the habitat of C. caffer. The possibility of a dual habitat for a single intertidal fish species appears to have been largely ignored by previous workers. Gibson (1970a) studied the diet of Gobius cobitis Pallas, an intertidal fish with a similar vertical distribution on the shore to C. caffer (Gibson, 1972), but he made no mention of collecting from different pool types. Miller (1961) treated Gobius paganellus L. as having an uniform feeding pattern up the shore, despite the fact that this species occupies pools similar to the high pools used by C. caffer. The argument could be put that, as the majority of the goby population were found in low level pools, it was not necessary to study fish from the marginal areas as they represent only a relatively small percentage of the entire population. The results obtained in this study indicate that to ignore fish from the high level pools would be to ignore an important part of the feeding population.

For each sampling, significant differences in diet between the two areas were found (Table 2). The similarity in the diet of the fish from the high and low level pools over the whole year was unexpected. Thus on a monthly basis the fish from each area were filling different 'sub-niches', but over a longer time span they occupied the same feeding niche. The reason for the differences in monthly data was probably due to differences in food availability rather than to upper pool fish having different diet preferences from the low level pool fish. The presence of these dietary differences, for whatever reasons, meant that it is valid to use either area as an indicator of overall diet only if collections are made over an extended period. Thus, diet studies based on single collections of fish from either low or high level pools, should be evaluated with caution.

The diet data accumulated for the different size classes showed trends that have been described for other fish species (i.e. a change from a carnivorous diet to a diet containing plant matter). The trends seen for the low level pool fish were more clearly discernible than for the high level pool population. This difference can probably be ascribed to the more opportunistic nature of the diet of the fish from the high pools, which in turn is most likely due to the lower diversity of food organisms available to these fish. There was less algal growth in these pools and this factor could be assumed to account for the predominance of animal matter in the diet of fish from this area (Fig. 12a).

Gibson (1970a) reported that young Gobius cobitis fed mainly on small prey organisms such as copepods, ostracods and small amphipods, but as the fish grew its diet changed to include larger organisms such as crabs and large amounts of green algae. This mirrors the situation found for C. caffer. Christensen (1978b) reports a diet change from animal to algal matter with increasing size in Sarpa salpa with a concomitant change in dentition and gut morphology. The teeth changed from conical in the juveniles to incisiform at 35mm SL. The gut changed from that of a typical omnivore to one of a herbivore in the sub-adult. Pitt-Kennedy (1968) found no dental or alimentary changes with age in C. caffer, and he showed the gut to be of a carnivorous type.

The lack of digestion of Ulva as it passed through the gut, and the low density of bacteria and diatoms on Ulva in the environment, indicated that C. caffer ingested algae for reasons other than deriving nutrient solely from the epiphytic flora and bacteria or the alga itself. The results obtained from an examination of the epifauna on Ulva indicate that C. caffer ingests algae to gain the nutritional value of the epifauna, and possibly, to a lesser degree the bacteria and diatoms present. Thus, despite ingesting algal material, C. caffer can be considered as a true carnivore rather than an omnivore.

The importance of Crustacea in the diet of C. caffer tied in well with Beckley's (1977) work and it is possible that these and other prey types were obtained largely off algae, either by direct ingestion of the algae by the larger fish, or by picking at organisms moving on the algal turf. Observations in the field and laboratory showed that two techniques were used by C. caffer when feeding on or off Ulva. The first technique, employed mainly by small individuals which did not actually ingest the alga, was for the fish to remain motionless on or near the algal turf and to 'pounce' on individual organisms moving among the alga. The second method, exhibited by larger fish, was for the fish to 'pounce' on the algal turf, an action possibly initiated by movement of prey organisms, but instead of only ingesting the prey, a mouthful of alga was bitten off. To remove the alga from the substrate the fish would hold it firmly in its mouth and rotate the body rapidly along its long axis, thus twisting the alga free.

The lack of seasonality in the diet of *C. caffer* is not unique among fishes from the eastern Cape. Christensen (1978b) studied three sparid species at Clayton's Rocks of which only one, *Diplodus sargus*, showed seasonal variation in its diet. In the present study the taxonomic breakdown of the prey organisms used may well have disguised some seasonal variations in diet, individual prey species possibly having seasonal fluctuations in numbers and availability. A breakdown to species level was not attempted during diet analysis due to the diversity of prey species and the consequent low numbers per individual species in the stomachs examined. Thus, the apparent lack of seasonality was most likely artificial (at the species level) for animal prey. The results obtained indicated that *C. caffer* was fairly consistent in its choice of animal groups as food. Algae were present throughout the year and the lack of seasonality in the ingestion of this food type was understandable in the light of algal availability throughout the year.

As *C. caffer* had been found to be opportunistic in its selection of food items, the feeding periodicity of the species was studied so that a complete picture of the feeding strategy used by this goby could be obtained. The following chapter presents results from six 24h feeding studies analysed by three different methods.

DAILY FEEDING PERIODICITY

Introduction

Caffrogobius caffer has been found to be catholic in its choice of food items (see above) and was thus not affected by variable availability of any one food species. In order to determine whether C. caffer was also opportunistic in its utilisation of its food resources on a diel basis an investigation of the species' diel feeding periodicity was conducted.

Other studies have shown that two major factors influence the feeding activity of marine fish. Gibson (1967b) reported that Blennius pholis L. showed an endogenous feeding activity rhythm that corresponded with the tidal cycle of the fish's habitat. Peaks of feeding activity occurred over high tide, even if the fish was kept in an aquarium away from the effect of the tide. A similar rhythm has been shown for Coryphoblennius galerita (L.) (Gibson, 1970b). 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 authors examined the dawn and dusk behaviour of reef fish and their results suggest that the fish studied were capable of monitoring light intensity levels accurately.

These two phenomena, tide and light intensity, might have an effect on the feeding of C. caffer. In this chapter results are presented in relation to time of day (indirectly light intensity) and tidal cycles.

Fish collections.

Two 24h collections were taken from each of the three collection sites. Collections were made over spring and neap tides so that any changes in feeding periodicity due to tidal influence could be monitored. For the two West Bank collections fish were caught throughout the day, while at Sea

View approximately ten fish were caught every four hours and at Clayton's Rocks the same number of fish were captured at three hour intervals. The time of capture of each fish was recorded and the specimens immediately preserved in 10% formalin in sea water. In the laboratory the stomach contents of all six collections were examined in the same way as for the diet studies (see above).

No relationship was found to exist between the number of points awarded to indvidual stomachs and the time of capture or tide height. For this reason the data was combined for three hour periods. Apart from the comparison of points with time of day and tide height two other methods (described below) were applied to the Sea View and Clayton's Rocks collections.

Determination of the time of ingestion

At Sea View a preliminary digestion rate experiment was conducted so that the approximate time of ingestion for various food items could be back-calculated for the fish from the 24h collections made at this site. Seven groups of approximately ten fish were caught and placed into food-free cages situated in the fish's habitat. 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 minimise the effect of capture and impoundment 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 notes made on the state of digestion of food items following the method of Darnell & Meierotto (1962). These authors chose a standard food item, the choice of which was based on previous natural diet analysis, and fed a known amount of this food item to pre-starved fish (they recommended the use of a small crustacean of complex morphology for the standard food item). Fish were killed at set time intervals and the length of time the food had been in the stomach was related to the state of digestion reached. By examining the condition of the standard food item's exoskeleton and musculature they were able to recognise three stages of digestion and the length of time taken to reach these stages. 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. An initial group was killed on capture and later groups at set time intervals. They used these fish to discover the number of hours required for the stomach contents to become 25, 50, 75 and 100% depleted. This is similar to the approach used in the present study except that in this case the length of time for a particular food item to disappear from the stomach was noted as well as the state of digestion at hourly intervals. Using the data obtained from this experiment the time of ingestion of certain food items in the stomachs of C. caffer caught in the two Sea View 24h collections was back-calculated.

Several assumptions were made in the above experiment. Firstly, as well

Table 4.

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

fish caught for diet studies had been caught in the morning and a low incidence of empty stomachs had been found (5%), it was assumed that by working in the morning most of the fish caught for the digestion rate experiment would have fed prior to capture. Secondly, it was assumed that capture and handling had only a minimal effect on digestion rate.

The advantage of the method used over that of Darnell & Meierotto (1962) was that the time of ingestion of a variety of food types could be estimated directly. As the animals used in this study were freshly caught, laboratory acclimation could not affect the results.

For the two Clayton's Rocks 24h collections the dry somatic mass of the fish and the dry mass of the food items from the stomachs were measured. The fish and the stomach contents were dried to constant mass by placing them in a drying oven at 90°C for twenty four hours. In addition to the mass values the points value of each food type in the stomach was noted.

Results

Analysis of back-calculated ingestion time vs time of day and tide

In order to discuss the feeding periodicity data for the back-calculated ingestion times, it is necessary to first outline the results of the digestion rate experiment.

Digestion rate experiment

The presence of the various food items in the stomach after various time intervals is shown in Table 4. For an example of how the time of ingestion was back-calculated, adult insects can be used. Adult insects were found to be virtually unaffected after one hour in the stomach, while after three hours the body had become broken up with no trace remaining of the musculature or viscera. 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 four hours, with shorter periods being assigned according to the state of digestion reached. Although fish were killed at hourly intervals, interpolations for ingestion times at intermediate times were made to the nearest half hour. Although *Ulva* spp., *Enteromorpha* spp. and *Codium* spp. were found in all hourly samples, including that from the seventh hour, these algae had to be ignored when estimating ingestion times for food items found in the 24h collections. This was because no discernible change in the state of digestion could be determined for these algal types (see Food & Feeding, p. 43). Mollusca did show a change in digestion state but this change was so slow that no accurate assessement of ingestion time could be made for this food type (their slow digestion rate may have been due to the protection afforded by their shells).

The stomach contents from the two 24h collections from Sea View were analysed in the same way as for diet studies. Although points were allocated to all food items, only those food items which could be aged were used in the construction of the feeding periodicity curves (Figs. 16, 17). The points assigned to these ageable food items were combined as 'usable points' and the number of usable points occurring in each hour was expressed as a percentage of the total usable points from the entire collection.

A. Back-calculated time of ingestion vs time of day

The results obtained by back-calculation of food ingestion time proved to be inconclusive. One graph (Fig. 16) showed major feeding peaks occurring throughout the day with no discernible trend. In the second graph (Fig. 17) a crepuscular pattern of feeding peaks was evinced.

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

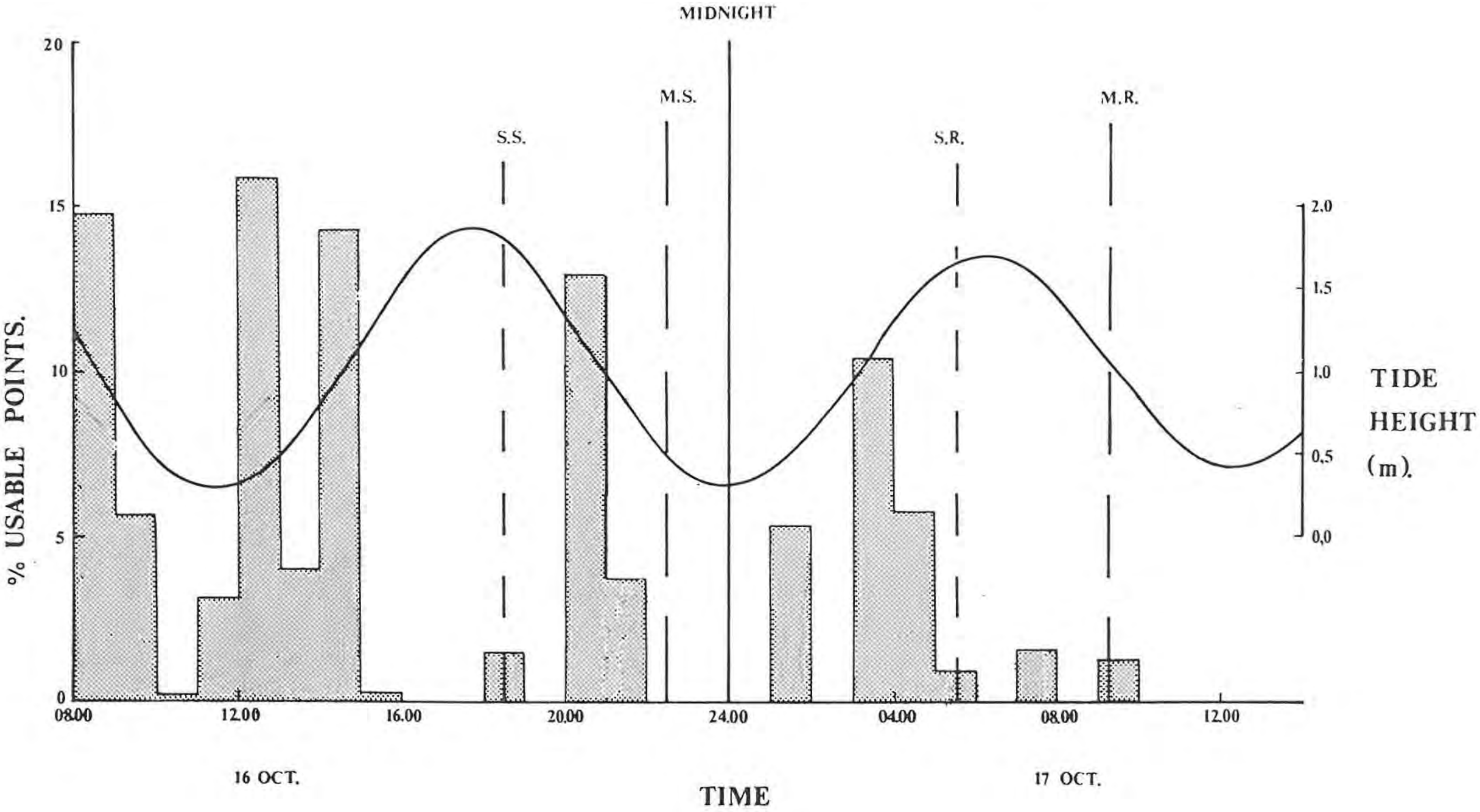


Fig. 16 Results of a 24h collection at Sea View taken on 16/17 October 1977 to examine daily feeding peaks in *C. caffer*. (Usable points are explained in the text. S.S. = sunset, S.R. = sunrise, M.S. = moonset, M.R. = moonrise. The sinusoidal curve represents predicted tide heights).

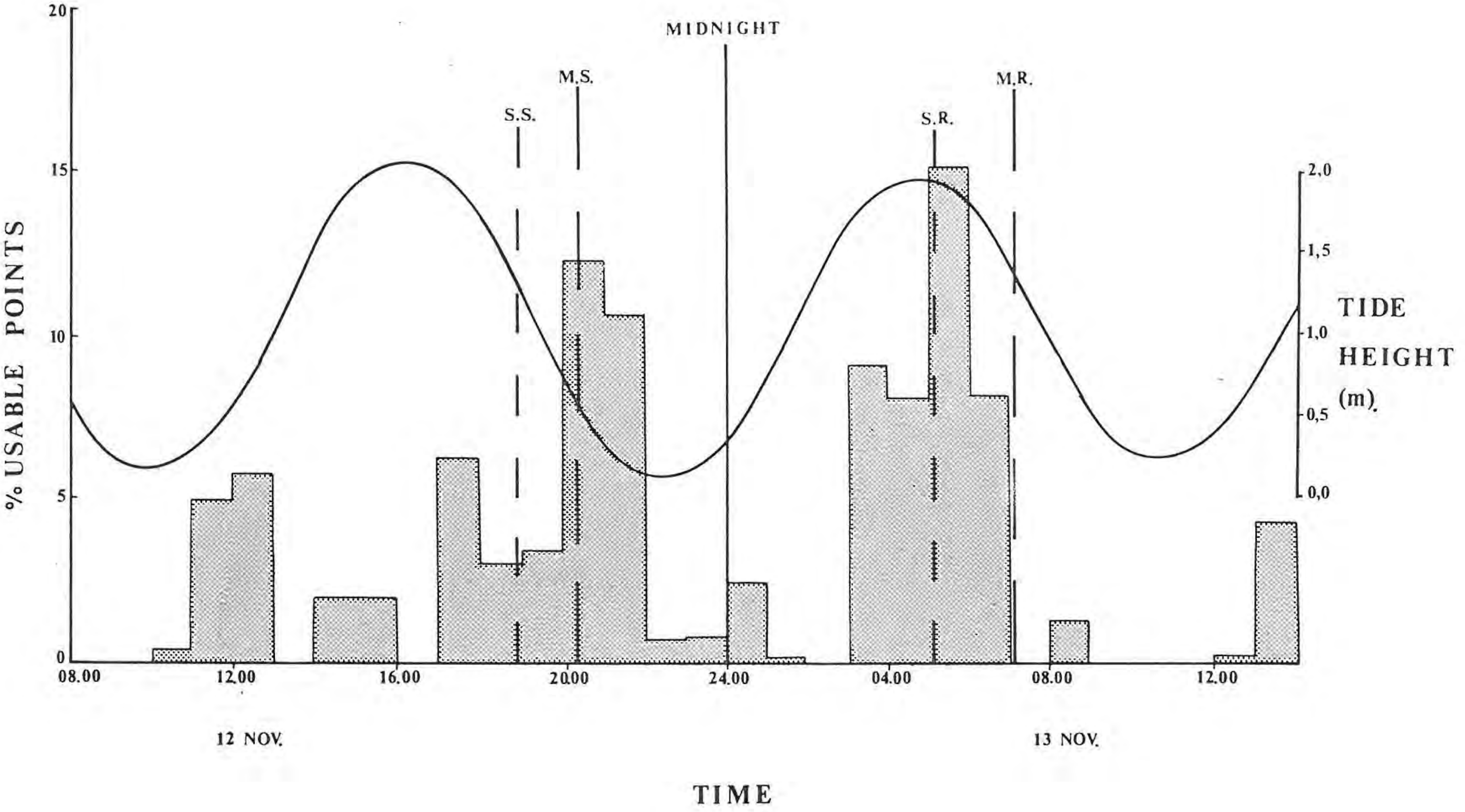


Fig. 17 Results of a 24h collection at Sea View taken on 12/13 November 1977 to examine daily feeding peaks in *C. caffer*. (Usable points are explained in the text. S.S. = sunset, S.R. = sunrise, M.S. = moonset, M.R. = moonrise. The sinusoidal curve represents the predicted tide heights).

peaks in the morning and evening, indicating the possibility of a crepuscular pattern of feeding. Both graphs also show that feeding activity took place throughout the day, and one graph (Fig. 16), with a major peak over midday, indicated that a definite crepuscular rhythm could not be postulated.

B. Back-calculated time of ingestion vs predicted tide height

Feeding was found to occur at any stage of the tidal cycle, with peaks occurring in both still and moving water. 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 (mainly wind-induced).

All specimens caught for 24h analysis were caught in pools lying between 0,78 and 1,13m above MSL. No note was made of the individual fish's pool of capture so the lower and upper limits were indicated on all relevant 24h graphs by a solid and hatched line respectively. During the time period spanned by these height limit lines the fish were experiencing minimal current velocities, if any at all.

When the recorded feeding peaks were examined in the light of the above no correlation between water movement, or absences of water movement, and feeding activity could be seen. Feeding peaks occurred during periods of both still and moving water with co clear cut pattern.

Analysis of points vs time and tide height

As has already been mentioned, neither individual capture time nor the tide height at this capture time showed any relationship with the specimens'

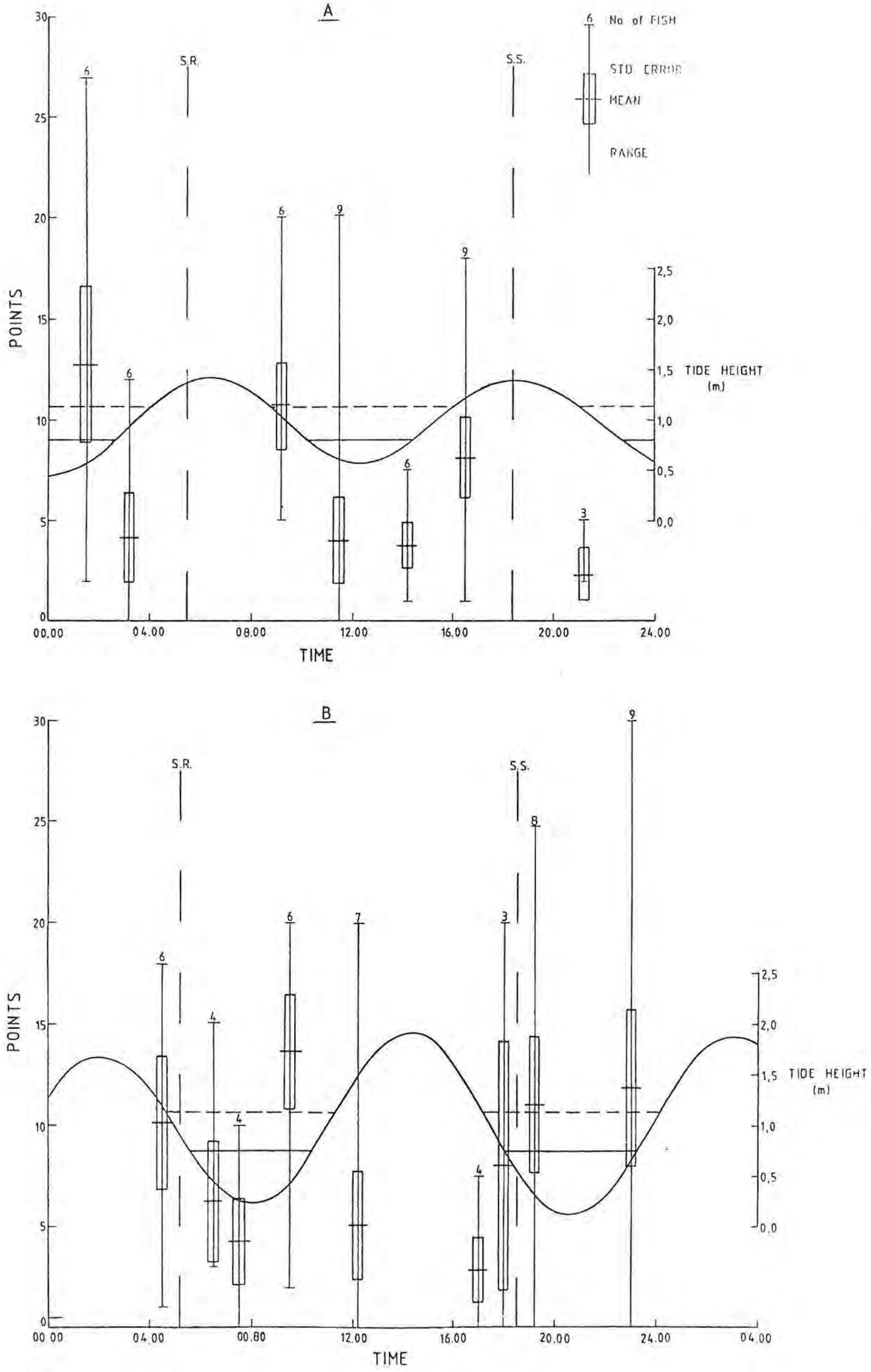


Fig. 18. Results from the two 24h diet collections made at West Bank analysed for points (A, 14/10/76; B, 21/10/76). The sinusoidal curve represents the predicted tide height, while the dashed and solid horizontal lines represent the upper and lower pool heights (relative to MSL) of the pools from which C. caffer were collected. During the periods spanned by these lines the fish were experiencing no water movement.

stomach fullness. When the individual points values were combined for three hour periods and the means and standard errors were calculated, a pattern emerged relative to time of day, but not to tide height.

Points vs time of day

The data from all six 24h collections were plotted as points vs time of day. Predicted tide heights and the limits of periods of still water were plotted on the same axes (Figs. 18 - 20). Time periods in these graphs which contain no data represent high tides during which the collection of specimens was not possible.

When the means 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. Fig. 20a showed the evening peak represented by a levelling off of the daytime decline in stomach fullness and this represents the most extreme deviation from the above mentioned pattern.

The time of the actual feeding peaks varied from collection to collection. This may have been due to differences in light intensity at the same time on different days. The possibility that light intensity may have played a rôle in determining feeding times is illustrated by the fact that on clear days morning peaks tended to occur earlier than was the case on overcast days. On cloudy evenings the peaks tended to be earlier than on cloudless days. It must be borne in mind that the graphs represent means for three hour periods and thus only indicate the approximate peak feeding times. This approximation is due to the fact that collecting large samples of *C. caffer* at hourly intervals would have had a marked effect on population densities and was thus avoided.

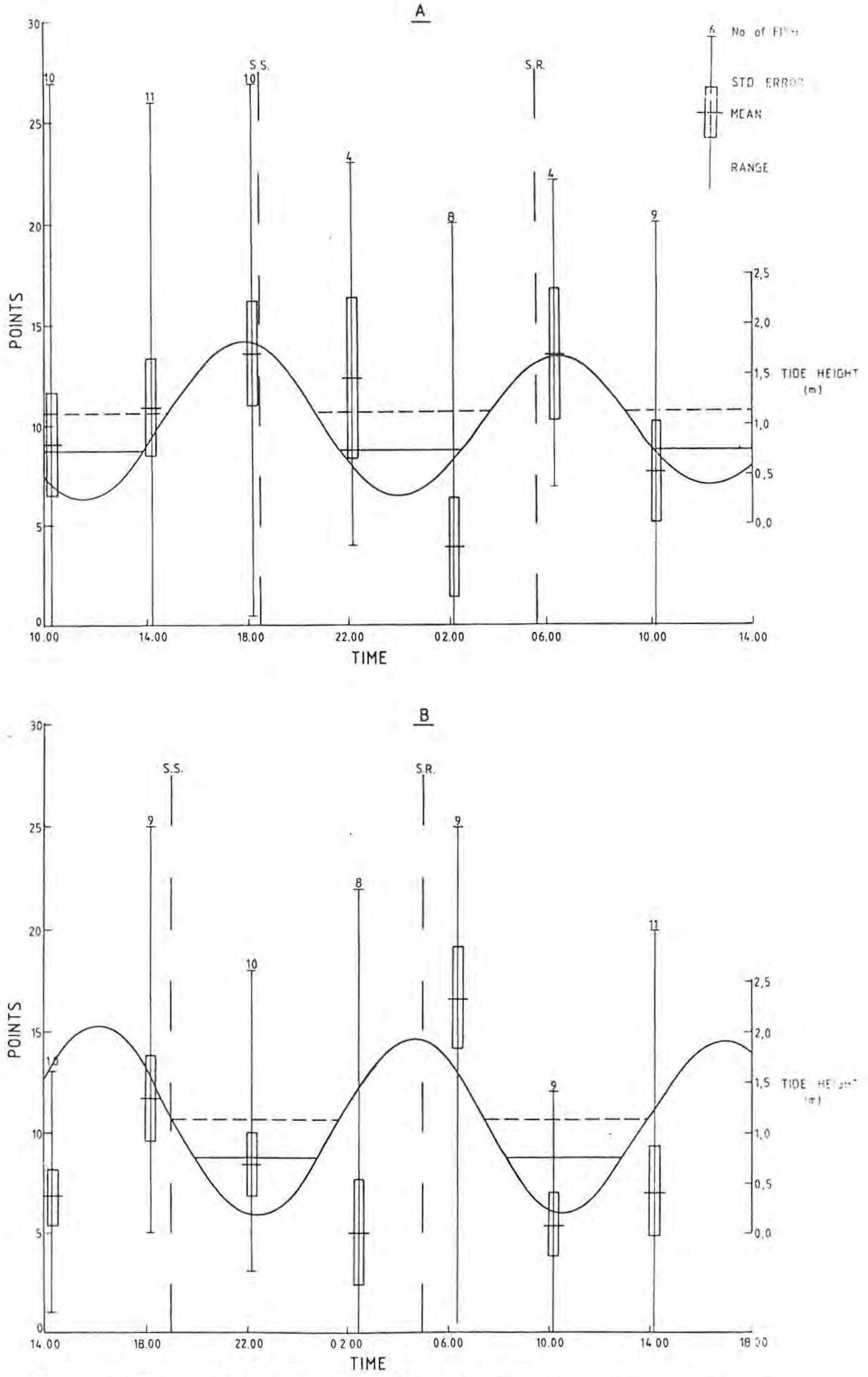


Fig. 19. Results of the two 24h diet collections made at Sea View analysed for points (A, 16-17/10/77; B, 12-13/10/77). The sinusoidal curve represents the predicted tide height, while the dashed and solid horizontal lines represent the upper and lower pool heights (relative to MSL) of the pools from which *C. caffer* collected. During the periods spanned by these lines the gobies were experiencing no water movement.

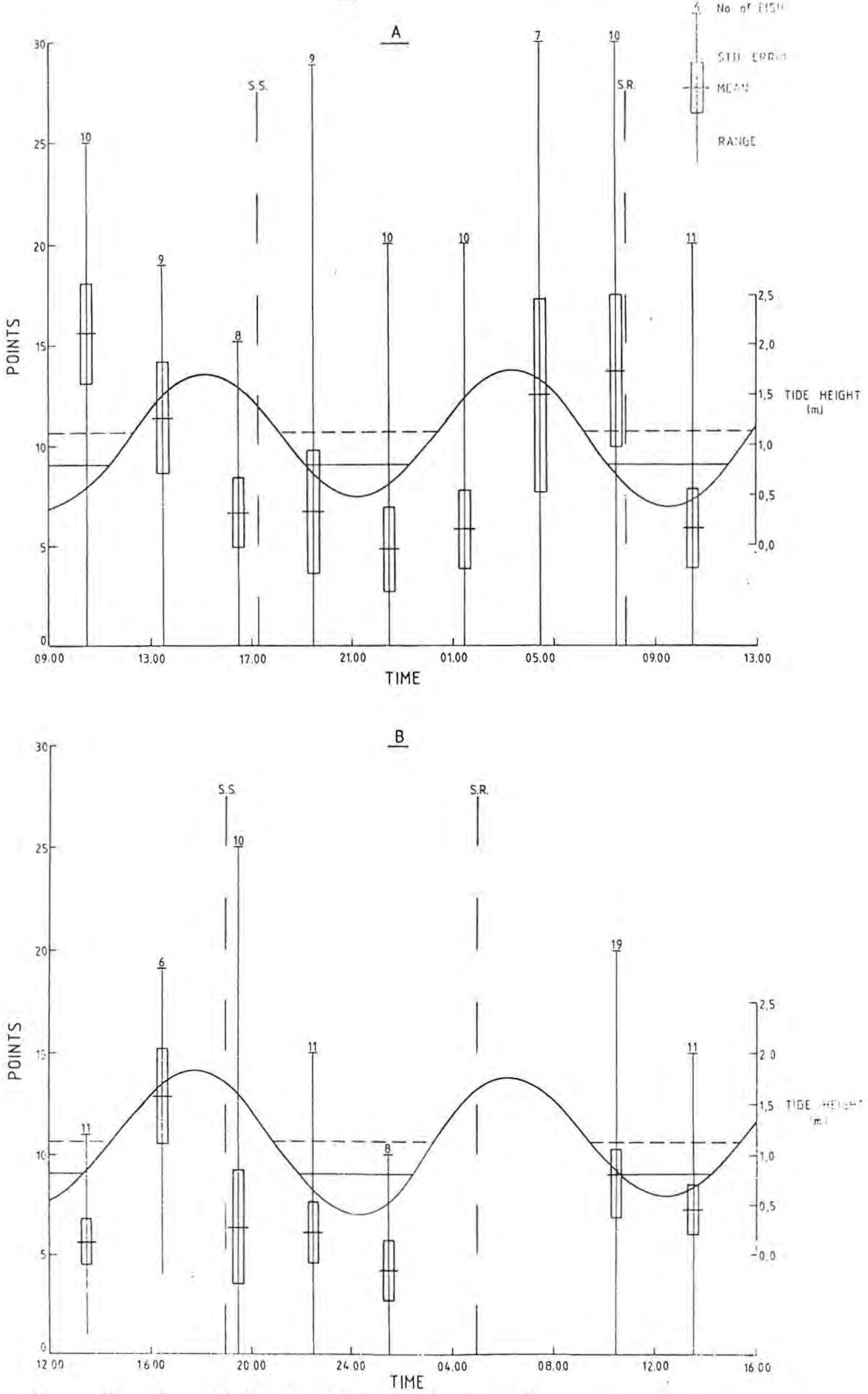


Fig. 20. Results of the two 24h diet collections made at Clayton's Rocks analysed for points (A, 23-23/6/79; B, 23-24/11/79). The sinusoidal curve represents the predicted tide height, while the dashed and solid horizontal lines represent the upper and lower pool heights (relative to MSL) of the pools from which *C. caffer* were collected. During the periods spanned by these lines the gobies were experiencing no water movement.

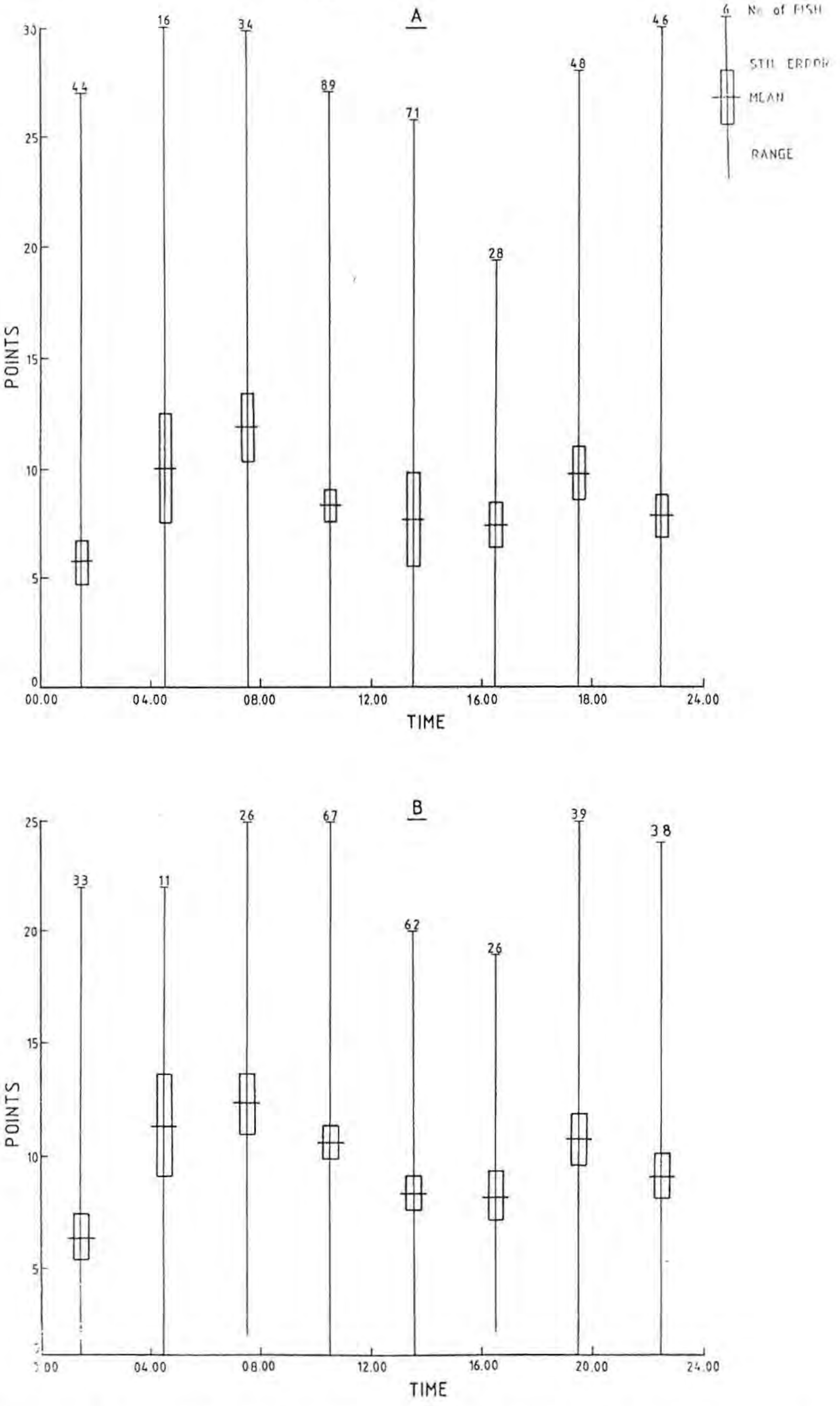


Fig. 21. A. Results of all 24h diet collections from the three collection sites combined and analysed for points vs time of day.

B. Results of all 24h diet collections from the three collection sites combined and analysed for points vs time of day. All points values above 25 or below 1 discarded.

The points data for all collections were combined into a single graph (Fig. 21a) to determine whether the crepuscular tendency evinced in the individual graphs could be considered to be a general trend. Fig. 21a showed the same pattern of feeding as found in the individual collection graphs, but the relative heights of the peaks was lower due to the variability of peak feeding time on different days.

Due to the overlap at the double, and even single, standard error level there were no significant differences between concurrent datum points. To exclude the effect of those fish which had not been feeding and those fish which had unusually full stomachs, all points values less than one and greater than 25 were discarded and the resultant data, presented in the same manner as for Fig. 18 - 20 & 21a are shown in Fig 21b. The choice of 25 points as the upper cut-off limit was made on the basis that all fish awarded more than 25 points contained food items which had been shown (Table 5) to have long gut residence times, for example Mollusca. the decision to set the lower limit at one point was made on the assumption that any fish awarded less than one point had not completed digestion of its last meal and was not feeding at the time the sample was taken. By ignoring fish with high or low points values the magnitude of the standard errors was reduced, but overlap still occurred at the level of two standard errors. Thus C. caffer feeds throughout the day with the possibility of slight increases in feeding activity at dawn and dusk.

Points vs tide height

When feeding peaks were compared with predicted tide heights (sinusoidal curves Figs. 18 - 20) no pattern could be seen. Some peaks were found to have occurred over high tide (Figs 18a, 19 & 20) while others occurred during still water, or continued into slack water periods.

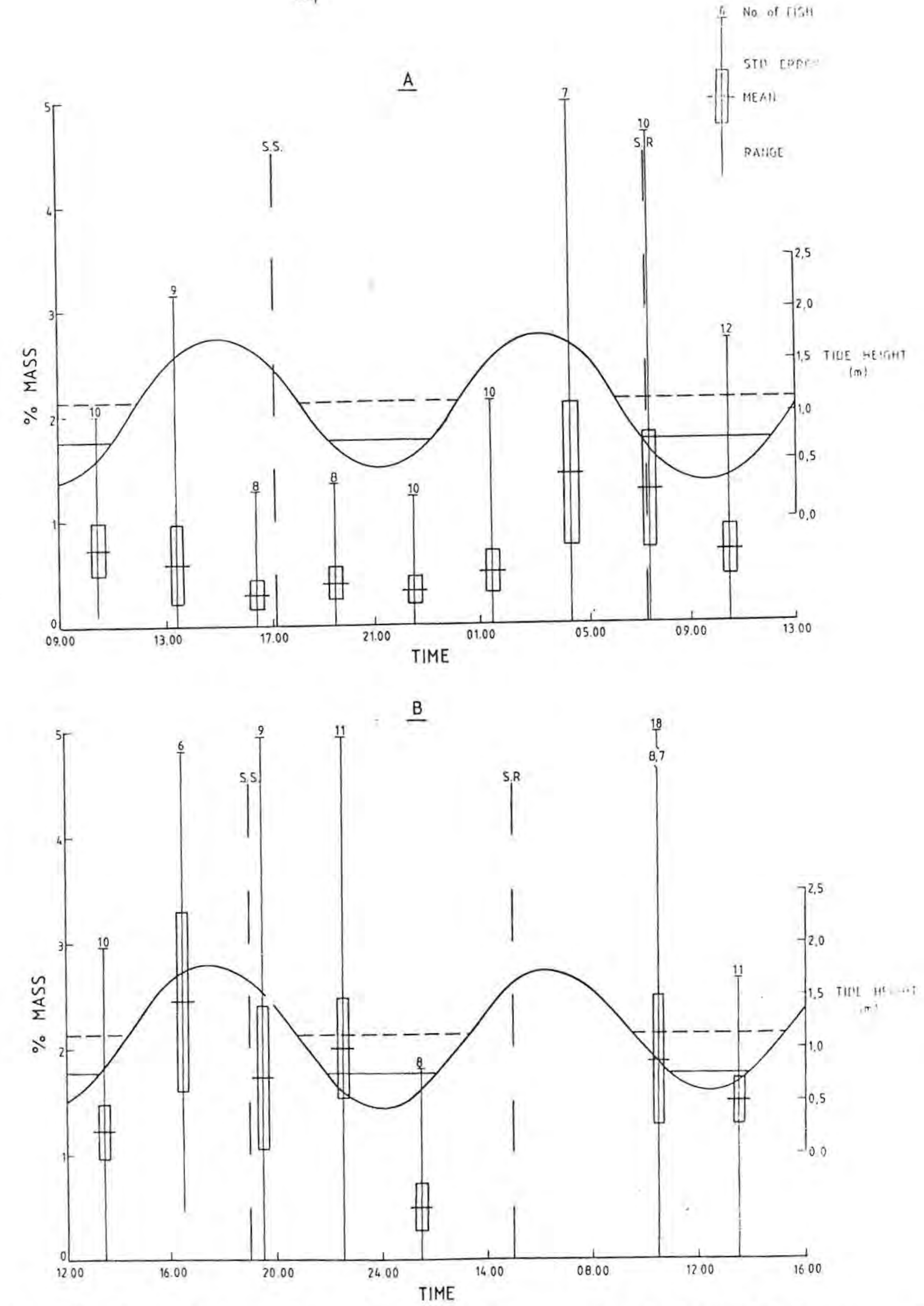


Fig. 22. Results of the two 24h diet collections made at Clayton's Rocks analysed for % mass (A, 23-24/6/79; B, 23-24/11/79). The sinusoidal curve represents the predicted tide height, while the dashed and solid horizontal lines represent the upper and lower pool heights (relative to MSL) of the pools from which C. caffer were collected. During the periods spanned by these lines the gobies were experiencing no water movement. % mass is explained in the text.

C. Analysis of stomach content dry mass as a percentage of dry somatic mass vs time of day and tide height

For the sake of brevity stomach content dry mass as a percentage of dry somatic mass will be referred to as % mass hereafter.

Time of day vs % mass

The results of the two Clayton's Rocks 24h collections (Fig. 22) show a similar trend to that found for the time of day vs points graphs. Figs. 22a and 22b show a morning and evening peak in % mass with troughs occurring overnight and over midday.

The data from the two collections were combined (Fig. 23). The resultant graph showed a trend very similar to that shown by the combined data graphs for points data. The morning peak occurred earlier than was the case for the points combined data graphs. This difference was probably due to the fact that Fig. 23 was based on data from only two collections as compared to six for the points graphs.

The large magnitude of the standard errors in the mass graphs was due 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 dried polychaete of a similar volume. Despite this reservation, an overall trend similar to that found for points data and one of the reconstructed ingestion time graphs was shown.

Tide height vs % mass

As with the two other methods employed to examine feeding periodicity, no correlation between tide height (or water movement) and % mass was found. In both collections (Fig. 22a & b) feeding took place over both high and low tides with no preference for either tide phase being shown.

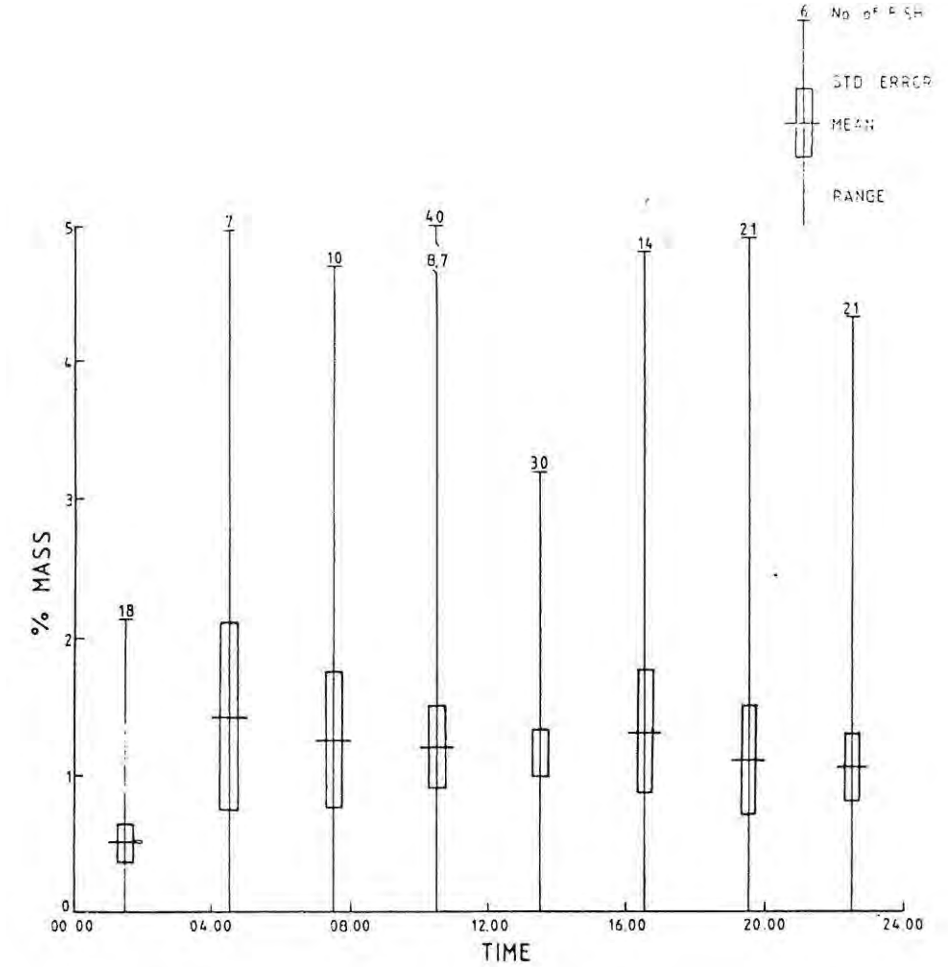


Fig. 23. Results of the two 24h collections from Clayton's Rocks combined and analysed for % mass. The term % mass is expained in the text.

Discussion

Pitt-Kennedy (1968) conducted no 24h 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 stomachs 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 by C. caffer as feeding occurred during both extremes of the tidal cycle.

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 (Fig. 16) 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 depict 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 minimise the effect of capture stress on the fish in the digestion rate experiment in that they were placed in food-free 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 24h experiments.

There are several factors pointing to the conclusion that Fig. 16 does in fact represent the true situation for this collection. Fig. 17 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 very 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 Fig. 16, 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 16 October collection could have led to a rise in feeding activity at this time.

CURRENT VELOCITY TOLERANCE BY CAFFROGOBIUS CAFFER

Introduction

Diving observations revealed that fewer gobies were in the open during high tide than at low tide. To test the validity of these observations transects were measured out at Sea View and Clayton's Rocks and the number of gobies seen in the open during both high and low tides was recorded. Transect counts showed significantly fewer gobies in the open over high tide relative to low tide and it was decided to test whether water movement affected the behaviour of *C. caffer*.

Experiments to test the current velocity tolerance of *C. caffer* were conducted in the laboratory and velocities over high and low tide were measured in the field. The laboratory-derived current tolerance could thus be compared with the actual conditions prevailing in the habitat of *C. caffer*. Jones & Demetropoulos (1968) considered that water drag on an organism was probably the single most important hazard affecting intertidal life. Gibson (1969b) reported that the intertidal goby, *Gobius paganellus*, could withstand only limited current velocities,an indication that the morphologically similar *C. caffer* would also only have limited current tolerance.

Materials and methods

A transect 27m long by 2m wide was chosen in pool G1 at Sea View and three counts of *C. caffer* seen in the open over consecutive high and low tides on two separate days were made. At Clayton's Rocks a transect 22m long by 2m wide was chosen in pool R3 and the same procedure as employed at Sea View was used except that counts were conducted on four different dates.

A count was made by an observer moving slowly along the transect and counting the number of gobies seen out of cover. After waiting 20 minutes a further count was made, and after another 20 minutes the third count was taken. When the tide changed the same procedure was repeated.

Current readings were taken both in the laboratory and the field. In the first preliminary experiment a current meter designed and built by the Department of Physics & Electronics, Rhodes University, was used. This meter consisted of a propellor (diameter 47mm) mounted in a nylon tube. As the propellor rotated the blades cut an infra-red beam and the pulses thus generated were counted by a digital impulse counter. The propellor used had different rotation speeds depending on the direction in which the water moved over the blades. In the field it was not possible to know in which direction the blades were turning and thus the calibration for the higher speed of rotation was applied to all field data obtained with this instrument. Thus the field readings were most probably an overestimate relative to the laboratory results which were obtained with the propellor oriented so that the fastest speed of rotation resulted.

There was a 10% difference in propellor rotation speed depending on the current direction. In the intertidal zone, however, the current is constantly changing direction by approximately 180° as the waves ebb and flow. It was assumed that the current spent approximately 50% of the time going in each direction and thus the field data was expected to represent a ± 5% overestimate of velocity. This level of accuracy was considered satisfactory for the preliminary experiment.

Later experiments were conducted using an electromagnetic current meter obtained from the National Research Institute for Oceanology of the Council for Scientific and Industrial Research in Stellenbosch. This

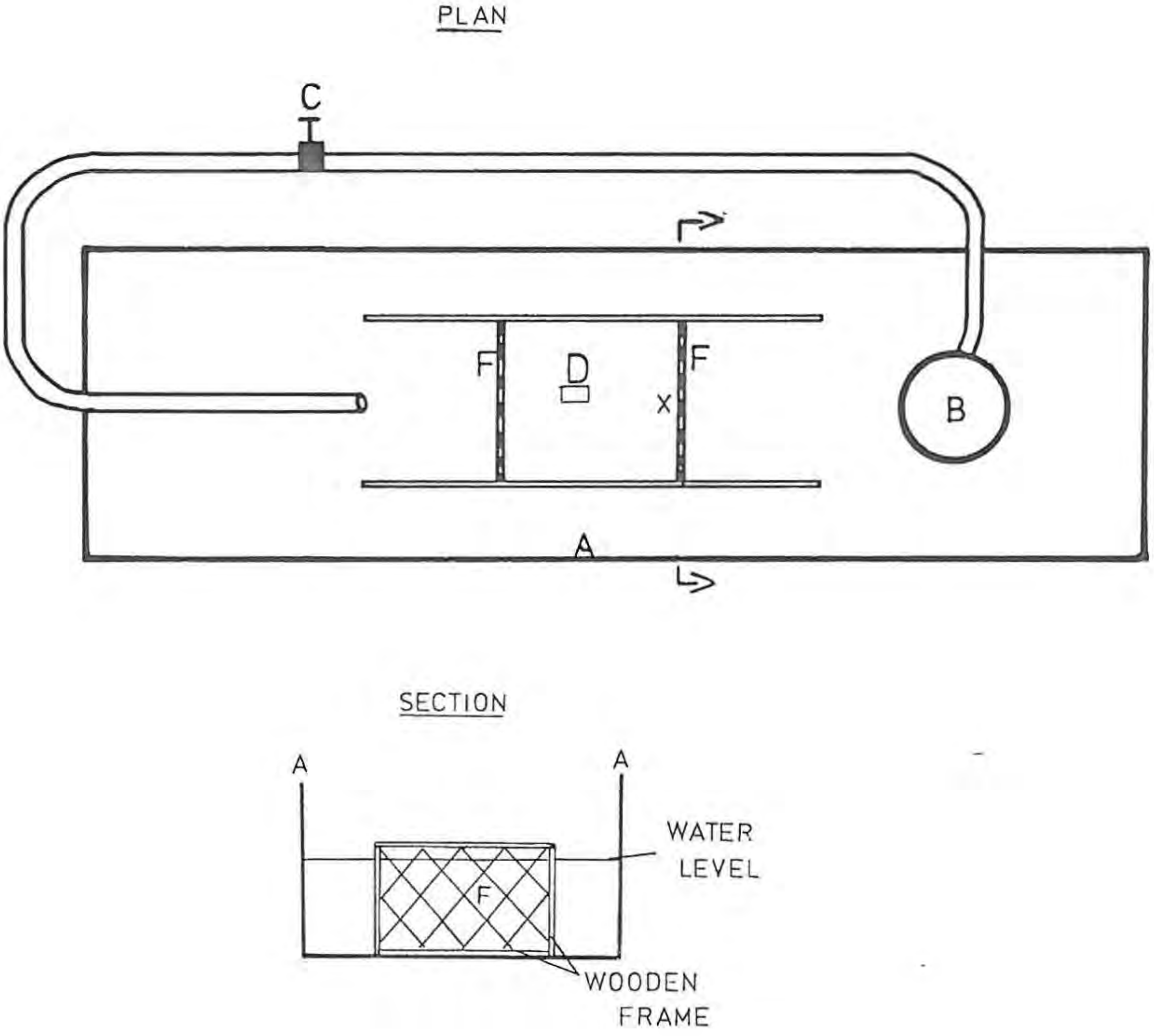


Fig. 24. Plan and section diagrams of the experimental tank used to determine the current velocity tolerance of *C. caffer*. (A = painted asbestos tank, B = submersible electric pump, C = tap regulating water velocity, D = current meter, E = enclosure for fish, F = netting restricting fish's movements, X = position fish would take up when subjected to current).

meter was not affected by current direction and for this reason field and laboratory results from this machine were directly comparable.

To ascertain the current velocity tolerance of C. caffer readings were taken in a painted asbestos tank (Fig. 24) in which a variable current was generated by a submersible electric pump. Six fish were tested for current velocity tolerance with the propellor meter, while 20 fish were tested with the electromagnetic meter. The means of five readings per fish were plotted. C. caffer, in common with other gobies, has a pelvic sucker formed by the fused pelvic fins. The velocity at which this organ could no longer hold the fish stationary on the painted asbestos tank was recorded for the six fish tested with the propellor meter.

With both meters the velocity at which C. caffer actively sought cover was recorded. Once the current velocity had passed the point at which the pelvic sucker could no longer hold them stationary, the fish would use a wooden frame (Fig. 24), part of the structure of the netted experimental enclosure, for support (x, Fig 24). In nearly all cases the fish would face the current with only the caudal region in contact with the frame, which was oriented at 90° to the current direction. Some fish did, however, orient themselves along the frame with their bodies at 90° to the current. The velocity at which the fish would leave the support of the frame and try to move out of the current was noted. This latter reading was interpreted as the maximum velocity the fish would withstand in the field even if they were supported by irregularities on the substrate.

At Clayton's Rocks current velocities were recorded in two areas. Readings were taken over rising spring tides with the recording device placed in pool R3 near this pool's junction with pool R2 (Fig. 2) (1,13m above MSL).

Table 5.

Number of *Caffrogobius caffer* seen in the open along transects at Sea View and at Clayton's Rocks over consecutive low and high tides on seven different days.

	Sea View.		Clayton's Rocks.			
	13/11/77	25/6/79	23/6/79	16/9/79	22/11/79	23/11/79
	23	27	9	17	10	12
Low tide	24	28	8	14	12	13
	28	24	11	17	14	14
Mean	25	26,3	9,3	16	12	13
	2	3	1	1	1	2
High tide	1	4	2	0	2	2
	0	3	0	0	1	0
Mean	1	3,3	1	0,3	1,3	1,3
t	14,70	18,44	7,91	14,86	8,88	13,23
p	<0,001	<0,001	<0,01	<0,001	<0,001	<0,001

where t = Student's t and p = probability.

Current velocity readings were taken with the mechanical meter in the marginally subtidal zone (± 0,2m above MSL).

In both areas the mechanical meter's digital counter was set such that it recorded and displayed the number of counts in each ten second period. Readings were taken for five minutes at fifteen minute intervals. The mean and standard error of the 30 readings from each five minute interval were calculated. The readout of the electromagnetic meter was analog and readings were taken every ten seconds for five minutes at fifteen minute intervals. The data from each five minute period were meaned and the standard errors calculated.

Current velocities were recorded at Sea View on a single occasion. The electromagnetic meter was situated in the middle of the mid-intertidal zone at the junction between pools F2 and F1 (Fig. 3).

Results

A. Transect counts

Table 5 shows the results from the transect counts taken on seven different days. For each of the seven days the high tide counts were statistically compared with the low tide counts from the same day by means of the Student's t test (Rohlf & Sokal, 1969; Sokal & Rohlf, 1969). These tests showed a significant difference between the number of gobies seen in the open during high tide and low tide for all the days for which data was collected. On all days, except for the counts made at Clayton's Rocks on 23 June 1979, where $p < 0,01$, the t values calculated gave $p < 0,001$.

B. Propellor meter

Laboratory results

Fig. 25 shows the mean values (in cm sec^{-1}) at which the pelvic sucker was

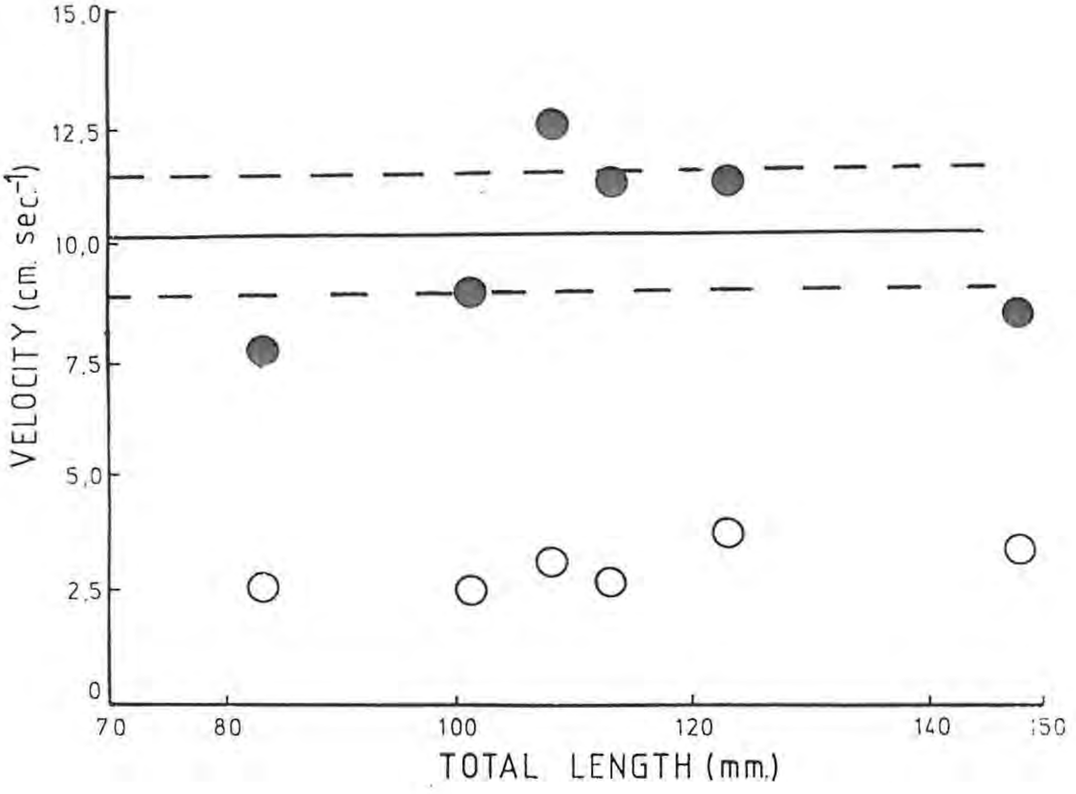


Fig. 25. Results of laboratory experiments to ascertain the current velocity tolerance of C. caffer using the propellor meter. The solid horizontal line represents the mean velocity withstood by all specimens tested and the dashed lines are the standard error about this mean. The black circles represent the mean velocity withstood by individual specimens derived from five tests per specimen. The open circles represent the mean velocity at which the sucker could no longer hold the individual specimens to the tank floor.

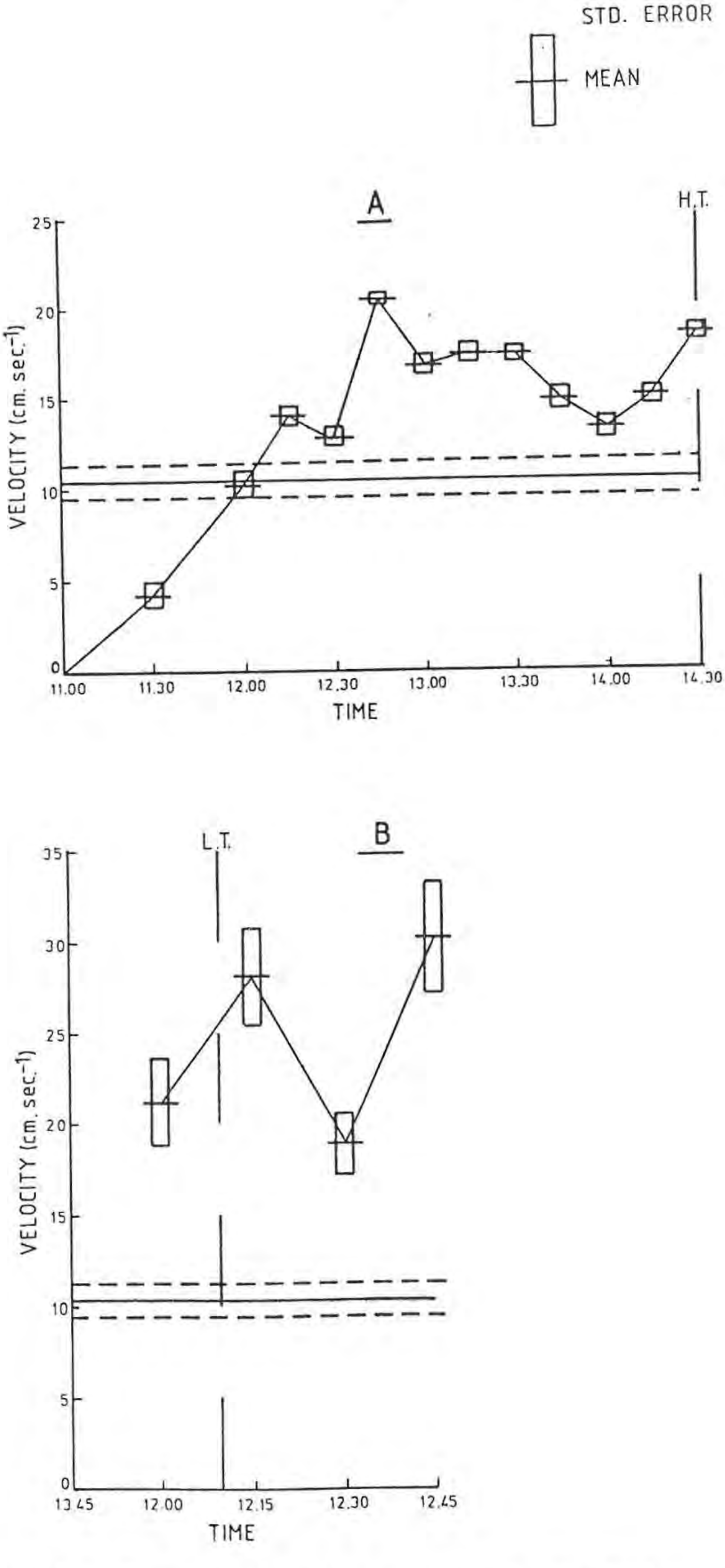


Fig. 26. Current velocities recorded in the field at Clayton's Rocks using the propellor meter. The solid horizontal line represents the laboratory derived mean tolerance of the fish tested using the propellor meter and the dashed lines are the standard error about this mean. A. Readings from the mid-intertidal zone (14/10/78) during the rising tide. B. Readings from the marginally subtidal zone (24/6/78) during low tide.

unable to hold the fish stationary on the bottom of the tank and the speeds at which specimens of C. caffer of different lengths sought cover from the current. The mean value of pelvic sucker tolerance was 3,0 cm $\sec^{-1}$ (SE 0,09). The mean value of the maximum tolerated velocities for all fish was 10,3 cm $\sec^{-1}$ (SE 0,9). These data are plotted on to the two field data graphs as well as on Fig. 25 as horizontal solid (mean) and dashed (SE) lines. No correlation was found between the mean velocity withstood by the fish and their total lengths.

Field results

The readings from low level pool R3 went from zero before the tide reached the pool, to mean velocities that exceeded the mean maximum velocity tolerated by C. caffer in the laboratory (Fig. 26a). When current velocity was recorded during low tide in the marginally subtidal region the velocities recorded far exceeded the mean maximum velocity withstood by C. caffer in the laboratory (Fig. 26b).

The results obtained with the propellor meter indicated that the behaviour of C. caffer was affected by current velocity. The electromagnetic meter was used for later experiments as it did not suffer the defect of the propellor meter in that the accuracy of the reading was not affected by the current direction.

C. Electromagnetic meter

Laboratory results

The test tank used with the electromagnetic meter was the same one used with the propellor meter (Fig. 24). Twenty fish were tested five times each and the mean current velocity at which each fish sought cover was plotted against the total length of the fish (Fig. 27). The mean of all

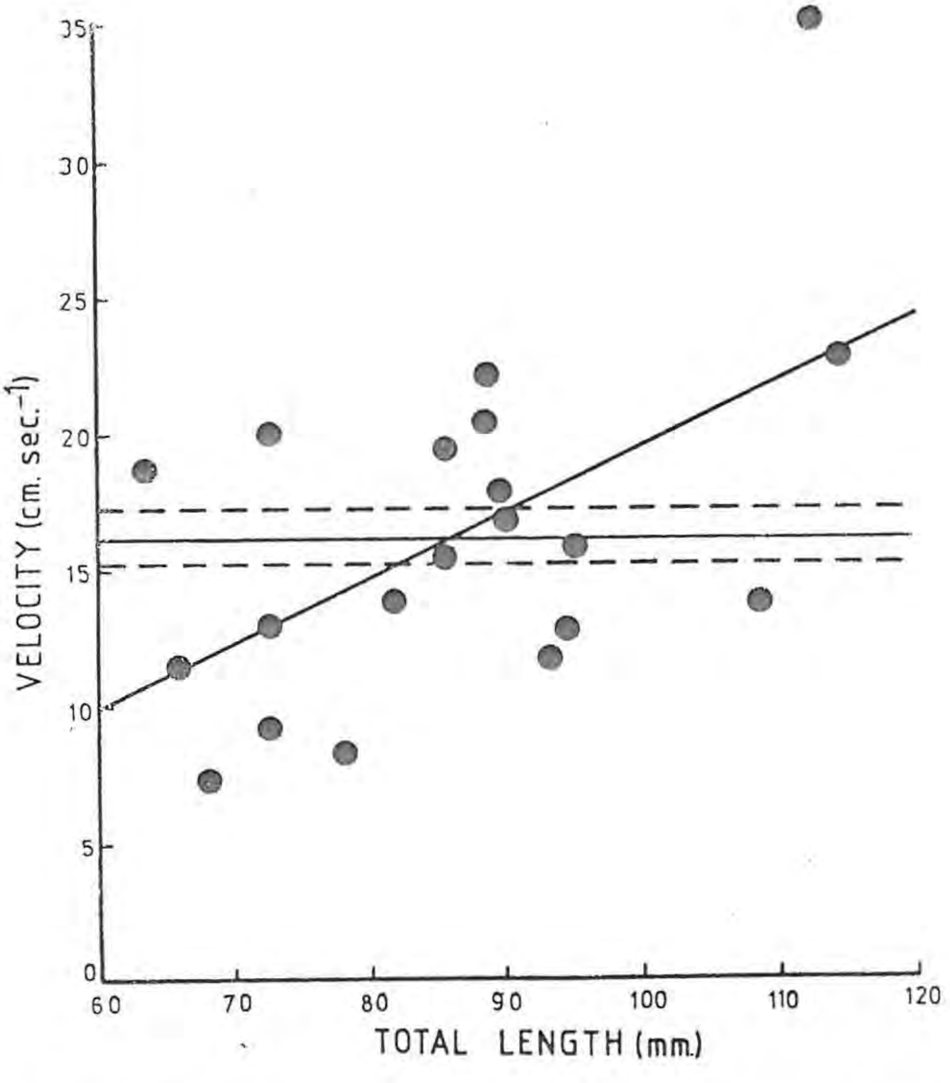


Fig. 27. Results of laboratory experiments to ascertain the current velocity tolerance of C. caffer using the electromagnetic meter. The solid horizontal line represents the mean velocity withstood by all specimens tested and the dashed lines are the standard error about this mean. The black circles represent the mean velocity withstood by individual specimens derived from five tests per specimen. The solid diagonal line represents the regression line calculated from the means of each fish ($r = 0{,}539$, $p < 0{,}01$).

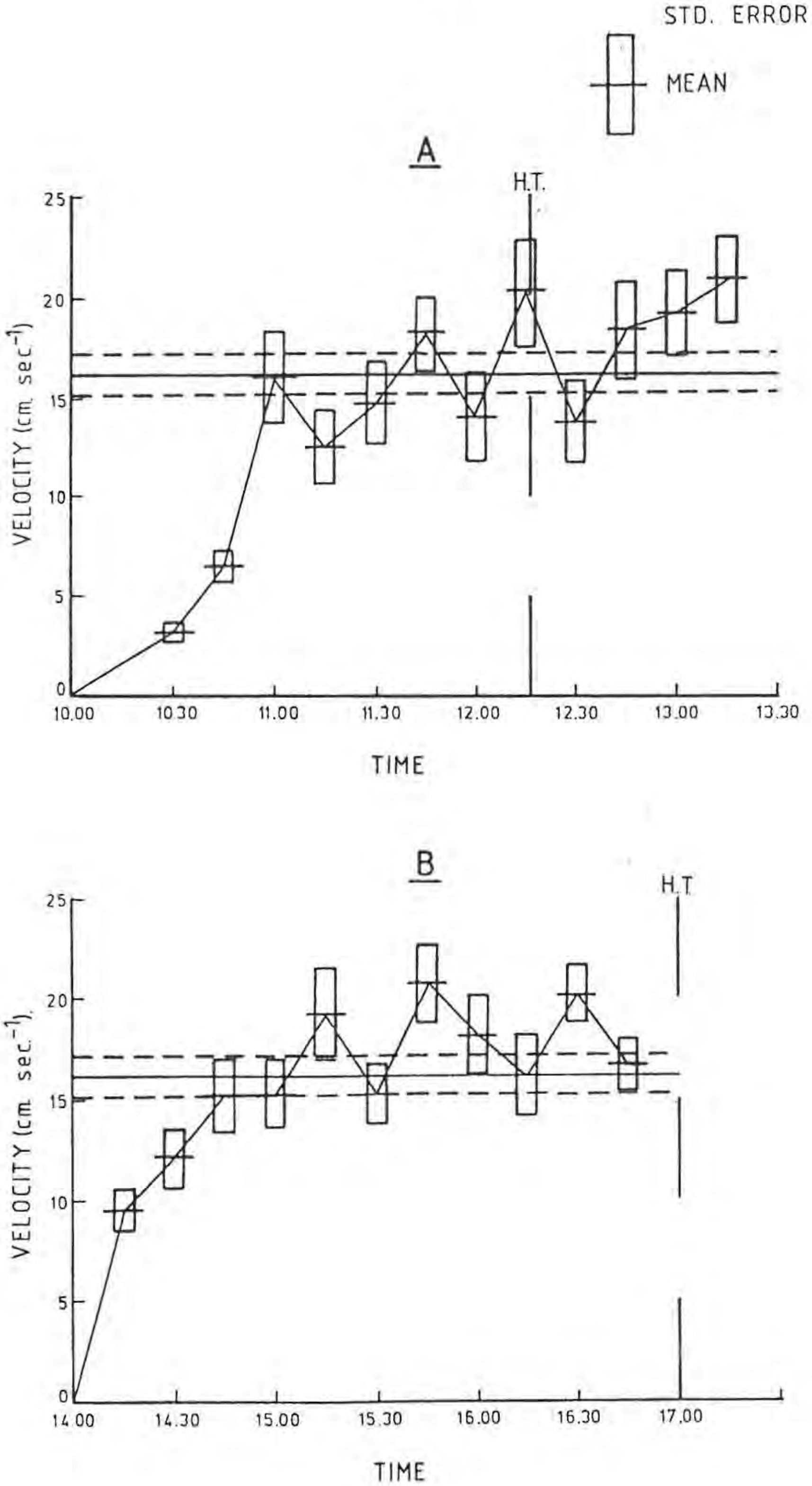


Fig. 28. Current velocities recorded in the mid-intertidal zone at Clayton's Rocks using the electromagnetic meter. A. 14/12/79. B. 19/1/80. The solid horizontal lines represent the laboratory derived mean tolerance of the fish tested using the electromagnetic meter and the dashed lines are the standard error about this mean. Readings on both days were taken during the rising tide.

fish (16,13 cm sec^{-1}) and the standard error (0,9 cm sec^{-1}) were plotted as horizontal solid and dashed lines respectively on all graphs based on data obtained with the electromagnetic meter.

A positive linear correlation between total length and the mean maximum velocity withstood by the specimens tested was recorded ($r = 0,539$, $p < 0,01$). This result differs from that recorded for the data from the propellor meter and was probably due to the larger number of fish used in the second laboratory experiment. The difference in magnitude between the mean maximum velocity tolerated by fish recorded by the two instruments is also probably due to the larger number of fish tested with the electromagnetic meter. The increase in tolerance of current velocity with increasing length is most likely due to the fact that the surface area of the animal increases as a function of a square while the volume increases in relation to the cube. Thus a larger fish has relatively less surface area on which the current can act, while the volume, and thus the mass, of a smaller fish is relatively lower than that of a larger fish and the mass of the fish obviously plays an important rôle in keeping the fish stationary on the substrate.

Field results

Current velocity readings were taken in the habitat of C. caffer on four different days using the electromagnetic meter. In all cases there was a rapid rise from zero velocity to values that approached and/or superseded the mean velocity C. caffer had been found capable of tolerating in the laboratory (Figs. 28 & 29). On only one occasion, at Sea View (Fig. 28a), did the average habitat current velocity drop markedly below the species' mean tolerance level. On the three other occasions, all at Clayton's Rocks, the mean habitat current velocity was found to fluctuate around the mean tolerance level,

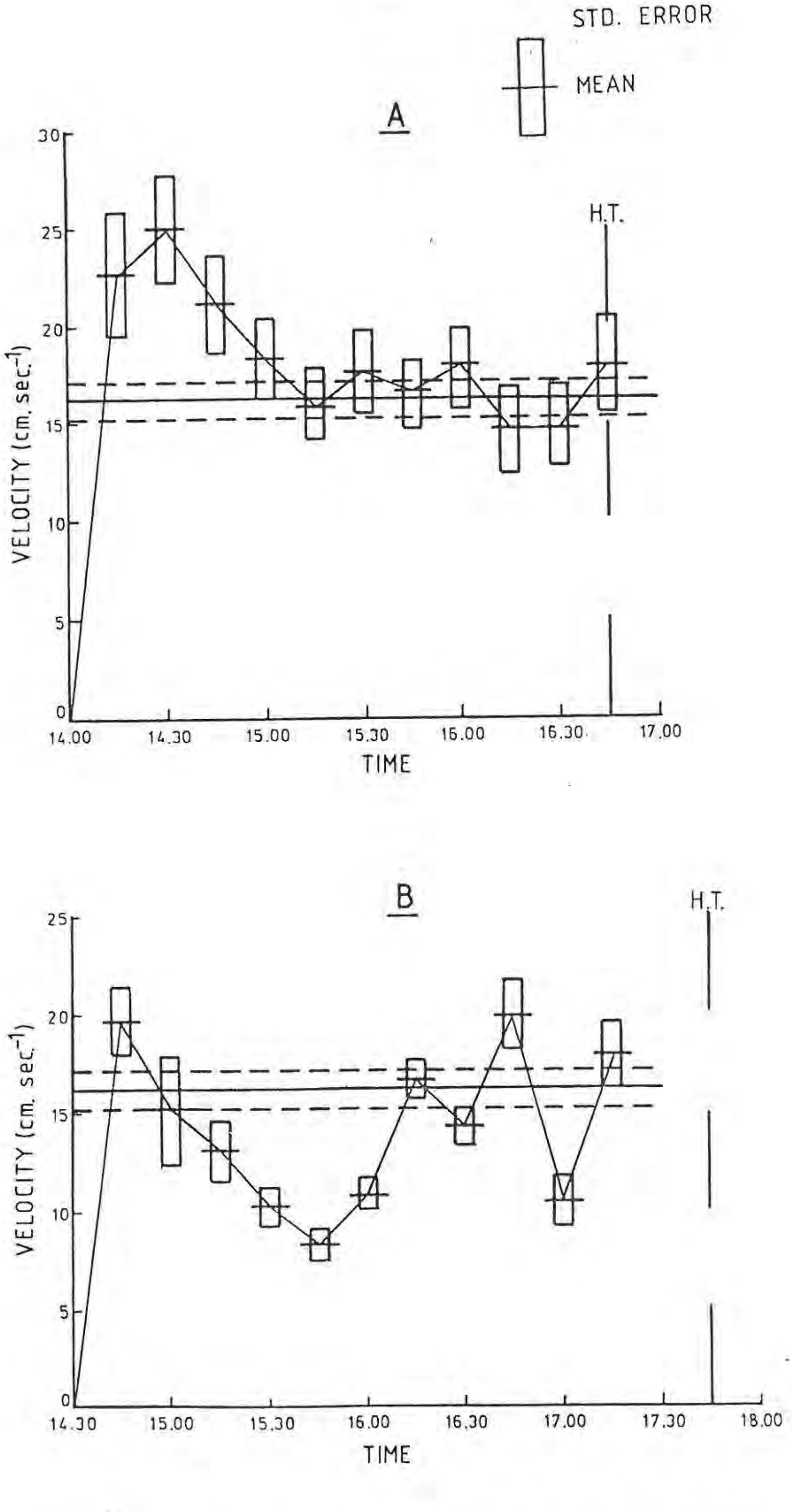


Fig. 29. Current velocities recorded in the mid-intertidal zone using the electromagnetic meter. A. Clayton's Rocks (17/2/80). B. Sea View (4/2/80). The solid horizontal line represents the laboratory derived mean tolerance of the fish tested using the electromagnetic meter and the dashed lines are the standard error about this mean.

(Figs. 28a, 29a & b). On all days on which readings were taken the mean habitat velocity exceeded the mean maximum tolerance level of C. caffer for considerable periods of the high tide cycle.

The data from the electromagnetic meter agree in general with the results from the propellor meter and also with the transect counts which revealed significantly fewer gobies in the open during high tide relative to low tide. This absence of gobies over high tide is explained by the current velocity graphs which show that over high tide the field current velocities are frequently of such a magnitude that the gobies would be under cover avoiding the current.

Discussion

Gibson (1969b) reported that Gobius paganellus, a goby with a similar intertidal distribution to C. caffer, could withstand a current velocity of $\geqq 10$ cm sec^{-1}. This value compares well with the results obtained in the present study for C. caffer (i.e. 10,3 cm sec^{-1}, propellor meter; 16,13 cm sec^{-1}, electromagnetic meter). Despite the fact that the current experienced in the intertidal zone frequently exceeded the mean maximum tolerance level of C. caffer over high tide there were periods over high tide during which the current velocity was below the fish's tolerance level (these periods occurred when the direction of flow of the water reversed). During these slack periods the gobies could remain motionless in the open, but the time available was limited as the periods of slack water were of short duration only. No gobies were seen swimming freely during high tide except for short darts out of or into cover; individuals were seen to retreat under cover during wave surges. As evidenced by the transect counts, C. caffer appeared to spend most of its time avoiding the current by remaining in hiding during high water and thus extensive water movement would appear to have been behaviourally avoided. Jones & Demetropoulos (1968) maintained that such adaptations had the effect of minimising the chance of mechanical damage to the organism and the behaviour of *C. caffer* would certainly appear to confirm this statement.

Gibson (1969b) found that *Gobius paganellus* could withstand a current velocity which the present study has shown to be comparable with the current velocity withstood by *C. caffer*. Gibson postulated that the main function of the weak sucker for *G. paganellus* was to allow the fish to lay and guard eggs on the underside of rocks. He felt the sucker of gobies was not primarily an organ of attachment to overcome water movement and that these fish avoided displacement from the substrate by pressing their bodies close to the substrate and keeping close to, or beneath, stones and boulders. Gibson also noted that fish with more efficient suckers were observed to be much less strongly thigmotactic than *G. paganellus* or members of the suckerless Bleniidae. Gibson's (1969b) postulate for the use of the sucker in gobies should be extended. The sucker also allows the gobies to attach themselves to vertical faces near food patches. This means that the fish can position themselves such that they can feed on food patches by making only short darts to capture food.

The results presented in this chapter show that *C. caffer* is limited in its movements by water current velocity and that most of the time over high tide is spent in cover. Diet studies had shown that fish from pools which were *Ulva*-free (high level pools) included this food type in their diet, a finding that was also reported by Pitt-Kennedy (1968) for *C. caffer* in the western Cape. This meant that the fish were moving about over high tide despite the restraint current placed on their movements. For this reason the system of space utilisation employed by C. caffer was investigated and the results of this investigation are reported in the following chapter.

INTERTIDAL MOVEMENT

Introduction

Caffrogobius caffer collected over spring tides when the sea reached the algae-free high pools were found to have included algae in their diet (Pitt-Kennedy, 1968; pers. obs.). This was interpreted as showing that C. caffer, or at least those from the high pools, moved about the intertidal zone to feed over high tide. Homing, territoriality or fidelity to a home pool have been reported for several intertidal marine fish species (Aronson, 1951; Carlson & Haight, 1972; Sasaki & Hattori, 1969; Gerking, 1959; Green, 1971). The possibility that C. caffer might also show some form of territoriality and/or interpool movement was investigated by means of two tagging experiments. From the results of these experiments it was hoped that a better understanding of the way in which C. caffer used their food resources would result. Behaviour was observed in the laboratory so that the behaviour seen in the field could be better understood.

Materials and Methods

A sketch map of the pools used for the tagging experiments at Sea View is given in Fig. 3. The pools prefixed G were gullies which, except for G3, were isolated from the sea at low tide. The maximum depth (± 1m) at low tide was in pool G3. The pools prefixed F were in an area of flat lying rocks had an average depth ± 0,2m at low tide, with a localised maximum of ± 0,75m in pool F3. The pools at Clayton's Rocks, represented in Fig. 2, were similar to the F pools at Sea View. The map of the pools at Clayton's Rocks was superimposed onto graph paper and the resultant grid thus formed allowed recognition of areas $1m^2$ in the field. This meant that accurate records of a specimens location in a pool could be kept.

Initially fish were marked by freeze branding (Laird et al., 1975) but modified Floy FD 67 spaghetti tags were used for all the results presented here. Several factors influenced the change to tags. The first was that, due to the small size of the fish, neither distinguishable letters nor numbers could be successfully branded onto the fish. This necessitated a coding system of dots on various parts of the fish. Laboratory control experiments showed, however, that brands did not always "take" successfully, some becoming indistinct within a week. The loss of a single dot could substantially alter the code branded onto a fish and an inaccurate resighting could result. The most important reason for the change to spaghetti tags was, however, the fact that branded fish had to be caught for the brand to be read. Recapture of fish proved to be a time-consuming process which was not suitable for regular, short interval, resighting observations due to the repeated interference with the fish. Modified spaghetti tags required only one capture and could be "read" at a distance of several metres when implanted in C. caffer.

For the preliminary Sea View experiment tags which allowed recognition of the initial pool of capture were used and, in certain cases, individual fish. At Clayton's Rocks all fish were tagged with individually recognisable tags and the pool of capture recorded. Standard Floy FD 67 tags with numbers would have required that the fish be recaptured for the numbers to be read. Furthermore, the tags were too long to be used with the smaller fish.

Differentiation between tags was made possible by the addition of coloured insulation tubing to provide a variety of colours. To increase the number of combinations, coloured plastic discs were cut and the disc threaded onto the shaft of the tag. The end of the shaft was melted

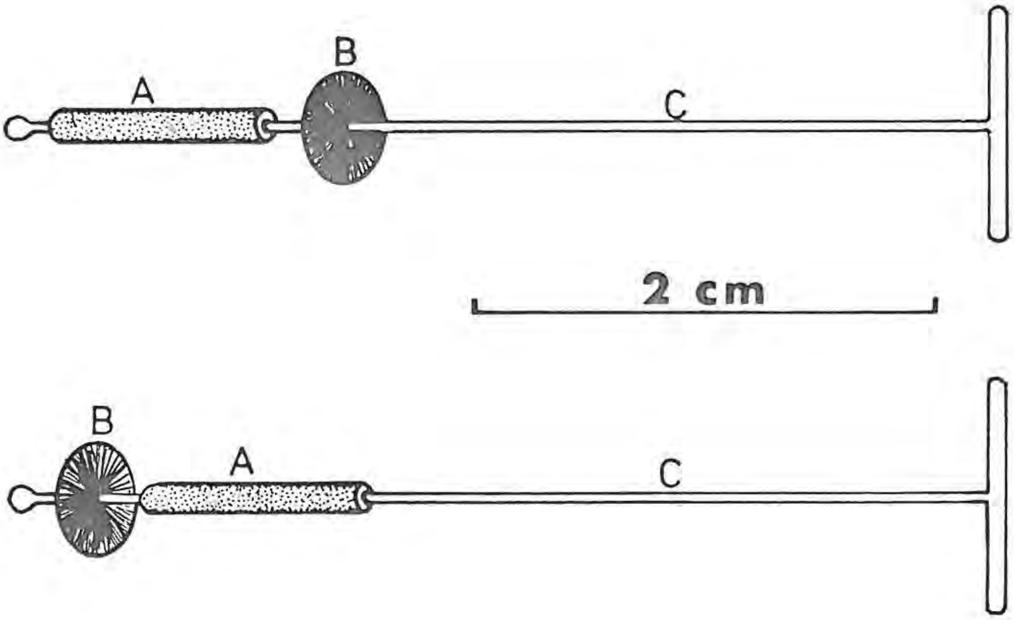


Fig. 30. Diagram of modified Flov FD 67 tags used for tagging C. caffer. (A = coloured plastic tubing, B = coloured plastic disc, C = shaft of tag).

into a bulge over which the plastic tubes and discs could not slide. Due to the relatively small size of the fish the tags were shortened. Tags were identified according to the colours and relative positions of the component parts (Fig. 30).

The tags were attached through the dorsal body musculature between the anterior and posterior dorsal fins using a standard Floy tag gun. A tag placed in this position did not appear to affect the swimming of the smallest fish tagged (60mm). Tagging had little effect on the behaviour of C. caffer (one fish was recaptured on a baited hook three times within an hour of being tagged). After tagging the fish were returned to the pool in which they had been caught. Capture of fish for tagging experiments was conducted using either baited hooks or hand nets.

Of the tagged fish kept in an aquarium for six and a half weeks only one died (when eaten by a conspecific). At the end of the six and a half week period a bacterial infection killed all the fish - including untagged controls. Behaviour of the tagged fish in the aquarium was not affected by the presence of the tag.

Two separate tagging experiments were conducted at Sea View. On the 4th and 5th April 1977, 124 fish were tagged with tags which identified the pool from which they had been captured. On 21st June 1977, 23 fish were fitted with tags that allowed recognition of individual fish. The first experiment was designed to investigate the possibility that C. caffer remained in or near a single pool through time, while the second, initiated due to the results of the first, aimed at examining whether fish had territories within the pool.

It was intended that resighting data be based on fortnightly observations taken over spring tides. Poor weather conditions over spring tide periods following tagging, however, prevented regular surveys. Seven resighting surveys were conducted over eight months. On five of these occasions three workers conducted the counts and on the other two occasions two people were involved. Resighting surveys could only be conducted during periods of low tide when there was no wind to disturb the water surface as fish could not be seen through the ripples caused by wind. Each survey took approximately one and a half hours to complete.

The tagging program at Clayton's Rocks differed from that at Sea View in that tagged fish were monitored each low tide, weather permitting, for three weeks after tagging. Between 16 and 19 August 1979, 150 fish from 10 pools (Fig. 2) were tagged with individually recognisable tags. Resighting surveys were conducted over low tides by, usually, two people. Surveys were made during both daylight and darkness at night was found to be easier than was the case during daylight surveys. At night the fish were often found in the open and could be blinded by torchlight and the tags easily read. During daylight fish would see the observer approaching and dart into cover, often before their tags could be identified.

Due to the ongoing nature of the experiment, rocks were not overturned to expose fish as had been done at Sea View, as it was felt that this might cause too great a disturbance to the habitat. The technique employed during surveys was for the two workers to walk slowly around the pool in opposite directions noting any tagged fish that were seen. The disturbance caused by someone walking through the pools often resulted in fish that had been in cover moving into the open so that they could be counted by the second worker as he retraced his colleague's footsteps. After the maps of the pools were complete the positions of

Table 6.

Percentages of resighted fish at Sea View that were displaced from the pools in which they were tagged. Separate = pools F1, F2, G1 and G2 considered as single entities; combined = data from pools F1 - F2 and G1 - G2 considered together.)

Date	Separate	Combined
5/4/77	66,7	55,6
6/4/77	36,4	27,3
16/4/77	46,4	21,4
21/6/77	75,6	25,0
13/11/77	14,3	0,0
10/12/77	28,6	0,0

The data for 21/6/77 should be treated with reserve as on this day the tagging of 23 fish from pool F3 was conducted. This allowed time for only a superficial count of previously tagged fish before the high tide reached the pools.

the fish in the pools were recorded within one metre square areas. Each survey took between two and two and a half hours to complete.

Eighteen fish were caught by hook and line from a high level pool at West Bank the day before the high spring tides started to reach the high pools. These fish were marked by truncating the caudal fins and thus they could easily be recognised when recaught. A week later the same pool was poisoned with Pro-Noxfish after the spring tides had stopped reaching the pool, and marked fish were collected.

Results

Interpool movements

One hundred and forty seven fish were tagged at Sea View, and 150 at Clayton's Rocks. At Sea View a total of 118 resightings were recorded while 99 fish (274 resightings) were resighted at Clayton's Rocks. (Note the distinction between a resighted fish and a resighting. A tagged fish could be resighted several times.) During the three weeks continuous observation at Clayton's Rocks six dropped tags were found and ten resightings of tag scarred fish were made.

At Sea View pools F1, F2, G1 and G2 were for the purpose of tagging considered as separate entities. These pools did, however, interconnect via shallow connections (Fig. 3) through which the fish could move if disturbed. Table 6 gives the percentage of resighted fish which were displaced from their original pools, with the pools considered as both complexes (e.g. pools F1 and F2 considered as one pool) and as single entities.

The results presented in Table 6 show that the percentage of resighted

Table 7.

Summary of the results of the 19 resighting surveys of tagged fish conducted at Clayton's Rocks. Note: A displaced resighting is one in which the resighted fish was found in a pool other than its original pool of capture.

Description	Number	%
1. Total fish tagged	150	100
2. Total fish resighted; as a % of total fish tagged	99	66,6
3. Total resightings	274	100
4. Fish resighted only in original pool of capture; as a % of total fish resighted (99)	67	67,7
5. Resightings of fish seen only in original pool of capture; as a % of total resightings (274)	217	79,2
6. Total displaced resightings; as a % of total resightings (274)	57	20,8
7. Displaced resightings within original pool complex; as a % of total resightings (274)	53	19,3
8. Fish displaced from original pool at least once; as a % of total resighted fish (99)	32	32,3
9. Fish displaced to new pools within original pool complex; as a % of total resighted fish (99)	29	29,3
10. Fish displaced into new pool complex at least once; as a % of total resighted fish (99)	3	3,0
11. Displaced resightings in a new pool complex; as a % of total resightings (274)	4	1,5
12. @Displaced fish remaining in new pools; as a % of total displaced fish (32)	7	21,8
13. @Displaced fish returning to original pool; as a % of total displaced fish (32)	12	37,5
14. @Displaced fish in new pool complex remaining in new pool complex; as a % of total displaced fish	1	3,3
15. @Displaced fish in new pool complex returned to original pool complex; as a % of total displaced fish (32)	?	?

(@ The data for numbers 12-15 inclusive may not represent the true situation. If the last resighting of a fish was a displacement, but preceding resightings were in the original pool of capture, then it was not possible to state that the fish in question had become a resident of the new pool. At least two consecutive displaced resightings were necessary before resident status could be recognised for a displaced fish.)

fish that were displaced from their original pool of capture decreased with time. This was particularly true if the pools were considered as complexes rather than single entities.

Of the 23 fish tagged with individually recognisable tags, only one was seen again. This fish was resighted in pool F3 (the pool in which it had been tagged) on 10/12/77, nearly six months after tagging.

The results of the 19 resighting surveys conducted at Clayton's Rocks are summarised in Table 7. The pools W1 - W4 and R1 - R3 were assumed to be two separate pool complexes at the time of tagging, an assumption that, so far as C. caffer was concerned, was proved to be correct by the results (Table 7). Fifty seven resightings (20,8%) representing 32 fish (32,3% of resighted fish) were of fish displaced from their original pool of capture. Of these 32 fish, only 3 (3%) (4 resightings, 1,5%) were seen in another pool complex. Of the 54 resightings of fish displaced within their own pool complex, 12 resightings were of fish in a narrow gully connecting pools W1 and W4 even at low tide. Thus the number of resightings of fish displaced from the original body of water in which they were captured was 45.

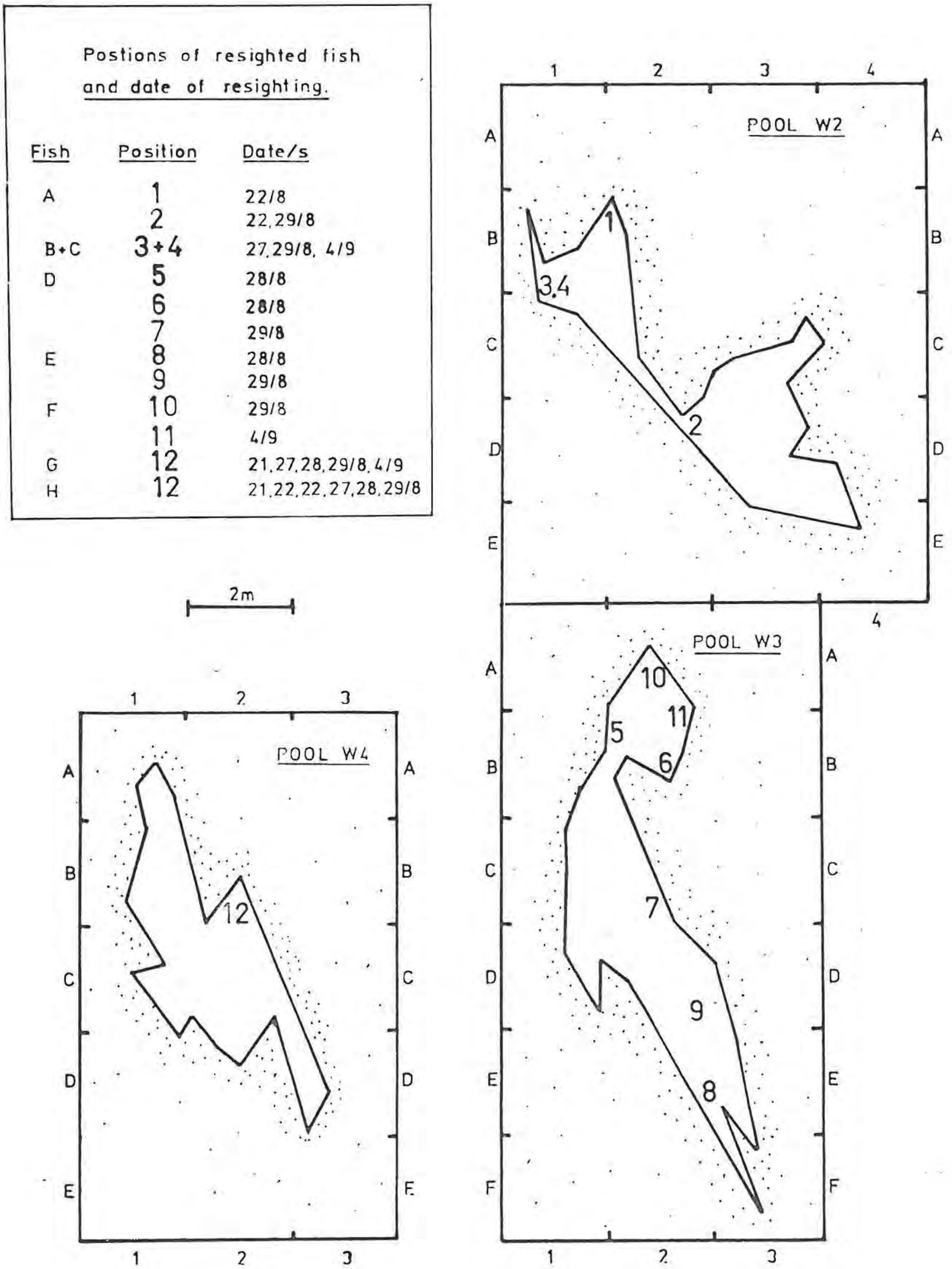
Maps of the pools were available for two weeks of the experiment. Only 15 fish were seen more than once after the grid maps were prepared. The reason for this low number of resightings was a deterioration in the weather, culminating in a storm with a reported wind velocity of 150km/h. The distances that these 15 fish had moved and the time between resightings is given in Table 8.

The maximum recorded distance moved was 6,7m and the minimum 0,0m with a

Table 8.

Distance moved by fish resighted during the course of the surveys at Clayton's Rocks. L = length in mm, D = distance moved in metres, T = time in hours between first resighting and last resighting.

L	D	T
83	6,7	170
108	1,0	146
69	1,0	193
63	1,0	193
85	3,0	170
113	1,0	25
73	2,0	34
66	1,5	63
112	4,0	359
65	0,0	167
98	6,5	62
72	1,0	24
81	1,0	23
150	6,0	210



Postions of resighted fish and date of resighting.

Fish	Position	Date/s
A	1	22/8
	2	22,29/8
B+C	3+4	27,29/8, 4/9
D	5	28/8
	6	28/8
	7	29/8
E	8	28/8
	9	29/8
F	10	29/8
	11	4/9
G	12	21,27,28,29/8, 4/9
H	12	21,22,22,27,28,29/8

Fig. 31. Movements recorded for eight C. caffer at Clayton's Rocks, showing distance moved and time taken for move.

mean of 1,5m (SE 0,46m). There was no relationship between the distance moved and the time taken for the move (r = 0,162, p 0,05) nor was there any correlation between the distance moved and the length of the fish (r = 0,131, p 0,05). The fish remained within restricted areas of the pools at low tide and did not utilise all the physical space available to them. Fig. 31 shows an example of the movements made by some of the 15 fish mentioned above. Of the 32 fish which were displaced and resighted at least twice, seven (21,2%) remained in the new area while 12 (36,4%) returned to their original pools. Of the 18 fish marked by caudal fin truncation at West Bank 14 were found in the same pool seven days later. The second collection, using ichthyocide, was made after the spring tides had stopped reaching the experimental pool.

Intra-pool movements

A total of 17,5 hours, comprising 19 different observation periods, were spent observing the movements and behaviour of *C. caffer* in pool W3. Fig. 32 shows the typical movements made by nine fish during an one hour period (09h00 - 10h00, 14/8/78). This figure shows that each fish remained within a restricted area of the pool. Although these areas, or ranges, did not in general overlap and fish seldom met, when they did some fish performed a frontal display (pectoral fins spread wide, pelvic sucker used to lift the fish off the substrate, head arched upwards). Under these circumstances the smaller fish would always retreat, even if the larger fish was trespassing in the range being used by the smaller fish. Any fish could enter the range of another and, even if the two fish met unexpectedly around a rock or projection, the resident would not always attempt to drive the intruder away. Agonistic behaviour was only displayed when the fish were of approximately the same size. If there was a large size difference the two fish ignored one another. There

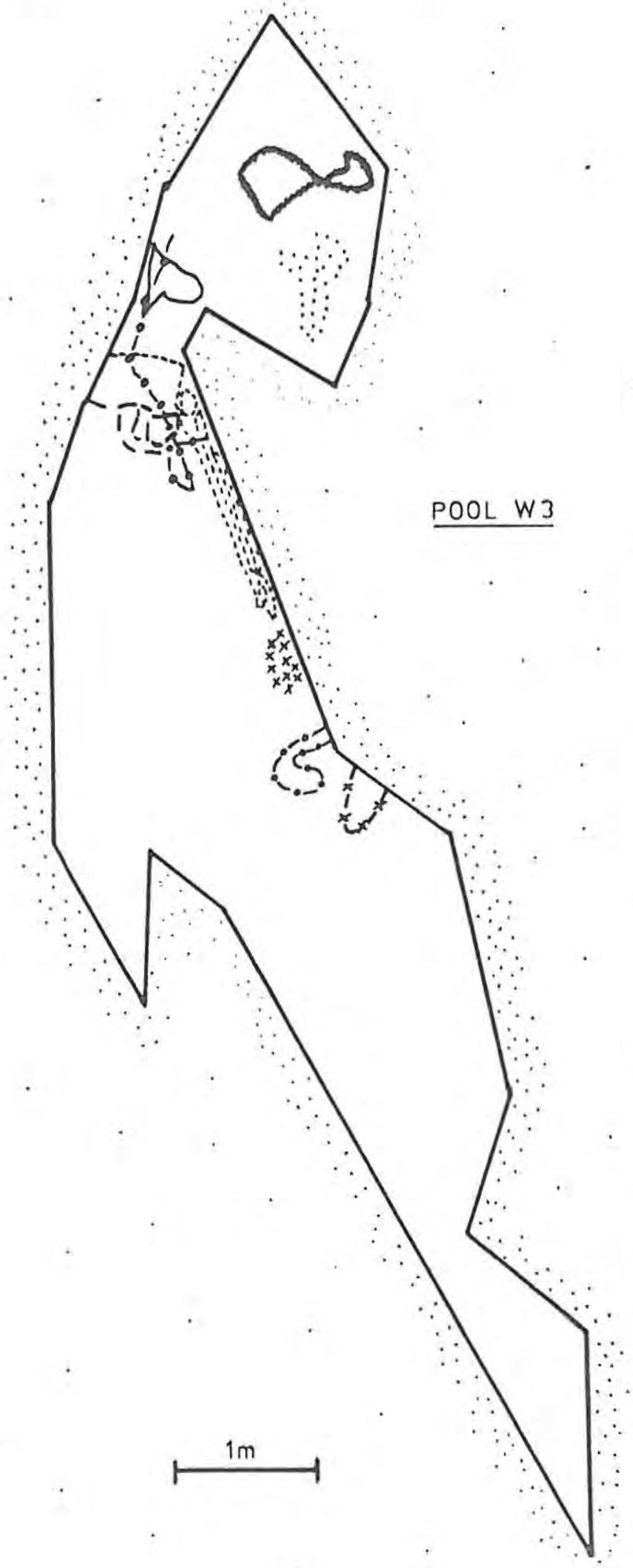


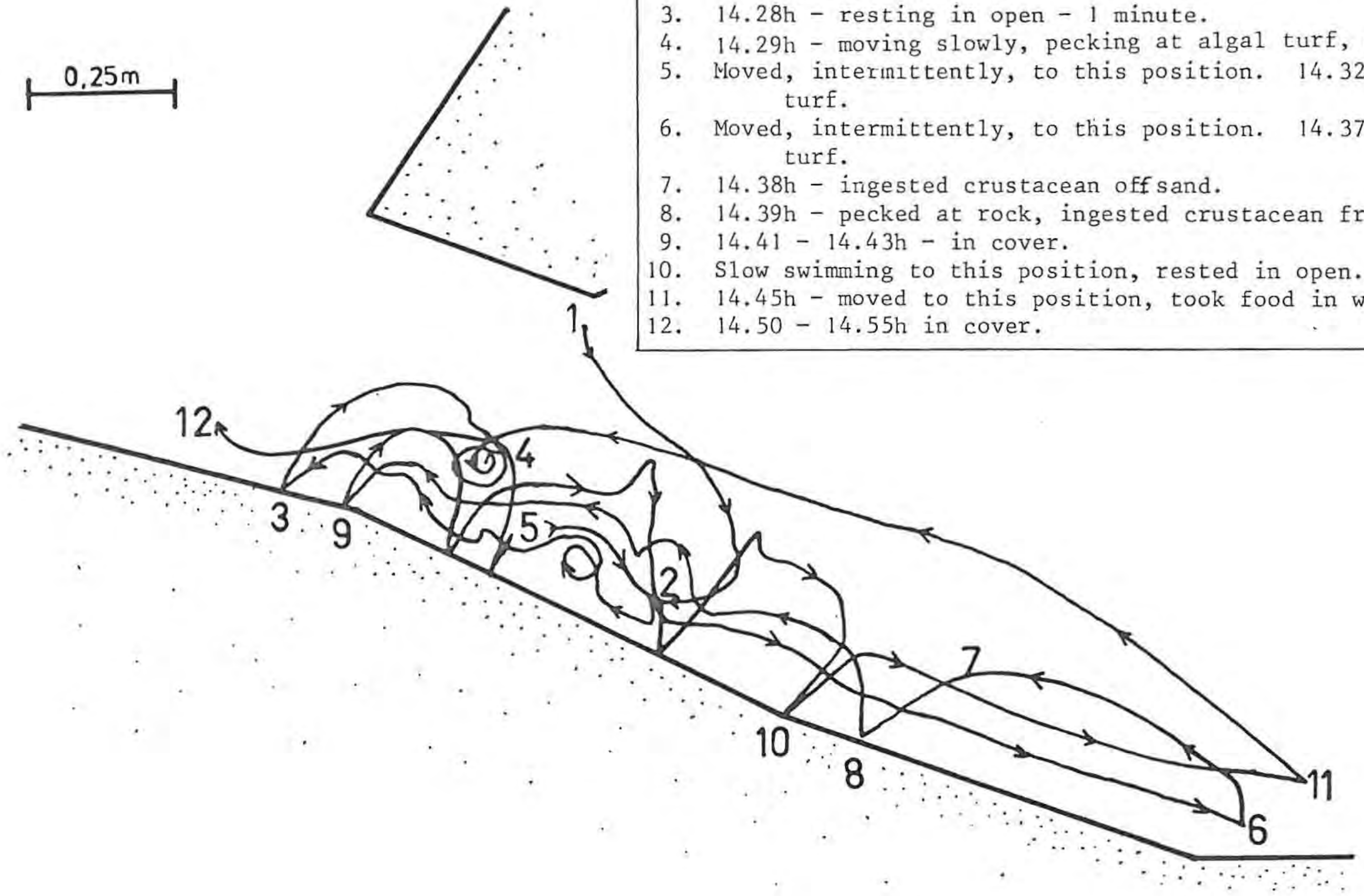
Fig. 32. Movements of nine C. caffer recorded in a one hour period (09h00 - 10h00, 19/8/78) in pool W3 at Clayton's Rocks.

was thus no territorial defence. Within its range the fish would spend its time resting, feeding, hiding in cover and in intraspecific displays.

The detailed movements and actions of a single fish (± 55mm) during a 30 minute period (14h25 - 14h55) are shown in Fig. 33. During this half hour period the subject made no contact with conspecifics (a situation found to be typical), although several other C. caffer did enter its range. Eight separate feeding movements were made, seven of which resulted in the ingestion of food. The fish moved about slowly, stopping intermittently for periods ranging from a few seconds to several minutes. The proximity to one another of the points reached at the ends of the range indicate that they represent the limits of normal movement. Similar behaviour was noted for all other fish observed.

No territorial defence was seen in the laboratory. All fish moved over the entire area of the aquarium. The fish, however, appeared to have a preferred area, or a home site (sensu Carlson & Haight, 1972) in the tank and would usually return to this area when alarmed, or when the illumination was switched off. Builders of cavities in the sand under rocks did not try to oust a conspecific which moved into the cavity while the owner was out of cover. When alarmed several fish might seek refuge in the same cavity; no agonistic behaviour was shown in such cases.

The only occasion when an area was seen to be truly defended and all intruders, including hermit crabs, were driven off was recorded in the laboratory when a male was guarding a clutch of eggs. The elongate eggs had been laid on the underside of a large stone in the aquarium. A cavity was hollowed out by the female and was maintained and enlarged



1. 14.25h - fish moved to 2.
2. 14.26h - fish attracted to hermit crab by movement - darted towards it - moved to 3.
3. 14.28h - resting in open - 1 minute.
4. 14.29h - moving slowly, pecking at algal turf, presumably for food.
5. Moved, intermittently, to this position. 14.32h pecking off algal turf.
6. Moved, intermittently, to this position. 14.37h pecking off algal turf.
7. 14.38h - ingested crustacean off sand.
8. 14.39h - pecked at rock, ingested crustacean from water column.
9. 14.41 - 14.43h - in cover.
10. Slow swimming to this position, rested in open.
11. 14.45h - moved to this position, took food in water column.
12. 14.50 - 14.55h in cover.

Fig. 33. Movements of a single C. caffer (± 55mm TL) observed for a half hour period (14h25 - 14h55, 23/8/78) in pool W3 at Clayton's Rocks.

by the guarding male. This male tolerated no other fish near the nest, including the female which had laid the eggs. With this latter exception the fish exhibited a size dependent heirarchy, smaller fish submitting to a larger individual in all parts of the tank. Fish, however, only used aggressive displays towards individuals of approximately the same size, ignoring much smaller or much larger individuals. During field observations no behaviour that contradicted conclusions drawn on the basis of laboratory observations was noted.

Low intensity red illumination provided by a photographic safe light was used to observe laboratory specimens in an attempt to observe nocturnal behaviour. Protasov (1968) reported that many species of fish can perceive colours and thus the finding that the behaviour exhibited by C. caffer under low red illumination was the same as seen under white light indicates that this species can perceive red light and that behaviour is not altered by low light intensity. The only difference noted was that fish spent longer periods resting under low levels of illumination relative to the amount of time spent resting at daylight light levels.

Discussion

Of the fish tagged at Sea View 11,3% were found eight months after they had been tagged. Tagged fish kept in aquaria suffered no tag induced mortality. Thus tag induced mortality did not affect the results of the three week study at Clayton's Rocks, although mortality due to tag presence might have had an effect on the results of the eight month survey at Sea View. Tag loss, however, could have affected the results at both study areas. Although no tagged fish kept in aquaria lost their tags, six dropped tags were found at Clayton's Rocks. Williams (1957) and Green (1971) used tags consisting of coloured embroidery beads attached by nylon monofilament line through the dorsal musculature of the fish. Green (1971) found that tags inserted into Oligocottus maculosus Girard (Cottidae) could be lost in the environment within a matter of weeks or even days. He ascribed this loss to the turbulent water and greater number of opportunities for the tag to become snagged on rocks in pools relative to aquarium conditions.

Williams (1957) used a variety of different coloured beads to identify individual fish, while Green (1971) used only two beads of different colours but clipped fins to increase the number of possible combinations. Williams' (1957) method was not used in the present study as the number of different colours was kept to a minimum and only colours that would not be confused, especially under artificial torchlight, were used. Fin clipping would have necessitated the recapture of fish for positive identification, as was done on the one occasion at West Bank. The modified Floy FD 67 tags used were susceptible to snagging and the six dropped tags might not have represented the true number lost.

The majority of fish resighted at Clayton's Rocks (67,7%) were found in the pools of their original capture. Of those fish resighted in new pools (32) not less than 37,5% returned to their original pool. It was not possible to determine exactly the number of tagged fish that returned to their original pool or remained in the new pool. Residence status in a pool could only be determined if more than one resighting, on separate occasions was made. Gerking (1959) quotes several authors as assigning residence status if a fish was resighted two or more times in the same pool. If these conditions were met the authors referred to by Gerking considered that the fish had a home range.

The 62,5% of displaced fish which did not return to their original pool either took up residence in another pool (at least 21,8%) or were not resighted again. Fish resighted in new pools would have moved during a high tide period and might have been caught by the receding tide and were thus not able to return to their original home pool. Fish which vacated their original tagging pool on a permanent basis could have been vagrants caught out of their home pool by the receding tide at the time of tagging. Once returned to their home pool such a fish would have been recorded as displaced while the true situation was that it was displaced when tagged.

Gerking (1959) commented that the design of an experiment can introduce bias to the results which makes accurate establishment of the size of the home range difficult. He pointed out that if the study area was small in relation to the home range few marked fish would be found in successive resightings. Williams (1957), discussing the same point, stated that a quantitative estimate of the size of a home range and the degree of straying (displacement) would describe the techniques used as much as the behaviour of the fish. The pool complexes studied at Clayton's Rocks almost definitely did not cover the entire home ranges of all the specimens tagged, especially as not all pools within each complex were monitored. This lack of coverage probably accounts for some of the missing 51 fish which were not resighted.

The results from Sea View and West Bank also indicate that C. caffer usually returns to a home pool. The experiment conducted at Sea View ran for eight months and tagged fish were found in the original pool complex throughout this period. On the basis of the results from the three study areas it can be said that C. caffer has a home pool and that they move into other pools over high tide, which constitute their home range, but return to the home pool unless caught by the receding tide. Gibson (1967a) described similar results for a tagging experiment with Blennius pholis. He suggested that his results were consistent with the concept of a home range, rather than a defended territory. He considered that B. pholis caught in any pool would include: '(i) individuals whose home range was centered on or near that pool, (ii)others whose home range included the pool within but not near the centre of the range, and (iii) fish outside their normal home range or whose home range only rarely included the pool in question' (p. 228). These conclusions fit the results obtained for C. caffer at Clayton's Rocks and Sea View.

The well-defined limits of movement of C. caffer within the home pool during low tide show that this species has a preferred area, or home site (sensu Carlson & Haight, 1972), within its home pool. This home site could not be considered as a territory, in the sense of a territory being a defended area (Noble, 1939; Nursall, 1977). Fish kept in the laboratory were never seen to defend a particular area of the aquarium with one exception, when a male was guarding a clutch of eggs. The only occasions when non-breeding aggressive behaviour was recorded both in the laboratory and the field was between fish of similar size, indicating that a size dependent heirarchy exists for C. caffer. Fish of different sizes probably did not show aggression to one another as their relative status could be established by sight.

C. caffer showed a dual system of space utilisation dependent upon the prevailing tide phase. Although non-breeding territories have been described for marine fish (Clarke, 1971; Nursall, 1977) and home pools have been reported for intertidal fish (Gibson, 1969a), no report has been made of a system similar to that used by C. caffer, i.e. a high tide home range covering several pools, and a home pool within which is a restricted home site. Previous work has centered on either establishing the true territoriality of a fish or its use of a home range. For those fish found to be territorial the associated behaviour has been studied in detail (Clarke, 1971; Nursall, 1977). Workers finding that a species has a home range seem to have been content with this finding alone and have not examined in detail the fish's utilisation of its home pool. It is likely that other intertidal fish species with a home pool use a restricted area of this home pool during low tide in a similar manner to that used by C. caffer.

Experiments on current velocity tolerance by C. caffer showed that this species spent most of the high tide period in cover. Two pool complexes at Clayton's Rocks were close enough to one another such that intervisiting could reasonably be expected (W & R complexes, Fig 2), but were separated by a low ridge of rocks. The pools of each individual complex were interconnected by the rising tide before the two complexes were joined. Examination of the field current velocity data and comparison with the established current velocity tolerance of C. caffer showed that movement between pools within a complex could occur as the limiting velocity had not been reached by the time the pools interconnected. By the time the two complexes were joined, however, the mean current velocities were approaching the tolerance level of C. caffer. Although current tolerance was measured only for the fish's ability to rest in the open, C. caffer took cover before its maximum tolerance level was reached and thus did not move between complexes. This is illustrated by the low number of fish that moved into another complex (3 individuals) and by the small number of fish observed in the open during high tide vs the number seen in the open during low water. Thus C. caffer probably only moved about its home range in the initial stages of tidal innundation, remained in cover most of the high tide period, and usually returned to their home pools as the current velocity decreased with the ebbing tide.

GENERAL DISCUSSION

Distribution of Caffrogobius caffer on the shore

The even distribution of *C. caffer* throughout the intertidal zone differs from the situation for some other intertidal animals (Gibson, 1970a; Branch, 1975a). The lack of size dependent zonation up the shore of *C. caffer* appeared to be in contradiction with the finding that larger fish could withstand higher current velocities than smaller individuals (Fig. 27). Although no current velocity readings were taken in the high level pools, it is most likely that the current velocities experienced by these pools would have been lower than the velocities occurring in the mid-intertidal pools. Lower velocities would be expected due to the protection afforded the high level pools by the rock strata of the low level areas. Assuming that the current velocities were lower in the high level pools it would have been expected that small individuals of *C. caffer* would have congregated in these pools. That such a congregation did not occur was attributable to several factors.

A small fish requires a correspondingly smaller crevice in which to hide relative to a larger specimen. Small fish could also use the hiding places suitable for larger fish and thus had a greater number of hiding places available to them than did larger individuals. It is unlikely that the current velocities under rocks would have approached the upper tolerance limit of the small fish, which could thus move feely under close cover even during high tide. The number of juveniles exceeded the number of adult fish (Fig. 6) and it is also possible that the upper pools alone could not have supported the entire juvenile population. The fact that larger individuals could withstand higher velocities does not imply that these large individuals would not utilise areas of low current velocity such as the high pools.

That C. caffer of all size classes did take cover over high tide was shown by the data from the transect counts. The smaller number of gobies in the open over high tide is explained by the finding that C. caffer had an upper limit of current tolerance that was exceeded over high tide. Jones & Demetropoulos (1968) stated that water drag on an organism was probably the most important single hazard facing intertidal life. It is probably for this reason that intertidal fish have a well developed thigmotactic response (Gibson, 1969a). So important can the presence of a substrate be that for juvenile Acanthurus triostegus (L.) this was the dominant factor affecting habitat selection, with cover availability playing a secondary rôle (Sale, 1969). C. caffer was found mainly on or near the substrate. During this survey this species was never seen making more than short darts into the water column and then only when capturing food.

Food and feeding

The main mechanism of prey detection in C. caffer appears to be sight (Pitt-Kennedy, 1968; pers. obs.). O'Brien et al.(1976) found that the apparent rather than the actual size of prey organisms determined whether the blue-gill sunfish, Lepomis macrochirus Rafinesque, would ingest a food item or not. O'Brien et al.conducted experiments in which prey of different sizes were offered to the sunfish at different distances. The fish always selected the prey that was apparently largest, either because of its proximity or its actual size. These authors suggested that by choosing the apparently largest prey under all conditions the sunfish alter their diet according to the abundance of prey and utilise the most rewarding food source. Whether prey size selection plays an important rôle in the feeding of all size classes of C. caffer is debatable. For the smallest size classes of C. caffer which feed solely on small animals, prey size probably plays an important rôle in prey selection. Whether prey size plays an important part in the ingestion of algae by the larger size classes depends on the mechanism that initiates the feeding movement. O'Brien *et al.*(1976) found that *Lepomis macrochirus* would only take moving prey items and the same seemed to be true for *C. caffer*. *C. caffer* would often ignore a baited hook that was motionless, but would readily take the bait if it was moved. In aquaria food that fell to the tank floor would often be left untouched. Movement of prey organisms on or in the algal turf is probably the stimulus that initiates feeding movements and the ingestion of algae. Whether it is purely movement, or movement coupled with the size of the moving organism, that triggers the feeding movement is not known.

By ingesting algae *C. caffer* obtains more prey items for a single feeding movement than would be the case if a single animal was ingested. The amount of time available to *C. caffer* for feeding on algae depends on two factors. Those fish which have home sites containing algae can obtain this food source throughout the day. For those fish with no algae in the home site, algae is mostly obtained during the initial stages of the incoming tide and the final stages of the ebbing tide, when current velocity is below the fish's tolerance level and interpool movements are possible. The dual system of space utilisation employed by *C. caffer* (a home range with a discrete core area) spaces the individuals out in such a way that little time or effort is wasted on agonistic displays and ensures the availability of cover for predator avoidance. This dual system and the size dependent heirarchy in no way denies any population member access to algal resources. Coupled with this species' ability to feed throughout the day the ingestion of algae and the catholic range

Table 9.

Comparison of points vs occurrence data from the high and low level pools at Clayton's Rocks. Spearman's rank correlation coefficient, converted to Student's t, was used to assess the level of significance.

	High pools				Low pools			
Date	rs	t	p	df	rs	t	p	df
Mar	0,8477	3,9143	<0,005	6	0,4386	1,6906	<0,05	12
Apr	0,5835	2,4889	<0,025	12	0,5832	1,8950	=0,05	7
May					0,5159	1,9044	<0,05	10
June					0,5868	2,4035	<0,025	11
July	0,4420	1,4782	<0,1	9	0,7530	3,4330	<0,005	9
Aug					0,8675	5,5148	<0,0005	10
Sep	0,7010	3,1084	<0,01	10	0,7182	2,7308	<0,025	7
Oct	0,				0,3933	1,3527	<0,1	10
Nov	0,3701	1,2594	<0,2	10	0,6781	2,7679	<0,025	9
Dec					0,5492	2,3695	<0,025	13
Jan	0,6682	2,9788	<0,01	11	0,8542	6,3628	<0,0005	15
Feb	0,8804	3,7130	<0,01	4	0,5187	1,9185	<0,05	10
Combined data for entire year;								
	0,9755	20,7978	<0,0005	22	0,9832	25,2648	<0,0005	22

Comparison of points vs % mass from the Clayton's Rocks 24h collections.

23-24/6	0,7000	2,5934	<0,025	7
23-24/11	0,7500	2,5355	<0,05	5
combined	0,8333	3,6923	<0,01	6

The term % mass is explained in the text (p. 65).

of food items in the diet allows the fish to optimally utilise the patchy resources of their habitat.

The finding that feeding did take place over high tide appeared to contradict the results of the current tolerance experiments which showed that the current velocities prevalent over high tide prevented C. caffer from remaining in the open. This apparent contradiction is probably explained by the fact that C. caffer could make use of lulls in water movement to capture food over high tide. Also, it is possible that feeding could have taken place while the fish were under cover, feeding on organisms found in the shelters or brought in by the tide. Diving observations showed that few C. caffer were in the open during high tide and thus feeding while in cover seems to be the more likely possibility.

Hynes (1950) commented, 'There are grounds for stating that, for a fish with a generalised diet, provided that a large number of specimens is examined, any of the commonly accepted methods of assessing the composition of the diet of fish gut contents will give substantially the same results' (p. 39). This statement seems to be too wide and results from subsequent studies have shown that it is correct only in certain cases. Bruton (1979b) used numerical and gravimetric methods to analyse the diet of Clarias gariepinus (Burchell). He found that these methods gave different results for C. gariepinus which ate food of different sizes. The results obtained in the present study from the three methods used to analyse diet were compared statistically by means of Spearman's rank correlation coefficient (Table 9). The three methods, points, occurrence and % mass, were compared and the points method results were found to be, in general, significantly similar to

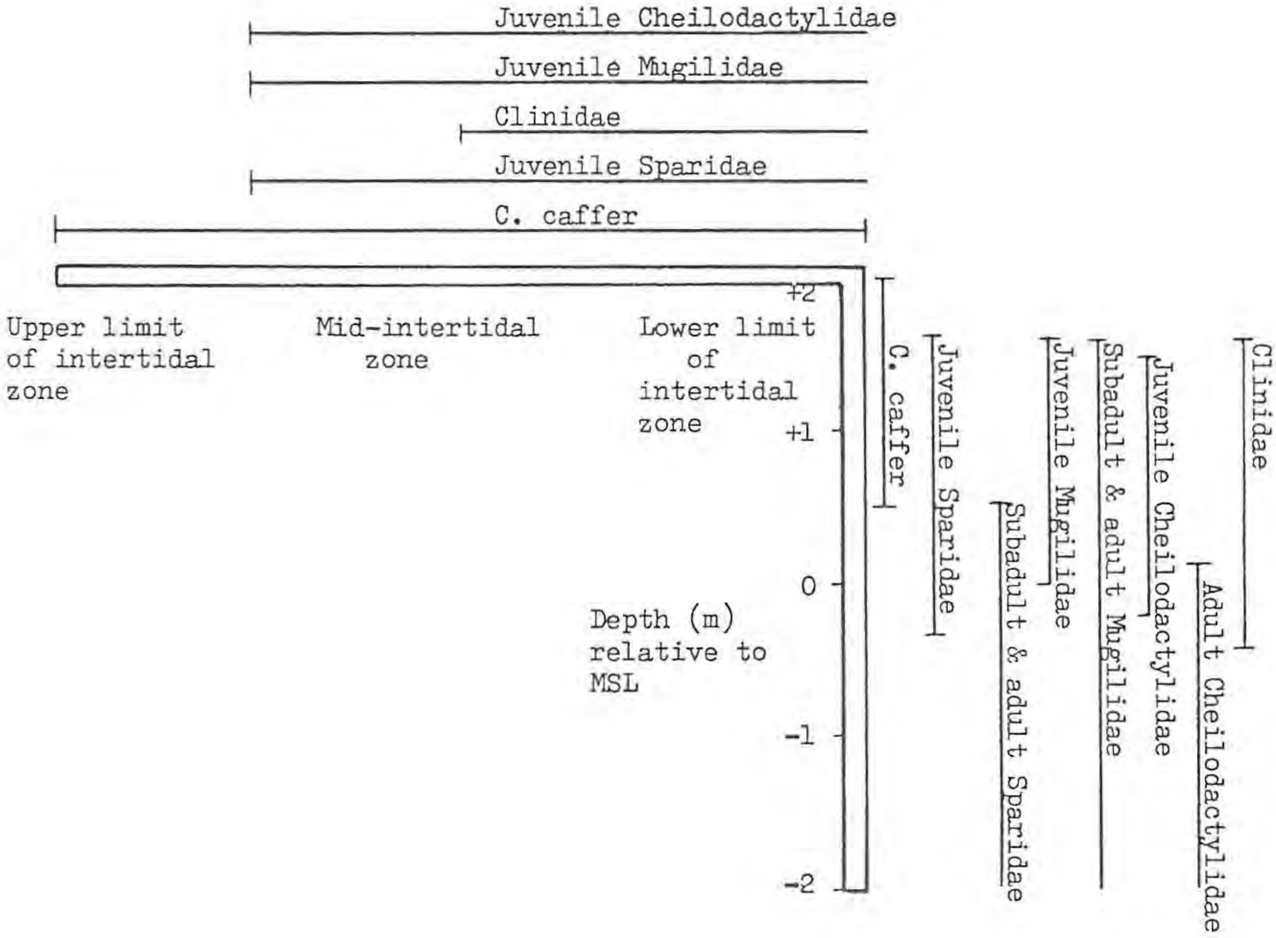


Fig. 34. Approximate distribution on the shore of some common intertidal fish species in the eastern Cape. The horizontal axis represents a cross section through the intertidal zone, while the vertical axis represents the depths at which the different species occur (relative to MSL). (Note; although this diagram only shows depths to 2m below MSL some of the species or families mentioned are found below this depth.

the results obtained by the other two methods. Thus it appears that Hynes' (1950) comment is correct in some cases but cannot be considered to be of general application.

Intra- and interspecific competition

Branch (1975a) found that competition between limpets was mainly for food and in Patella species in which the adult diet was similar to that of the juveniles, the adults moved up the shore away from the juvenile feeding grounds. This movement tended to reduce intra-specific competition. Patella species which did not partition their population up the shore overcame intra-specific competition by having different diets in the juvenile and adult stages. C. caffer had a uniform distribution on the shore relative to size class and this species used the strategy of changing diet with growth to overcome intra-specific competition. This strategy mirrors the method used by those limpets which remained in the same area of the intertidal region throughout their lives.

Other than the change in diet with growth, little is known about the mechanisms which C. caffer uses to overcome competition. Other fish species with distributions on the shore that overlap with that of C. caffer have been found to ingest food types similar to those eaten by C. caffer (Butler, 1975; Christensen, 1978a,b & c; Jackson, 1950; Penrith, 1965). Fig. 34 shows the approximate distribution on the shore of some other common fish species in the eastern Cape in relation to the distribution of C. caffer. The niche separation between C. caffer and other species probably results from quantitative differences in diet between the species. Closely related fish species that co-exist in the same pools have been found to have quantitative, and sometimes qualitative, differences in their diets which effectively separate their niches (Butler, 1975; Christensen,1978a,b;

Pitt-Kennedy, 1968; Nakamura, 1971). The ingestion of Ulva ecologically separates C. caffer from all other eastern Cape intertidal fish studied with the exception of Sarpa salpa (Christensen, 1978b). S. salpa, of the size classes which ingest algae, spends the low tide in the deeper pools of the intertidal zone and in the subtidal area (Christensen, 1976). S. salpa moves into the intertidal area over high tide to feed and thus the temporal and spatial separation between it and C. caffer is incomplete. Apart from the spatial and temporal aspects of their niche separation S. sarpa ingests algal species not utilised by C. caffer and there is a quantitative difference in the amount of Ulva ingested by the two species.

Predation on Caffrogobius caffer

Another aspect of competition for which there is little evidence is the predation pressure on C. caffer. C. caffer undoubtedly forms part of the diet of larger piscivorous fish which enter the intertidal zone over high tide, but there are no records in the literature to prove that such predation occurs. Only two animals are definitely known to eat C. caffer. These are C. caffer itself and the sea anemone Pseudactinia flagellifera (Hertw.). Cannibalism by C. caffer was observed on several occasions both in the laboratory and field, while the sea anemone was identified as a predator of C. caffer by the presence of a tag protruding from the mouth of an individual. Other potential predators are birds. Skead (1966) lists the birds that frequent the intertidal region of the Cape peninsula and recorded several species that are piscivorous. At Clayton's Rocks several bird species which might have fed on C. caffer were seen. These included the pied kingfisher, Ceryle rudis (L.), and the little egret, Egretta garzetta (L.). Marsh et al. (1978) refer to Larus dominicanus (Licht.), the black-backed gull, as a potential predator of intertidal clinids. Skead (1966), however, recorded that L. dominicanus fed on sand hoppers in washed-up kelp and made no reference to this species fishing in the tide pools. McLachlan & Liversidge (1975) described L. dominicanus as feeding on shellfish and offal. Thus the black-backed gull does not appear to be a predator on intertidal fish. Rand (1960) reported that Gobius nudiceps (= Caffrogobius caffer in part, see Taxonomic Status) comprised a very minor part of the diet of the Cape cormorant, Phalacrocorax capensis (Sparrman), and that Gobius spp. occurred rarely in the diet of the bank cormorant, Phalacrocorax neglectus (Wahlberg). The term rockfish used by Rand to describe unidentifiable remains of intertidal and subtidal fish in cormorant stomachs may conceal the importance which gobies have in the diet of these birds. Bruton (1979a) examined the stomach contents of eight specimens of Phalacrocorax carbo (L.), the white-breasted cormorant, shot at Lake Sibaya and found that gobies dominated the diet of this sample.

Predation may, along with interspecific competition, play a rôle in excluding C. caffer from the subtidal area. Cormorants were frequently seen in the subtidal area at all three collection sites and C. caffer in the subtidal region would be exposed to predation by piscivorous fish throughout the day while in the open. Although little is known of the interspecific competition affecting C. caffer it remains a possibility that competition with other fish species plays a part in excluding C. caffer from the subtidal region. The absence of Ulva, an important source of invertebrates for C. caffer, from the subtidal zone (Seagrief, 1967) could also be a factor limiting this species to the intertidal region. The only real evidence at present, however, which suggests why C. caffer is found solely in the intertidal region is the low current tolerance of this species. The continuous movement of water in the subtidal zone (Fig. 26b) may prevent C. caffer from colonising this area.

Space utilisation by Caffrogobius caffer

In describing the movement of fish within their habitats some workers have tended to use the term 'migration' to describe these movements (Gerking, 1959; Gibson, 1969a; Hobson, 1973). Some confusion exists in the literature as to the meaning of the word migration. Southwood (1962) considered that the movements of animals consisted of two broad types, trivial movements and migrations. He stated that migratory movements take animals away from their population territory or habitat and frequently result in an increase in the mean distance between individuals of the original population. The movements of Patella spp. described by Branch (1975a) fit this description of a migration. Trivial movements, according to Southwood (1962), are restricted to the animal's habitat and hence can only lead to a limited increase in the mean distance between individuals. Southwood claimed that during migration animals change direction less frequently than is the case during trivial movement. He considered that all migratory movements have a fixed period during which there is persistent locomotor activity. A migrating animal will not stop for food or other vegetative stimuli. Although the upshore movements of Patella spp. described by Branch (1975a) fit the description of a migration as proposed by Southwood (1962) they also fit his description of trivial movement during which an animal will respond to a vegetative stimulus. Furthermore, the Patella spp. moving up the shore cannot be considered to leave their habitat at any time. Southwood (1962) notes that there is no clear distinction between migratory and trivial movement and the Patella spp. described by Branch (1975a) illustrate this point well. Various other definitions of migration have been put forward but none cover all cases of 'migratory' behaviour (Kennedy, 1961; Hassell & Southwood, 1978). Despite the uncertainty over the definition of migration it is safe to say that

C. caffer do not migrate between pools but that such interpool movement is an example of trivial movement within the habitat.

The word 'habitat' was defined by Partridge (1978) as the conglomerate of physical and biotic factors which together make up the sort of place in which an animal lives. She noted that habitats can be described with different degrees of precision for different animals. For example, an animal's habitat may be restricted to a particular plant and also to a particular part of that plant. This is opposed to the situation in which a generalist animal may utilise several host plants or portions of the host plant. Hassell & Southwood (1978) pointed out that the habitat itself may be discontinuous and be broken up into patches of suitable areas. These authors considered that the habitat should be considered at the level of the patch as the usefulness of this approach arises when trying to distinguish between migrations between habitats and trivial movements between patches within the habitat. The food resources of *C. caffer* are not continuous throughout the intertidal zone. *Ulva* for example has a patchy distribution. *Ulva*-covered areas can be considered as one type of food patch which does not necessarily contain cover units, or cover patches. The movement of *C. caffer* between pools can thus be considered as trivial movement between food and cover patches. The movement within the area of the home site ('core area', *sensu* Keenleyside, 1979), or cover patch, is also trivial movement with the purpose of satisfying the vegetative stimulus of hunger. The core area can be considered as a cover patch as each individual knows its core area intimately and is able to dart into cover rapidly if threatened. Considering the core area as a cover patch in no way implies that feeding does not take place there, but rather that the prime reason for having a core area is to ensure that the fish is in a locality in which it is not far from suitable cover.

The restriction of C. caffer to discrete patches during low tide brings about the question of whether this patch is a territory or a home site. The generally accepted definition of a territory is a 'defended area' (Noble, 1939). Davies (1978) used a broader and less rigid definition of a territory. He recognised a territory whenever animals were spaced out more than would be expected from a random occupation of suitable habitats. He noted that the spacing between individuals may be maintained by overt aggression or by the effect of subtle signals such as scent, but that aggression was not necessarily a component of territoriality. In the present study Davies' (1978) wider concept of a territory implies that the low tide core area used by C. caffer is a territory. Davies' definition has not been accepted and the definition proposed by Wilson (1975), 'an area more or less exclusively used by an animal or a group of animals by means of repulsion through overt defense or advertisement', (p. 256) has been accepted. This definition combines the two concepts of aggression and exclusive use, neither of which is shown by C. caffer. By retaining Wilson's definition of a territory it is possible to use the terminology 'territory' and 'home range' to indicate the concept of aggressive or non-aggressive use of space. The patches within which C. caffer spends low tide are considered to be home sites or core areas and not territories as no active defense of the patch took place.

Bruton (1977) discussed the benefits that accrue to individuals by spacing out and not crowding together. He pointed out that spacing out allows avaiable food resources to be maximally utilised and that predation and the spread of disease are reduced. Davies (1978), discussing the same point, concluded that territories, by his definition, are formed for a variety of purposes, e.g. feeding or breeding. He felt that territory formation depended on the availability of resources. When resources are of an unpredictable nature animals tend to live together in groups without fixed territories. Where resources are predictable, territories (home ranges) can be formed. *C. caffer* has available dependable but scattered resources and is thus able to limit its movements to a restricted area, the home range. Only trivial movements are necessary for *C. caffer* to satisfy all vegetative stimuli. The only occasion when a territory was found to exist for *C. caffer* was during breeding.

The system of space utilisation used by *C. caffer* appears to result in the slow recolonisation of vacant areas. After two pools at Clayton's Rocks had been poisoned with the ichthyocide Pro-Noxfish a check was kept on the length of time taken for *C. caffer* to recolonise the pools. A visual check one month after poisoning revealed so few gobies that the pools were not repoisoned as had been planned. Six months passed before the goby population appeared to have returned to a normal density. Bussing (1972) poisoned a tide pool in the Marshall Islands with Pro-Noxfish and repoisoned the same pool after 22 days. His general finding was that the fish population density was much reduced in species diversity, numbers and biomass, although the trophic structure was not substantially altered. Bussing cited the reduction of certain invertebrates, odour of rotenone and the habits of juvenile fish as possible reasons for the delay in repopulation of the pool.

When the two pools at Clayton's Rocks were poisoned most of the fish whose home pools these represented were killed. The first fish to 'recolonise' the denuded pools would have been residents trapped by the tide in other pools at the time of poisoning. Fish within whose home range the poisoned pools lay would have been transient visitors over high tide, with some in time making the poisoned pools their home pool. The pools were poisoned soon after the juvenile fish appeared in the intertidal zone and juveniles were found in a density similar to that of other pools within two months. At this point the adult population was still below normal levels; approximately 30 fish were seen compared with the 381 specimens obtained from the poison collections.

Recolonisation of a pool by new residents of a species with a home range necessitates that the new residents be juveniles as yet unattached to a home pool, adults which change their home pool or adults that are strays with no home pool. Nursall (1977) found that it took, on average, 34 minutes before the territorial blenny, Ophioblennius atlanticus Silvester, made the first transgression of a neighbouring territory from which the resident had been removed. A territorial fish only controls an area which it is capable of defending and constant vigilance is required if the territory is to be held. Huxley (1934) and Manning (1967) compared territories to elastic discs with the resident animals at their centres. When population density increases and pressure builds up along the border the size of the territory decreases. When the surrounding population decreases the territory expands to utilise the available space. There is a limit beyond which the territory will not grow resulting in discontinuous territories in sparse populations (Wilson, 1975). A fish with a home site and home range does not have its movements restricted by defended borders, but rather by its 'knowledge' of its range and the time available for movement. Aronson (1950) suggested that Bathygobius soporator learned its home range over high tide and was thus able to jump from pool to pool to avoid predation. Fish which were transported well away from their pool of capture would not jump, despite the fact that handling had not been found to inhibit jumping. The motivation for a fish with a home range to colonise a denuded area

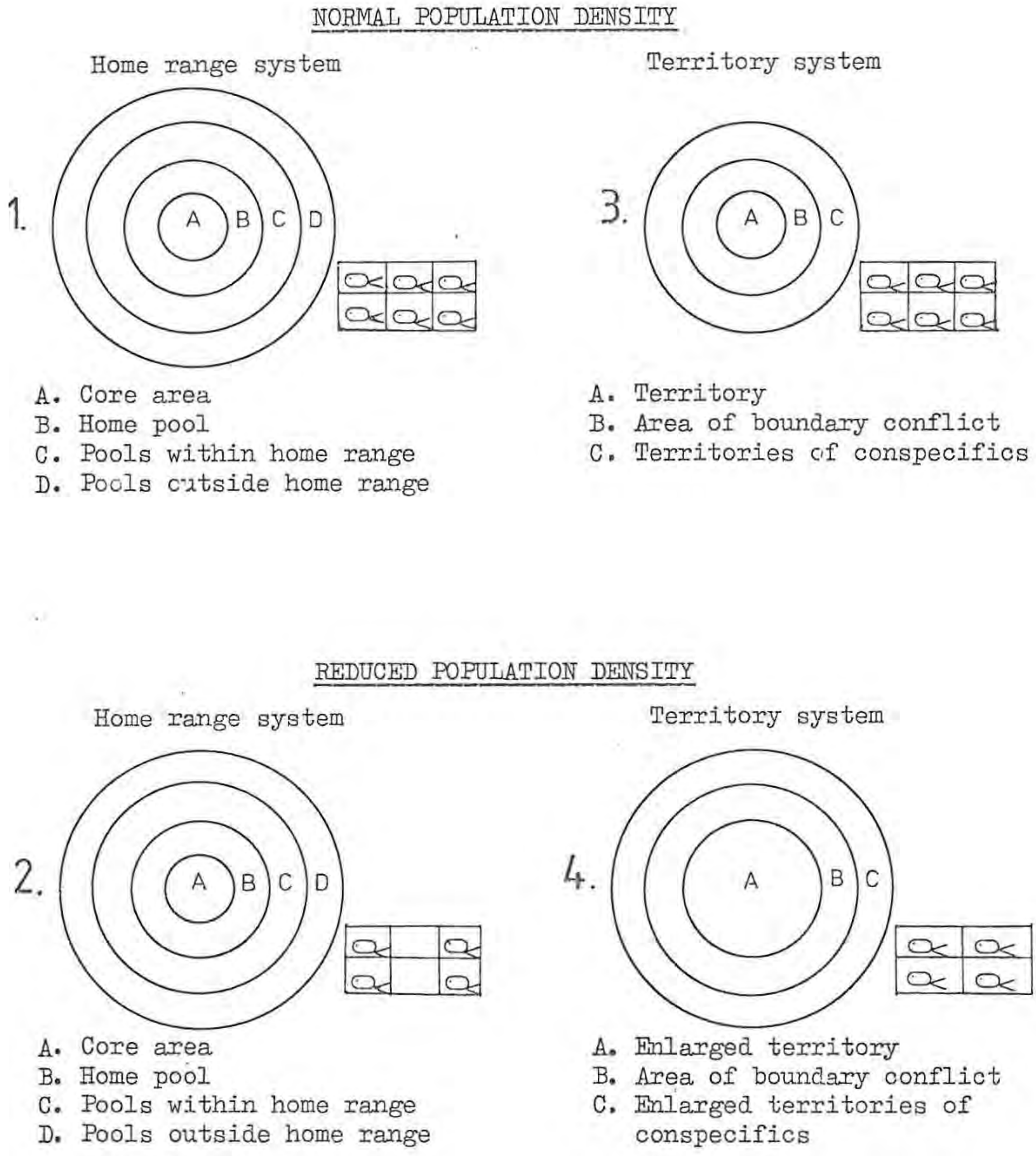


Fig. 35.
Diagram to illustrate the differences between home range and territorial behaviour when population density is reduced. Block diagrams illustrate spatial arrangement of the fish before and after population density reduction for the two space utilisation systems.
1. Illustrates the situation for a species with a home range under normal population density.
2. Illustrates the situation for a species with a home range when the population density is reduced. Note that there is no enlargement of the range and that vacated spaces remain vacant, at least initially.
3. Illustrates the situation for species with a territory under normal population density.
4. Illustrates the situation for a species with a territory when population density is reduced. Note that the size of the territory increases and vacated areas are incorporated into existing territories.

is probably not as high as for a territorial fish such as Ophioblennius atlanticus. A territorial fish that transgresses its borders will be forced to return to its territory by conspecifics, but if these neighbouring territorial fish are removed then the movement into the denuded area can be expected to be rapid as the remaining fish expand the areas they control. In contrast to this a fish with a home range returns to its home site by 'choice', not due to pressure from aggressive conspecifics. Thus the length of time taken for a denuded area to be recolonised will be longer than is the case for a territorial fish. Fig. 35 illustrates the differences between the situation for a territorial fish and a home range system species when conspecifics are removed. The upper two diagrams of Fig. 35 show the situation when a normal population density exists, the two lower diagrams show the situation resulting when some of the population is removed. In the case of the home range system there is no change in the area utilised by individual fish. In the case of a territorial fish, the fish enlarge their territories and thus maximally utilise the available space.

Summary

The strategy employed by C. caffer for survival in the harsh intertidal environment is made up of several facets. The opportunism shown in both diet and feeding times, the avoidance of strong currents that could injure the fish, together with their strong thigmotactic response and the way in which space is utilised, combined with their morphological adaptations such as small size, add up to form a strategy which enables C. caffer to be a successful coloniser of an environment which few other fish species can utilise.

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APPENDIX 1

Extract from Hynes (1950) discussing the merits and faults of the points method of diet analysis:

'Facts in its (points methods) favour are that it is rapid and easy, requires no special apparatus for measurement, is not influenced by frequent occurrence of a small organism in small numbers, nor of heavy bodies, like snail shells and caddis cases, and does not involve trying to count large numbers of small and broken organisms. It also does not give the spurious impression of accuracy which is given by some of the other methods.

Two critcisms of this method are offered. First, it is subjective, and the investigator may be influenced by prejudice in his allotment of points; but where large samples are analysed over a period of months this difficulty is to some extent overcome. It should also be realised that this criticism applies to all such work. In identifying the broken, and often partly digested, remains of organisms, ordinary taxonomical characters are usually obscured, and the investigator relies entirely on general facies. He is therfore equally liable to be influenced by prejudice, and the accuracy of his determinations depends on his knowledge of the food organisms. As most investigators of the food of fishes are people whose primary interest is in the fish themselves, rather than in the fauna which form their food, it seems that great opportunity exists for such subjective inaccuracy. The same type of argument can be brought against counts of the number of organisms. Apart from the fact that unless great care is taken some food particles are not removed from the gut for examination, some at least of the organisms are normally broken, especially in those fish which chew their food, and it is often only possible to estimate the number present. ... This applies particularly to such important food organisms as copepods. Where plant tissue is involved counts become meaningless as inaccurate.' (p. 37).