THE FEEDING ECOLOGY OF CURLEW SANDPIPERS CALIDRIS FERRUGINEA IN THE SOUTH - WESTERN CAPE, SOUTH AFRICA

by

GILLIAN MARGARET PUTTICK

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CONTENTS

ABSTRACT

Spatial and temporal changes in the distribution of food organisms potentially available to curlew sandpipers *Calidris ferruginea* at Langebaan Lagoon (33°S, 18°E), South Africa, are described for the period February 1974 - March 1975. Seasonal changes in the diet of curlew sandpipers foraging in the intertidal sandflats and marshes were studied, and the food taken by male and female, and immature and adult, birds was compared. The daily and seasonal activity of curlew sandpipers was monitored during March 1974 - March 1975 and this also provided information on the birds' foraging behaviour and foraging techniques, their use of microhabitat and their foraging related to shore level. Variations during the austral summer in the density and the foraging of curlew sandpipers related to the density of their prey was investigated in the light of Royama's (1971) theory of profitability. The foraging behaviour and spatial distribution of foraging male and female curlew sandpipers at Kommetjie (34 08°S, 18 19°E) was compared, since curlew sandpipers show sexual dimorphism with females having longer culmens. The energy requirements and energy intake of curlew sandpipers at Langebaan Lagoon are described. The gross annual production of the benthic invertebrates potentially available to the birds was estimated, as well as the birds' impact on this.

INTRODUCTION

The study of trophic relationships within the world's major ecosystems has provided a significant thrust to ecological investigations over the past fifteen years. Ecologically 'sensitive' areas such as wetlands and intertidal zones, which form the interface between different ecosystems, have been receiving attention more recently. However, apart from terrestrial ecosystems, very little information is available on trophic relationships within other southern African ecosystems and within wetlands in particular. Furthermore, although Siegfried (in prep.) has described the seasonal abundance of migratory birds at southern African wetlands as 'a major ecological phenomenon', there is at present no clear understanding of resource partitioning among Palaearctic waders on the one hand and resident species on the other in southern Africa. This dissertation attempts to contribute information useful in understanding the trophic relationships within a marine lagoon ecosystem in the south-western Cape, South Africa, and to elucidate the resource utilization of the most abundant Palaearctic migrant there, the curlew sandpiper <u>Calidris ferruginea</u>.

The curlew sandpiper is a common member of the avifauna of estuaries and lagoons around the coast of South Africa (McLachlan & Liversidge 1970). In particular, the population of curlew sandpipers varies between 37 000 and 55 000 birds at Langebaan Lagoon (33°S, 18°E) during the austral summer (Pringle & Cooper 1975, Summers 1977), and is as high as 12 000 in the austral winter (Pringle & Cooper 1975). Curlew sandpipers comprise 64% of the wader population which migrates seasonally to Langebaan Lagoon (Pringle & Cooper 1975).

I studied the food, aspects of the feeding ecology, and the energetics of curlew sandpipers at Langebaan Lagoon during March 1974 - March 1975 and December 1977 - April 1978. Specifically, the aims of the study were :

1. to describe spatial and temporal variations in the food potentially available to curlew sandpipers at Langebaan Lagoon;
2. to describe seasonal changes in the birds' diet related to these variations;
3. to investigate several other aspects of the birds' feeding ecology such as the differential utilization of potential foraging areas at Langebaan, seasonal changes in foraging behaviour and daily activity, microhabitat utilization, and foraging related to tide and shore level;
4. to investigate the effect of prey density on foraging behaviour;

5. to compare the resource utilization and foraging behaviour of male and female birds, since curlew sandpipers show sexual dimorphism;
6. to describe the energy budgets of curlew sandpipers in a wintering area; and
7. to estimate the impact of curlew sandpiper predation on the gross annual production of the benthic invertebrates potentially available to them at Langebaan Lagoon.

The International Convention on Wetlands at a conference held in Heiligenhafen, West Germany, in 1974 recommended, _inter alia_, that wetlands supporting not fewer than 20 000 wading birds should be classified as being of international importance for nature conservation (Anon. 1974). Since populations of waders at Langebaan Lagoon regularly exceed this number, informed conservation and management of the lagoon is necessary in the face of present large-scale industrial and associated development at Saldanha Bay nearby, especially since only one other wetland in the south-western Cape, the Berg river estuary (32°S, 18°E), supports at least this number of waders (Cooper _et al._ 1976). Certain of the projected development plans entail closing the mouth of the lagoon and establishing a new mouth; this scheme would seriously reduce available wader habitat in the lagoon. In view of this, and also in view of a possible future influx of waders due to a decrease in available wader habitat in the rest of the south-western Cape (Cooper et al. 1976), an attempt has been made in this thesis to determine whether the lagoon has reached carrying capacity for curlew sandpipers with respect to food.

This dissertation comprises six separate parts; the thesis has been arranged in this way to facilitate publication of the material presented. The first two parts have already been published as scientific papers.

SYNTHESIS

Spatial and temporal variations in the food (intertidal benthic invertebrates occurring in the top 60 mm of the substrate) potentially available to curlew sandpipers at Langebaan Lagoon (33°S, 18°E), were studied during March 1974 - March 1975. The diet of the birds was affected by fluctuations in their food supply. Hence, temporal variations affected different components of the birds' diet during the course of the year, while spatial variations, in conjunction with short-term temporal ones caused by tidal fluctuations, determined where and when the birds foraged. Biomass and numbers of prey potentially available increased by about 50% from midwinter to spring and from midsummer to autumn. The autumn peak coincided with the birds' accumulation of fat reserves prior to migration in mid-April and presumably facilitated pre-migratory fattening. The biomass of invertebrates occurring in the *Arthrocnemum* marshes increased in winter, at a time when wintering immature curlew sandpipers had fewer daylight hours in which to forage. In addition, the birds' energy needs at this time were presumably increased due to lower ambient temperatures; the higher numbers and biomass of prey occurring in the marshes presumably contributed towards the birds' ability to meet these needs. Part of the winter peak in marsh biomass and numbers was due to stratiomyid larvae (O. Diptera) and these formed a relatively high percentage of the birds' diet then. The small hydrobiid gastropod *Assiminea globulus* accounted for 62,5% of the total biomass and this organism dominated overall fluctuations in prey numbers and biomass. *A. globulus* was an important component of the birds' diet during all seasons; nereid worms (mainly *Ceratonereis erythraensis*), amphipods (mainly *Urothoe grimaldi*) and the crabs *Hymenosoma orbiculare* and *Cleistostoma edwardsii* were also important items. *A. globulus* was recruited in spring and autumn, and therefore numbers of this species were high then. However, the proportion of snails in the birds' diet dropped in spring, presumably since the smaller size of individual snails made them energetically less rewarding, and the birds selected more nereids, crabs and amphipods instead. The seeds of *Salicornia* sp. were important dietary items in autumn and early winter, when they were abundantly available, and they may have been an important energy subsidy for birds increasing their pre-migratory fat load. The birds also increased their energy intake by selecting larger prey items than those generally available.

A. globulus was distributed on the marshes and on the upper shore where very high densities occurred. Size classes appear to have been segregated, with largest individuals occurring in the marshes and smaller individuals occurring lower on the shore. Nereid worms and crabs were distributed from below high water to low water and amphipods and bivalves from low water to above mid-tide level. The birds foraged on the sandflats when these were exposed by the tide, first taking Assiminea and then including worms, crabs, amphipods and bivalves as these became available on the receding tide. The birds' foraging and success rates reflected the density and distribution of potentially available prey. Hence, foraging and success rates were highest at the top of the shore in the Assiminea zone where prey density was high and decreased down the shore. Prey behaviour appears to have affected foraging and success rates, since the birds fed faster on incoming than on outgoing tides. This was presumably a response to increased prey activity after quiescence during the preceding exposure period.

Apart from the effect on their activities of spatial and temporal variations in the seasonal availability of food, curlew sandpipers showed changes in activity which were responses to seasonal variations in energy requirements. Hence, they foraged for 55-65% of daylight hours in spring and summer but up to 80% in autumn and winter. During autumn and winter, the birds foraged on the salt marshes at high tide, where they took <u>Assiminea</u>, small crustaceans and insect larvae, mainly Stratiomyidae. This meant that birds extended their foraging habitat in autumn presumably to help meet their energy needs for pre-migratory fattening, and in winter presumably because fewer daylight hours were available for foraging and because lower ambient temperatures increased their energy needs. The birds also modified their foraging behaviour by foraging faster in autumn and winter, and the foraging efficiency of adult birds increased towards late summer and autumn. The diversity of foraging techniques used by the birds appeared to change seasonally in response to changes in prey density, although the data were equivocal. Optimal predator strategy should lead to more selective feeding (i.e. less foraging diversity) and a more restricted diet if food density increases (Emlen 1966, MacArthur & Pianka 1966, Schoener 1971). However, birds foraging by tactile methods, i.e. probers, presumably cannot be as selective as peckers can, since they presumably cannot 'evaluate' items until after they have grasped these with their bills. Curlew sandpipers tended to peck on the marshes, where 90% of the prey were epifaunal; foraging diversity on the marshes was high when prey numbers were low, consistent with this prediction. Contrary to expectation, foraging diversity on the sandflats was high when prey numbers were highest, but this may have been because birds mostly probed when foraging on the sandflats.

The foraging and success rates of curlew sandpipers clearly resembled Holling's (1959) type-3 predator response to prey density, which indicates that the birds responded to the density of their prey in a way consistent with Royama's (1971) profitability model. Royama (1971) proposed that a birds' choice of a suitable area in which to forage was determined by the 'profitability' of different areas, and that birds which sampled many feeding areas quickly but concentrated their search effort in a few highly productive areas would capture the most prey with the least expense of time and energy. The biomass of prey taken per unit time also accorded with Royama's (1971) profitability model, although figures for biomass taken were extrapolated values. Evidence in support of the profitability model (Royama 1971, Alcock 1973, Smith 1974, Goss-Custard 1977a, 1977b, O'Connor & Brown 1977) showed predators responding to variations in the density of one prey type or to a preferred prey type. However, curlew sandpipers responded not only to the profitability of different areas within one prey habitat but also to a spectrum of prey habitats. Such a response is implicit in Royama's model : a predator choosing a particular foraging habitat with a particular prey spectrum optimizes its intake as much as it does by choosing optimum prey density areas within that habitat. Evidence that at high prey densities individual Assiminea (a major prey item) were smaller and that size classes of Assiminea were spatially segregated, may mean that profitability was decreased at high prey densities, and this would account for a lower success rate. Hence, a feature not represented in the model was that small prey may have reduced the foraging and success rates of curlew sandpipers by decreasing profitability at high prey densities.

The density of foraging birds increased with increasing prey density up to an asymptotic level, meaning that they concentrated their foraging effort in areas of greatest profitability. Birds foraged more successfully in groups than when they were foraging alone. However, higher levels of aggression when the birds were closer together counteracted further increases in bird density.

Immature curlew sandpipers foraged more slowly and less successfully than adult birds and they generally took smaller prey items than adults did. It appears that inexperienced foraging prevented immature birds from accumulating sufficient fat reserves for migration, and this would explain why they normally overwinter in the southern hemisphere. An inability to forage successfully in competition with adults could be another reason for immatures overwintering in the southern hemisphere. However, there did not appear to be competition between adults and immatures during the adults' pre-migratory fattening period, since very few aggressive interactions were observed and since prey numbers and biomass were relatively high then.

Curlew sandpipers exhibit sexual dimorphism with females being significantly larger than males (Elliott *et al*. 1976). Females took slightly different food types from males at Langebaan Lagoon, which implies that spatial segregation between the sexes occurred to reduce competition for food. A comparison of resource utilization by male and female curlew sandpipers was made at Kommetjie beach where it was easier to colour-ring birds for later identification than at Langebaan Lagoon. At Kommetjie, males and females foraged more often in segregated than in mixed groups, and agonistic behaviour was higher in single sex groups. Females appear to have foraged faster and more successfully than males did. Since food did not appear to be limiting at Kommetjie, it is possible that spatial segregation occurred because bird density was high in relation to a relatively small area available for foraging. Baker & Baker (1973) concluded that food was limiting in North American wader wintering areas and that population size was regulated by competition in the wintering rather than the breeding areas. However, food did not appear to be limiting at Langebaan Lagoon, and it is possible that conditions outside the wintering grounds favour sexual dimorphism in the species. Local and seasonal food shortages do occur on curlew sandpiper breeding grounds (Holmes 1966) and competition between the sexes may be crucial then. Related to this may be the fact that males seem to leave the breeding areas soon after egg-laying (Holmes & Pitelka 1964). Also, sex differences may minimize competition on migration routes to and from the breeding grounds (Recher 1966). The fact that only the females incubate the eggs (Holmes & Pitelka 1964) may be another equally important factor favouring sexual dimorphism in the species, since females presumably require extra energy reserves for this.

The mean estimated energy intake of a curlew sandpiper at Langebaan Lagoon was 180 kJ per day, of which 144 kJ per day was assimilated (an assimilation efficiency of 80% was assumed). This agrees fairly well with the mean estimated energy requirement of a free-living curlew sandpiper which was 125 kJ per day. A substantial positive energy balance existed in late summer and autumn, when adults moult and also accumulate fat reserves for migration, but overwintering immature birds appear to have had a negative energy balance in winter. However, actual values of energy ingested and expended are not as important as the indication they give of the efficiency of time and energy partitioning in free-living birds. Curlew sandpipers foraged for increasing periods of time during the pre-migratory fattening period in autumn. The relatively high energetic cost of this was presumably unimportant when compared with the advantage (and necessity) of accumulating a fat store prior to migration. The estimated gross annual production of benthic invertebrates potentially available to curlew sandpipers at Langebaan Lagoon was 705 kJ/m^2 per year. The birds took an estimated 10,3, 11,1, and 17,2% of the production potentially available to them on the marshes, the Assiminea zone and the lower shore respectively. Thus they took an estimated mean of 12,9% annually, or 91 kJ/m^2 per year, which is higher than the estimated 87 kJ/m^2 per year taken during 1975 by the total wader population at Langebaan Lagoon (Summers 1977). Exploitation of the lower shore (17,2%) was 50% greater than that of the marsh and Assiminea zones. However, the tide acted as an important temporal regulator of the availability of foraging space on the lower shore, since this area is only exposed for a relatively short time each tidal cycle. The marsh and Assiminea zones were exploited almost equally by the birds, meaning that the marshes provided an indispensable proportion of the birds' diet. The percentage (12,9%) of the estimated gross annual production of prey taken by curlew sandpipers appears to be relatively small. However, not all gross annual production of prey is available to predators, since prey species use part of this for growth, reproduction and metabolic activities. Hence, the proportion taken by curlew sandpipers would be higher if expressed as a percentage of nett production.

It is not clear whether the carrying capacity of Langebaan Lagoon for wading birds has been reached. A definitive answer may only be provided by studies of prey productivity and by investigation of the energy requirements of other predators, including fish. However, it seems possible that the carrying capacity of the lagoon for curlew sandpipers has not been reached with respect to food, since

1. at no time during the year do the birds spend all their daily time foraging even though the marshes are almost always available when the sandflat foraging areas are not;
2. both intra- and interspecific agonistic behaviour was infrequent; and

3. some potential foraging areas were not exploited during the whole period that they were accessible (e.g. the marsh and Assiminea zone were mostly vacated by curlew sandpipers when the lower shore was uncovered by the tide).

Food may not be the single limiting factor for curlew sandpipers at Langebaan Lagoon. Other factors, such as the availability of suitable roosting sites, are also likely to be important. Elucidation of the impact of birds and other predators on estuarine ecosystems in southern Africa is critical before management and conservation of such ecologically 'sensitive' areas can be implemented.

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PART 1

Spatial and temporal variations in inter-tidal animal distribution at Langebaan Lagoon, South Africa

SPATIAL AND TEMPORAL VARIATIONS IN INTER-TIDAL ANIMAL DISTRIBUTION AT LANGEBAAN LAGOON, SOUTH AFRICA

by Gillian M. Puttick

(FitzPatrick Institute, University of Cape Town)

Summary

Spatial and temporal changes in the distribution of food organisms potentially available to curlew sandpipers *Calidris ferruginea* at Langebaan Lagoon (33 °S, 18 °E) are described for the period February 1974–March 1975. The inter-tidal benthic fauna at sandy sites showed spring and autumn peaks in biomass and numbers. The fauna was dominated by the gastropod *Assiminea globulus*, which comprised 62,5 % of the total biomass. A Production : Biomass ratio of 4,96 was found for this species, and 1,36 for the amphipod *Urothoe grimaldi*. The fauna at sites containing macrophytes (*Spartina*, *Zostera*, *Arthrocnemum*) showed winter peaks in biomass and numbers. Classification and ordination confirmed the discreteness of macrophyte and non-macrophyte sites, each having its own characteristic benthos. There was a positive correlation between the distribution of benthos and sediment parameters at the different sites, macrophyte sites having a higher fine fraction and organic content.

Opsomming

Ruimtelike en temporale veranderings in die verspreiding van voedselorganismes, wat potensieel beskikbaar is vir die strandlopertjie *Calidris ferruginea* by die Langebaan-strandmeer (33 °S, 18 °O), word vir die periode Februarie 1974–Maart 1975 beskryf. Die tussentyse bentiese fauna by sanderige gebiede het maksimumwaardes in biomassa en getalle gedurende die herfs en lente getoon. Die fauna is deur die slak *Assiminea globulus* (Gastropoda) gedomineer. Hierdie organisme het 62,5 % van die totale biomassa uitgemaak. 'n Produksie : Biomassaverhouding van 4,96 is ook vir hierdie spesie verkry, terwyl *Urothoe grimaldi* (Amphipoda) 'n verhouding van 1,36 getoon het. Die fauna by gebiede wat makrofiete bevat het (*Spartina*, *Zostera* en *Arthrocnemum*), het maksimumwaardes in biomassa en getalle gedurende die winter getoon. Klassifikasie en ordinering het die onderskeid tussen die makrofiet- en nie-makrofietgebiede bevestig en elkeen van hierdie gebiede het 'n kenmerkende bentos besit. 'n Positiewe korrelasie tussen die bentosverspreiding en die sedimentmaatstawwe by die verskillende gebiede is ook gevind. Die makrofietgebiede het 'n hoër fynfraksie en organiese inhoud bevat.

INTRODUCTION

Among species of wading birds which migrate seasonally from their breeding grounds in the Arctic tundra to the Southern Hemisphere, the curlew sandpiper *Calidris ferruginea* is a common member of the avifauna of estuaries and lagoons around the coast of South Africa (McLachlan & Liversidge 1970). Curlew sandpipers occur abundantly at Langebaan Lagoon (33 °S, 18 °E) during the austral summer (Pringle & Cooper 1975). The importance of Langebaan Lagoon to wading birds and to the curlew sandpiper in particular may be gauged by the criteria adopted by the International Convention on Wetlands. This convention recommended, *inter alia*, that wetlands supporting not fewer than 20 000 wading birds should be classified as being of international importance for nature conservation (International Waterfowl Research Bureau 1974). Populations of curlew sandpipers at Langebaan Lagoon regularly exceed 20 000 (Summers 1977).

I studied the food and feeding ecology of the curlew sandpiper at Langebaan Lagoon during February 1974–March 1975, first, because no work has been done in this field in South Africa and, second, to contribute information useful in understand-

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ing trophic relationships within the lagoon ecosystem. Such understanding is necessary for informed conservation and management of the lagoon in the face of present large-scale industrial and associated developments at Saldanha Bay.

This paper describes the kind and amount of food potentially available throughout the year to curlew sandpipers at Langebaan Lagoon. A paper dealing with the curlew sandpiper's feeding habits will be published later.

STUDY AREA

Study sites were chosen at Bottelary, Geelbek, Schrywershoek and Rietbaai in Langebaan Lagoon (Fig. 1). At Bottelary 500 m of fine sand is exposed at spring tides. The spring tide has a range of *ca.* 1,4 m. *Zostera capensis* is patchily distributed from HWN and *Gracilaria confervoides* occurs at lower levels. There is a salt marsh at Bottelary where *Arthrocnemum* plants grow densely between HWN and HWS, with interspersed patches of *Triglochin bulbosum* and *Chenolea diffusa.* Standing pools of water fill several depressions in the marsh. Geelbek, at the head of the lagoon, has a substrate consisting of fine anaerobic mud with a high organic content. There is an extensive bed of *Zostera capensis* at mid-tide level. The Geelbek marsh is similar to that at Bottelary. Schrywershoek on the western side of the lagoon has a sandy substrate with little silt. Sediments on the western shore have a lower fine fraction than those on the eastern shore, because prevailing winds effect the movement of the fine fraction both by their own action and by affecting current movements (Flemming pers. comm.). Rietbaai, in the north-western corner of the lagoon, has silt and fine sand covering patches of sandy calcrete, there is a fairly high proportion of large shell fragments, and *Zostera capensis* occurs in large patches at mid-tide level and below. There is also a salt marsh at Rietbaai.

MATERIALS AND METHODS

The benthos at Bottelary was sampled every month at springs during February 1974–March 1975; additional samples were taken every second month at the other three sites. Transects were established after the method of Day (1959) at each site. Five stations (A–E) were established along each of the four transects between LWS and HWN, because this was the area on the flats where the birds generally fed.

Ten cores of 50 mm diameter and 60 mm depth were taken randomly of the substrate at each station. The corer was a polyvinyl-chloride tube with the bottom sanded to a sharp cutting edge. A collar was glued to the outside of the tube, preventing insertion deeper than 60 mm. The corer was lifted out of the substrate by placing a hand under the bottom aperture. Curlew sandpipers have a maximum bill length of 45 mm, so a 60 mm core was assumed to include all the food potentially available to the birds. Note that this is not deep enough to sample all the animals present. One finds larger organisms, such as *Arenicola*, *Upogebia* and certain bivalves, much deeper in the substrate. However, Boltt (1975) states that 'there is evidence that the greatest part of the small forms of the fauna is to be found in the top 10 cm of muddy substrate'.

Samples at each station were taken at the edge of the tide, as it receded at Bottelary and as it came in at the other three sites. Waders tend to concentrate their feeding at

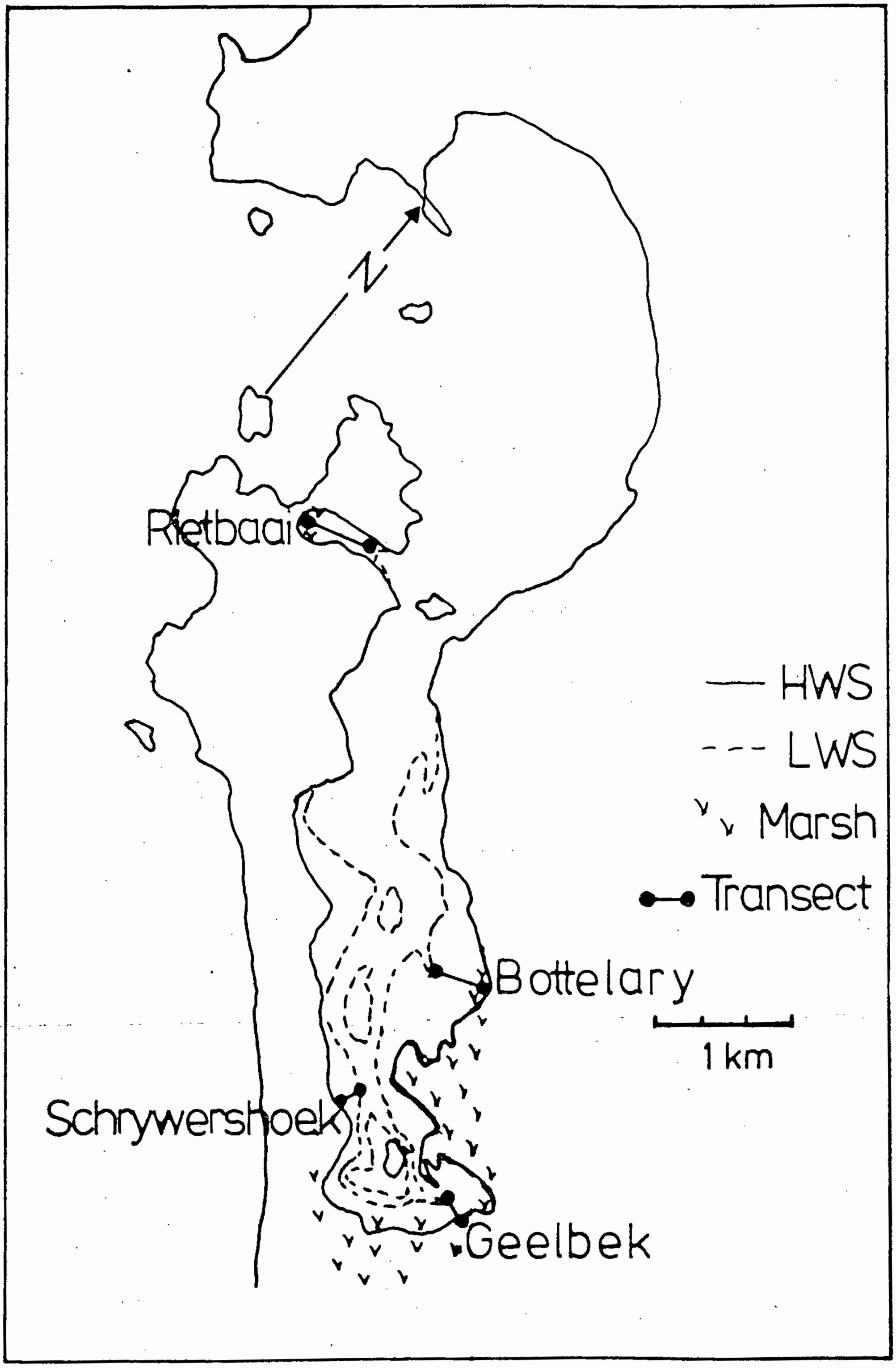

Fig. 1. Langebaan Lagoon, showing positions of transects.

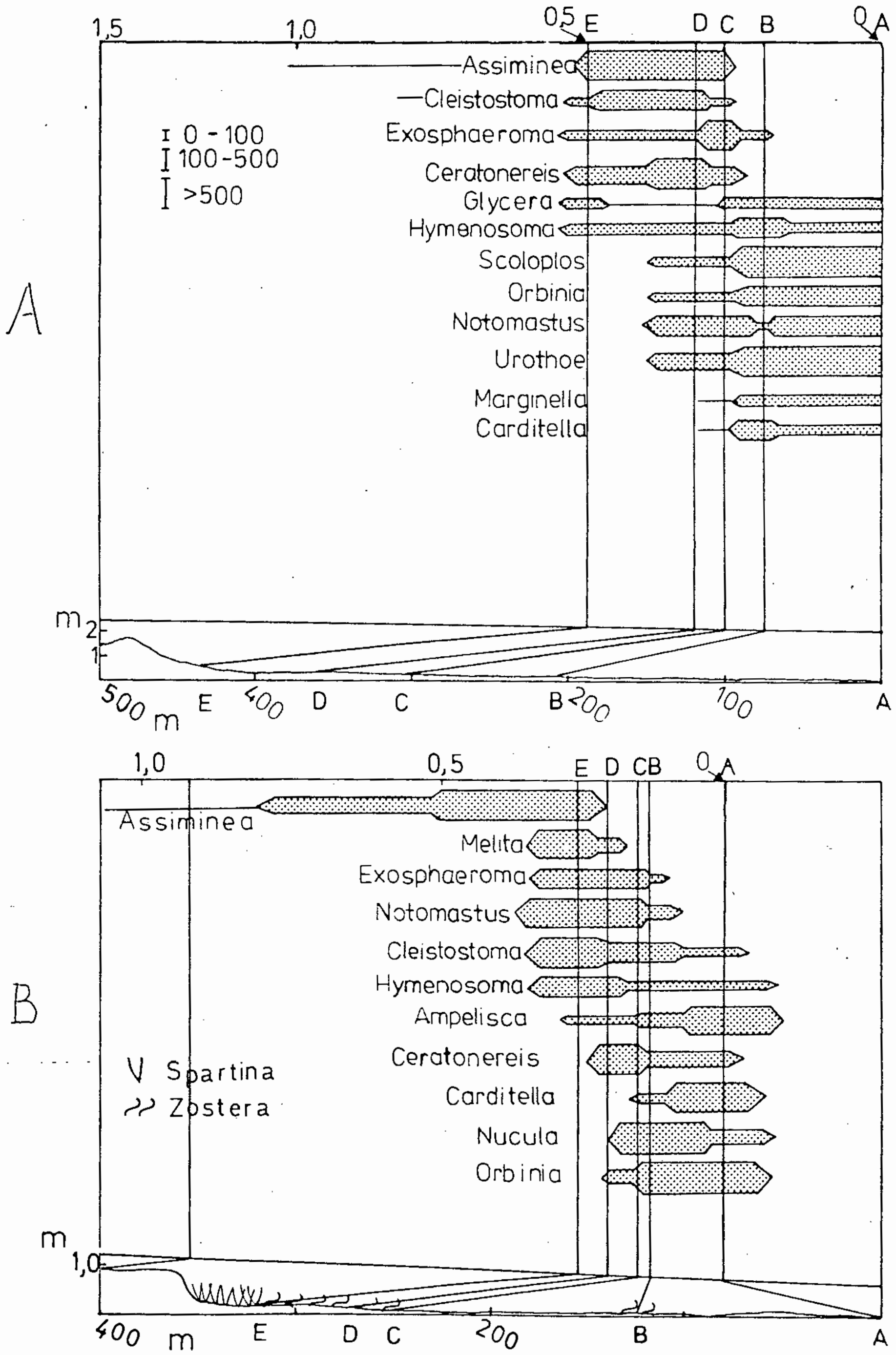

Fig. 2. Shore profiles and distribution of common organisms at Bottelary (A), Geèlbek (B), Schrywershoek (C) and Rietbaai (D).

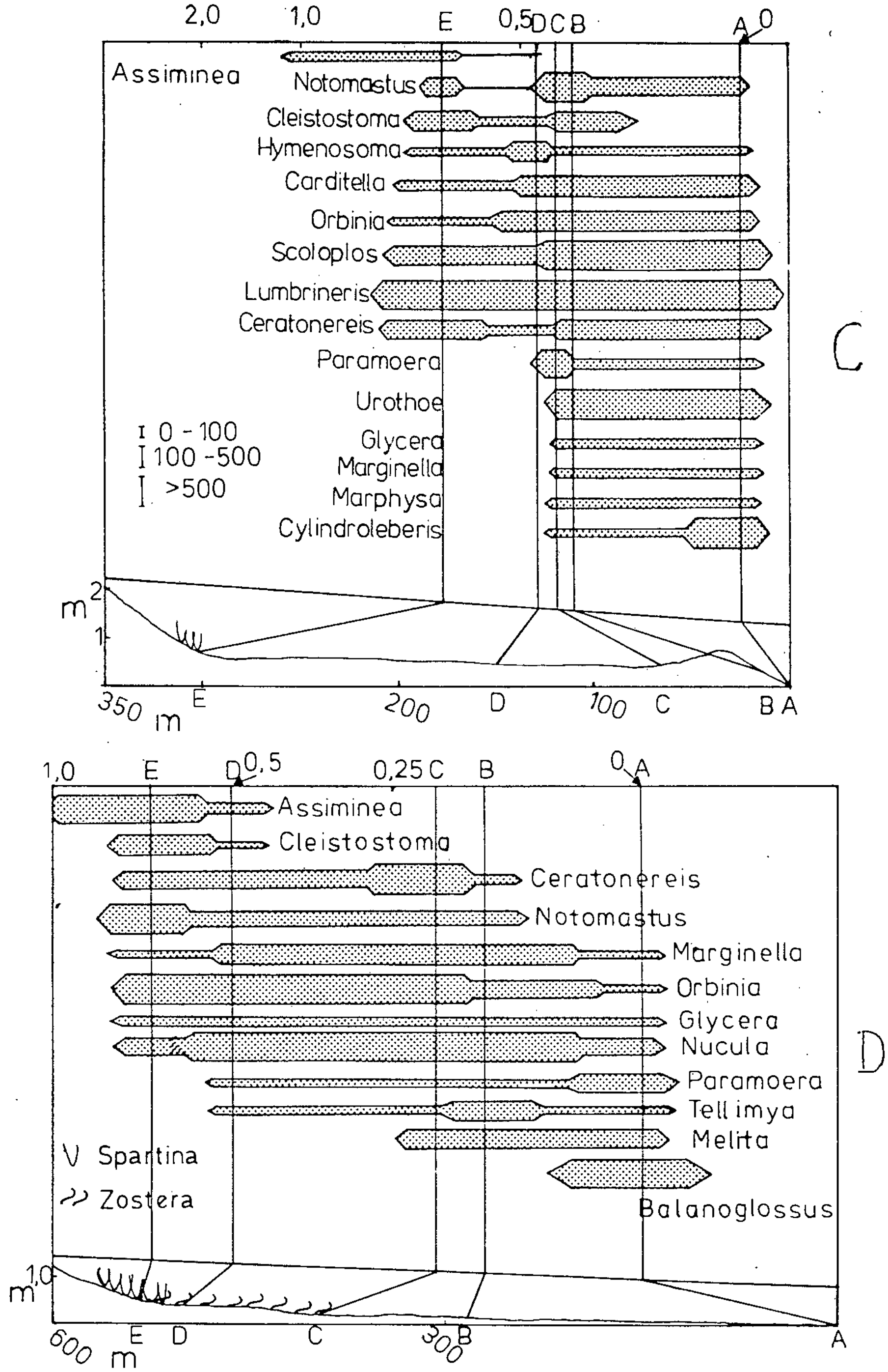
2,0
1,0
E
0,5
D C B
A
0
Assiminea
Notomastus
Cleistostoma
Hymenosoma
Carditella
Orbinia
Scoloplos
Lumbrineris
Ceratonereis
Paramoera
Urothoe
Glycera
Marginella
Marphysa
Cylindroleberis
0 - 100
100 -500
>500
C
m
2
1
350 m
E
200
D
100
C
B A
1,0
E
D
0,5
0,25 C
B
0
A
Assiminea
Cleistostoma
Ceratonereis
Notomastus
Marginella
Orbinia
Glycera
Nucula
Paramoera
Tellimya
Melita
Balanoglossus
D
Spartina
Zostera
m
1,0
600 m
E
D
C
300
B
A

Fig. 2 (*cont.*)

the edge of the tide, and prey animals are likely to be nearer the surface when the substrate is saturated (Vader 1964). The 10 samples from each station were pooled and sieved through a 1 mm-mesh sieve on site. The animals were hand-sorted and preserved in 5 % formalin for later identification in the laboratory. Anderson (1972) quotes Prater (in lit.) as saying that animals less than 1 mm in size are unimportant in the diet of curlew *Numenius arquata*, redshank *Tringa totanus*, knot *Calidris canutus* and dunlin *C. alpina*. Also, a preliminary study revealed no item smaller than 1 mm in the stomachs of 40 curlew sandpipers (Puttick 1972). However, subsequently items between 0,9 and 1 mm were found occasionally in the birds' stomachs. Consequently, 10 extra cores were taken at Bottelary monthly from September 1974 onwards and sieved separately through 0,7 mm mesh to determine whether a significant number of potential prey items had been missed before.

Cores were taken in the marsh at sites where curlew sandpipers fed. Flies, in the air above pools in the marsh, were caught in 0,5 mm-mesh net held at arm's length, while swept five times over a distance of 2 m.

Substrates were analysed for particle size and organic content, using five cores taken at each station, pooled and mixed, and then frozen as soon as possible after sampling (*ca.* 2 h).

Salinities and surface temperatures were measured at Bottelary. A pocket refractometer was used to determine salinity.

Animals were identified mainly to species but occasionally to family or ordinal level. All animals, except *Assiminea* spp. and polychaete worms, were counted and individually measured using a binocular microscope and graticule. The length of amphipods and isopods was measured from the base of the first antenna to the tip of the telson. In brachyurans the length of the cephalothorax was measured in the mid-line from the front (or rostrum) to the junction with the first abdominal segment. Bivalves were measured from the hinge line across the shortest length of the valve. Gastropods were measured from the tip of the terminal whorl to the base of the aperture. Polychaete worms were not measured, because they often break during sieving and sorting. *Assiminea* occurred in such large numbers that the animals were sorted by eye into five size classes—extra small, small, medium, large and extra large. Twenty-five individuals from each class were chosen randomly and measured to obtain the mean size in each class. Their shells (and those of the other molluscs) were removed, using 10 % nitric acid (Boltt 1975).

Animals were dried to constant mass at 60 °C. Mass was determined to four decimal places. Dry mass and not ash-free dry mass was determined for three reasons: Calorific values cannot be obtained for ash-free dry animals; the birds consume the animals containing sand so that an analysis of the relative importance of different prey items is only valid using actual dry mass; and, very little sand is left in animals which have been formalinized.

Actual mass of *Assiminea* was obtained only in September 1974 and in March 1975, because these animals were so numerous. Student's t-test was applied to the length/mass regressions for the two samples and showed that they were not significantly different ($p > 0{,}01$). Hence, figures for *Assiminea* mass for all the other months were obtained by extrapolating September and March values. *Assiminea globulus* and *A. isosceles* occur together at Bottelary. The latter accounted for 2 % of the total numbers so, although *A. isosceles* has been included in total biomass figures, references to *Assiminea* hereafter refer to *A. globulus*. Biomass and numerical fluctuations were determined on a monthly basis for *A. globulus* and *Urothoe grimaldi* only, due to the low numbers of the other organisms occurring in each sample. Production and P : B ratios were determined for *U. grimaldi* and *A. globulus*, using Crisp's (1971) method as modified by Chambers & Milne (1975*a*).

The Czekanowski or Bray–Curtis coefficient (Field 1971) was used as a measure of overall species similarity between the stations at all four transects. The stations were sorted using a group-average method based on the Czekanowski coefficient. The resulting hierarchy was used to construct a dendrogram showing which stations had similar faunistic groupings. The significance of the differences between the groupings was tested using information statistic tests (Field 1969). Position vectors ordination was also applied in which the relationships between individual stations (and not between groups of stations) were investigated (Field & Robb 1970).

Body length : mass relationships were established for those species present in sufficient numbers and of a representative size range. In addition, the jaw length : body mass relationship for three polychaetes and for stratiomyid larvae, whose jaws occur frequently in curlew sandpiper stomachs, was established by obtaining the dry mass of individual whole animals and then dissecting out and measuring the length of the jaws. The chela length : body mass relationship for *Hymenosoma* and *Cleistostoma* was also established.

Subsamples of about 150 g, taken from the frozen cores, were used for analysing particle size of sediments. The animals and pieces of vegetation were carefully removed, before each sample was tied in a 15 mm-length of dialysis tubing and suspended for 18 h in fresh running water to remove the salt. Wet sieving then removed the silt and clay fraction ($< 63\ \mu$). The coarse fraction was oven-dried at 105 °C, weighed and separated into five fractions (very coarse, coarse, medium, fine and very fine) according to the Wentworth scale (Newell 1970). The silt and clay fraction was allowed to settle for five days until the supernatant was clear. The supernatant was decanted and the remaining sediment oven-dried at 105 °C and weighed. Fractions were expressed as percentages of total dry mass. Particle size was plotted in cumulative percentages, using the phi-scale. Percentiles were read from each curve to calculate median particle size (Md_ϕ), phi quartile deviation (QD_ϕ) and phi quartile skewness (Skq_ϕ). The Mann–Whitney U-test was applied to test differences between sediment parameters corresponding to observed differences in animal distribution. Organic content was determined by weight differences of samples after combustion at 580 °C.

RESULTS

Physical factors

QD_ϕ indicates the degree of sorting of a sediment, i.e. the proportion of similar size to Md_ϕ. Skq_ϕ indicates which fraction, coarse or fine, is better sorted (Newell 1970). Md_ϕ values at Schrywershoek stations were small, indicating a coarse sediment

Table 1

Sediment characteristics of substrates at sampling stations in Langebaan Lagoon
Wentworth scale

	Very coarse	Coarse	Medium	Fine	Very fine	Silt + clay	Mdϕ	QDϕ	Skqϕ	Percent organics
	(%)	(%)	(%)	(%)	(%)	(%)				
Bottelary										
A	0,63	3,99	43,32	30,04	20,98	1,06	2,08	0,66	0,12	0,82
B	0,27	0,59	54,9	27,21	10,9	0,79	2,92	0,56	−0,77	0,70
C	0,06	1,08	23,27	34,18	41,06	0,35	2,88	0,66	0,05	0,66
D	0,21	2,03	24,99	28,51	43,01	1,27	2,85	0,79	−0,1	0,8
E	0,69	6,69	63,18	25,98	1,8	1,67	1,76	0,32	0,06	1,08
Geelbek										
A	0,17	3,4	33,95	47,6	7,35	7,52	2,09	0,4	0,08	1,89
B	0,16	2,59	28,35	49,67	8,4	10,84	2,26	0,46	0,08	1,71
C	0,13	2,13	4,0	63,34	9,17	21,24	2,47	0,65	0,38	3,89
D	0,18	1,69	22,55	42,57	5,72	27,29	2,56	1,34	0,78	3,83
E	0,27	0,12	1,74	6,86	2,01	88,99	4,78	0,26	0,1	8,63
Rietbaai										
A	5,73	31,06	25,52	20,1	17,06	1,56	1,5	1,03	0,11	0,89
B	0,18	15,38	29,15	28,45	23,8	1,39	2,23	0,86	0,01	1,0
C	1,95	7,27	20,28	28,07	36,24	6,19	2,77	0,77	−0,17	1,27
D	1,55	4,35	13,41	20,6	44,38	15,7	3,3	0,71	−0,26	1,57
E	4,36	9,41	20,17	20,67	32,73	12,66	2,85	0,92	−0,19	2,17
Schrywershoek										
A	0,93	8,33	64,41	20,37	4,31	1,65	1,52	0,44	0,12	0,97
B	0,24	6,22	66,37	22,17	3,68	1,38	1,55	0,44	0,11	0,87
C	0,34	6,91	59,1	25,73	4,87	3,1	1,65	0,5	0,1	1,49
D	0,27	6,24	67,74	22,16	1,81	1,78	1,52	0,89	0,64	1,36

(Table 1). QD$_\phi$ values were similar, i.e. the sediment was well sorted. Bottelary, Geelbek and Rietbaai had finer substrates, relatively less well sorted (Fig. 3). Bottelary and Schrywershoek had a very small silt and clay fraction; Rietbaai had more and Geelbek had a high proportion (Table 1). The organic content of the substrate increased as the fine fraction increased (Table 1). At Schrywershoek, Md$_\phi$ was the same at all the stations. At Bottelary Md$_\phi$ increased up the shore, whereas at Geelbek and Rietbaai it decreased up the shore (Table 1).

Salinities and temperatures (Table 2) were within the ranges measured by Day (1959).

Invertebrates

Bottelary

Fairly well-marked seasonal fluctuations in biomass and numbers of invertebrates occurred at Bottelary (Fig. 4). There were peaks in spring (September) and autumn (February–March) and lower winter and summer levels. Biomass and numbers at each sampling station (Fig. 5) showed different fluctuations due to the vertical distribution of the benthos. *Assiminea* was present chiefly at the high-water level (Fig. 2a), and polychaetes were distributed from low to high water. Crustacea and bivalves occurred from low water to above the mid-tide level. (A checklist of the fauna at Bottelary, and mean biomass and numbers of invertebrates per month, are given in Appendix 1.)

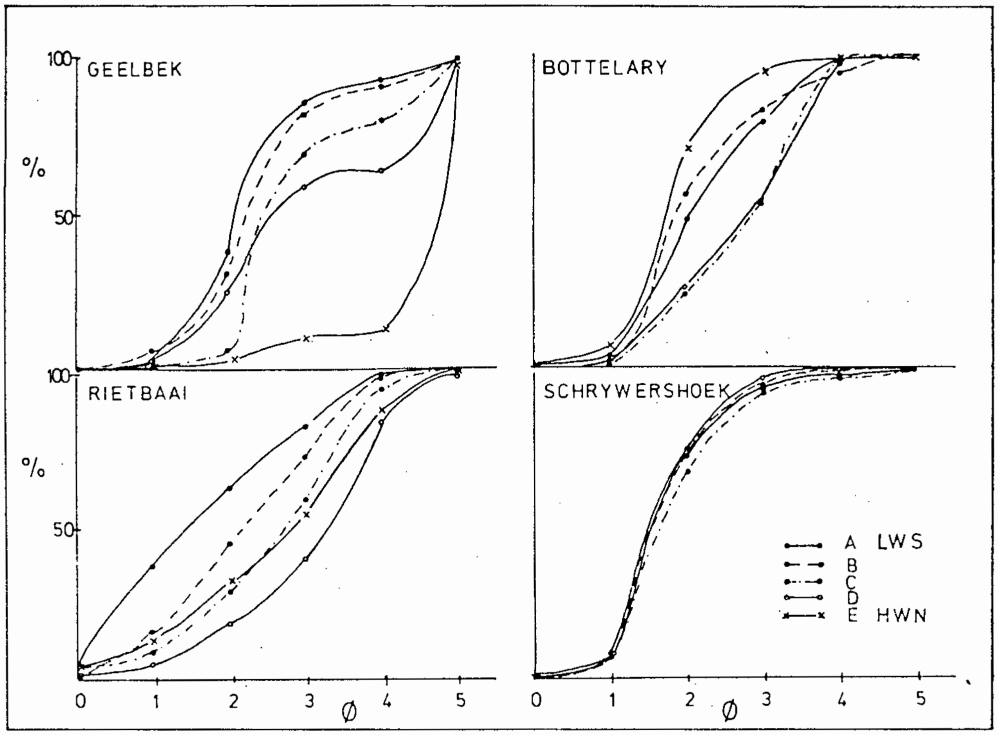

Fig. 3. Particle-size cumulative curves for sediments at five sampling stations at each of four transect sites. The *y*-axis shows cumulative percentage of sediment by mass, the *x*-axis particle-size classes measured on the phi-scale.

Table 2

Salinities (‰) and temperatures (°C) at Bottelary. Low-water and high-water readings taken at springs, marsh readings at neaps. All figures are averages of three readings

	Sandflats		Marsh pool
	Low-water	*High-water*	
Salinity			
Spring (Sept.–Nov.)	35,0	35,5	38,0
Summer (Dec.–Feb.)	36,3	36,5	50,0
Autumn (March–May)	36,0	35,0	57,0
Winter (June–Aug.)	33,5	34,0	34,5
Temperature			
Spring	17,0	18,0	20,0
Summer	25,0	26,4	28,5
Autumn	15,5	17,0	24,0
Winter	15,5	17,5	18,5

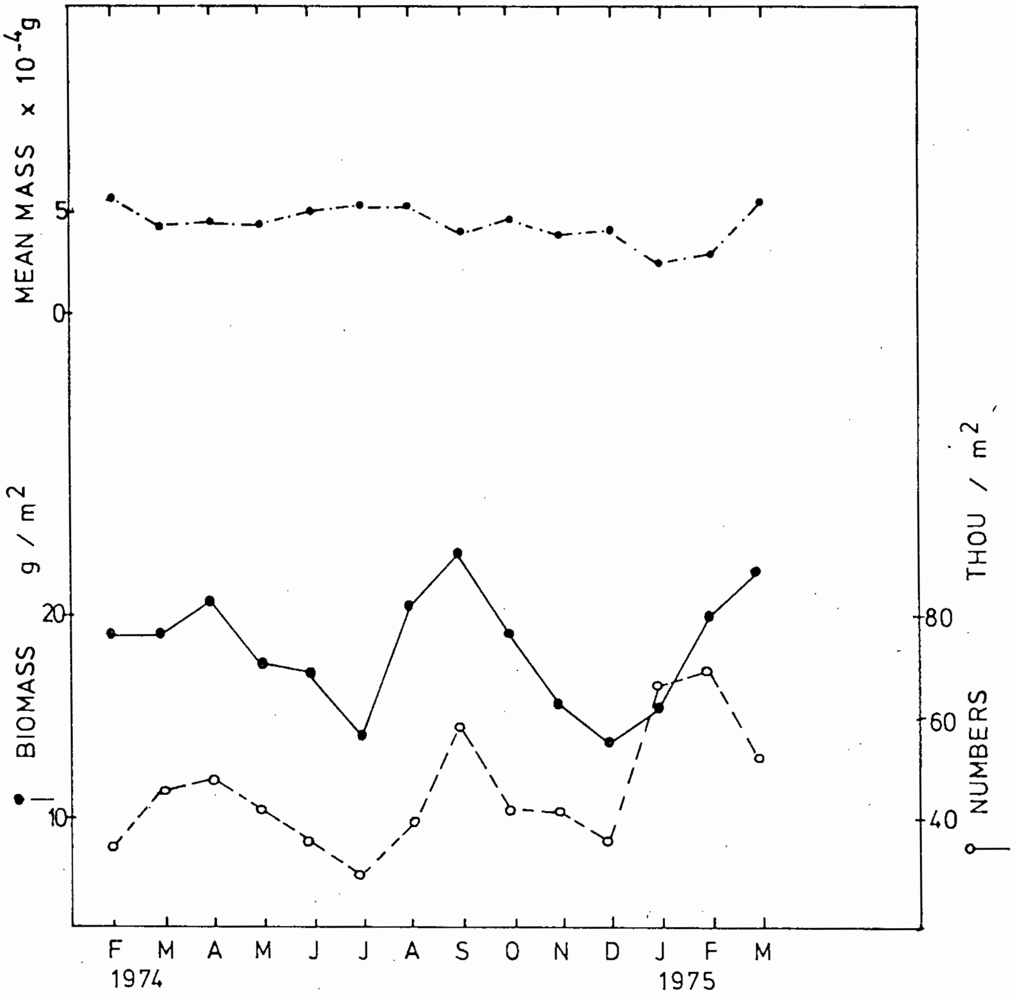

Fig. 4. Mean biomass, numbers and mean mass of the benthic organisms at Bottelary. Mean annual biomass was 18,44 ± 0,34 g/m^2 (± S.E.) and mean annual number was 45 347 ± 1 458,4 (± S.E.) per m^2.

Figure 6 presents a breakdown of the total biomass into major categories of animals. Gastropods (mainly *Assiminea*) comprised on average 62,5 % of the total biomass. Changes in total biomass and numbers at Bottelary were dominated by changes in *Assiminea* alone (cf. Figs 4 & 7). (Note that the biomass in Fig. 7 is mean biomass for stations C, D and E only as this is the range within which *Assiminea* was found.) *Assiminea* comprised all the animals smaller than 1 mm in the seven months during which these were sampled (Appendix 2).

Analysis of monthly samples of *Assiminea* from Bottelary for size distribution, number of juveniles and mean mass of individuals (Fig. 8) shows a major recruitment

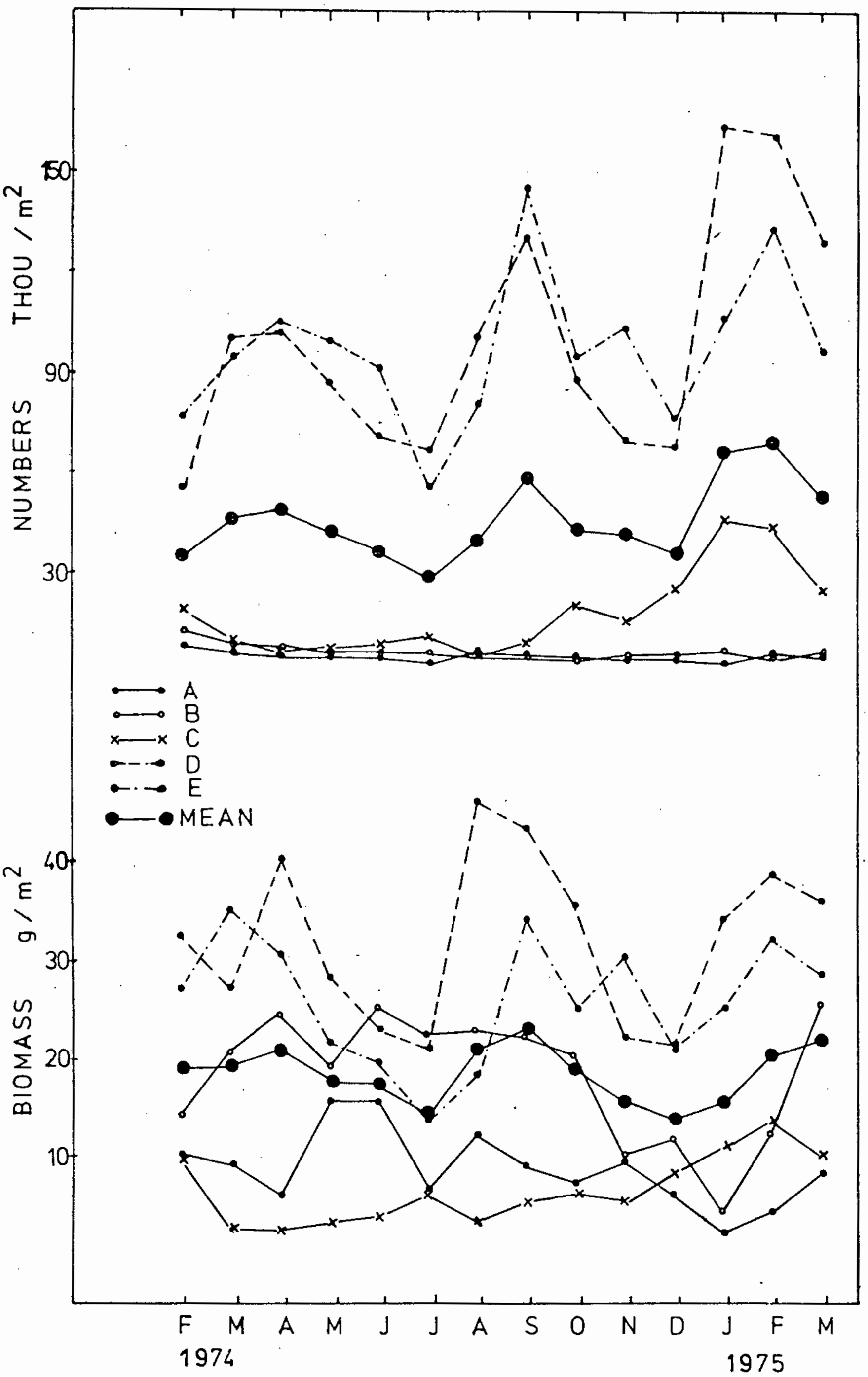

Fig. 5. Mean numbers (top) and biomass (bottom) at five sampling stations (A–E) at Bottelary. The total mean is also shown.

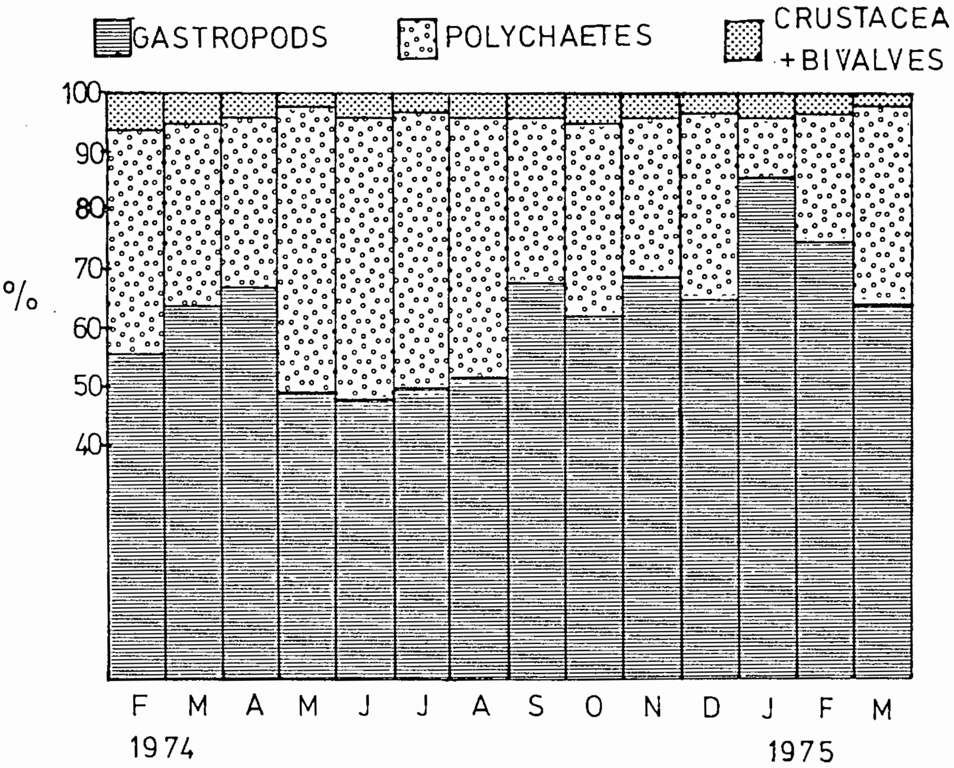

Fig. 6. Percentage occurrence of major categories of benthic organisms based on total biomass at Bottelary.

peak in January–February. The histogram for September 1974 indicates that another recruitment peak may have occurred in the preceding month. However, this could not be shown conclusively, because animals smaller than 1 mm were sampled only from September onwards. The small number of animals in the larger size classes suggests that the life cycle is short, probably one year. A growth rate of about 1,5 – 2,0 mm in 12 months can be deduced. Production was high (Table 3), because of the short life cycle.

Similar analysis for *Urothoe grimaldi* shows a major recruitment peak in December (Figs 9 & 10). Longevity in *Urothoe* appears to be 12 months, and the growth 5 mm in 12 months. Thus the high biomass achieved in winter and early spring was attributable to individual growth. Production was low (Table 4), despite the short life cycle.

A very high percentage of the Bottelary benthos consists of deposit feeders (Table 5), since Bottelary is a depositing shore.

Length: mass regression equations for common species are given in Table 6.

Geelbek, Schrywershoek and Rietbaai

There were seasonal fluctuations in mean biomass and numbers of invertebrates at Geelbek, Schrywershoek and Rietbaai, although the variation is somewhat obscured

Table 3

Summary of the data used in the calculation of total annual production (per m^2) of *Assiminea globulus*

	No./m^2	Mass ($\times 10^{-4}$ g)	Mass ($\times 10^{-4}$ g)	No.	Production (g/m^2)
Cohort 1					
1974 Apr.	73 084	9,6	—		
May	63 540	6,7	−2,9	68 312	−19,81
June	55 001	7,7	1,0	59 270,5	5,93
July	43 511	8,04	0,34	49 256	1,67
Aug.	60 275	8,79	0,75	51 893	3,89
Sept.	69 065	9,57	0,78	64 670	5,04
Oct.	3 767	19,01	9,44	36 416	34,38
Cohort 2					
1974 Sept.	25 005	4,8	—		
Oct.	62 959	8,1	3,3	43 982	14,51
Nov.	64 686	8,24	0,14	63 822,5	0,89
Dec.	55 629	7,8	−0,44	60 157,5	−2,65
1975 Jan.	53 274	9,16	1,36	54 451,5	7,41
Cohort 3					
1975 Jan.	51 579	3,14	—		
Feb.	106 737	6,89	3,75	79 158	29,68
March	79 645	8,43	1,54	93 191	14,35
					95,29 g/m^2/y

Mean annual biomass 19,21 g
P : B ratio 4,96

Table 4

Summary of the data used in the calculation of total annual production (per m^2) of *Urothoe grimaldi*

	No./m^2	Mass ($\times 10^{-4}$ g)	Mass ($\times 10^{-4}$ g)	No.	Production (g/m^2)
Cohort 1					
1974 Feb.	565	5,7	—		
March	565	4,2	−1,5	565	−0,0847
Apr.	722	6,8	2,6	643,5	0,1673
May	549	6,5	−0,3	635,5	−0,0191
June	671	8,0	1,5	610	0,0915
July	459	9,1	1,1	565	0,0622
Aug.	1 005	8,0	−1,1	732	−0,0805
Sept.	628	10,6	2,6	816,5	0,2123
Oct.	465	12,1	1,7	546,5	0,0929
Nov.	324	10,3	−1,8	394,5	−0,0710
Dec.	269	8,1	−2,2	296,5	−0,0652
1975 Jan.	332	11,6	3,5	300,5	0,1052
Cohort 2					
1974 Oct.	218	3,4	—		
Nov.	171	1,6	−1,8	194,5	−0,0350
Dec.	755	2,3	0,9	463	0,0417
1975 Jan.	489	1,9	−0,4	622	−0,0249
Feb.	1 036	5,3	3,4	762,5	0,2593
March	691	5,8	0,5	863,5	0,0432
					0,6952 g/m^2/y

Mean annual biomass 0,51 g
P : B ratio 1,36

Table 5

Trophic grouping of benthic organisms at Bottelary expressed as percentage total biomass. Classification of feeding type after Day (1969)

Trophic grouping	Mean ± S.E.
Herbivore	1,06 ± 0,49
Filter feeder	1,95 ± 0,48
Detritivore	89,56 ± 1,22
Carnivore	4,46 ± 0,89
Omnivore	3,01 ± 0,66

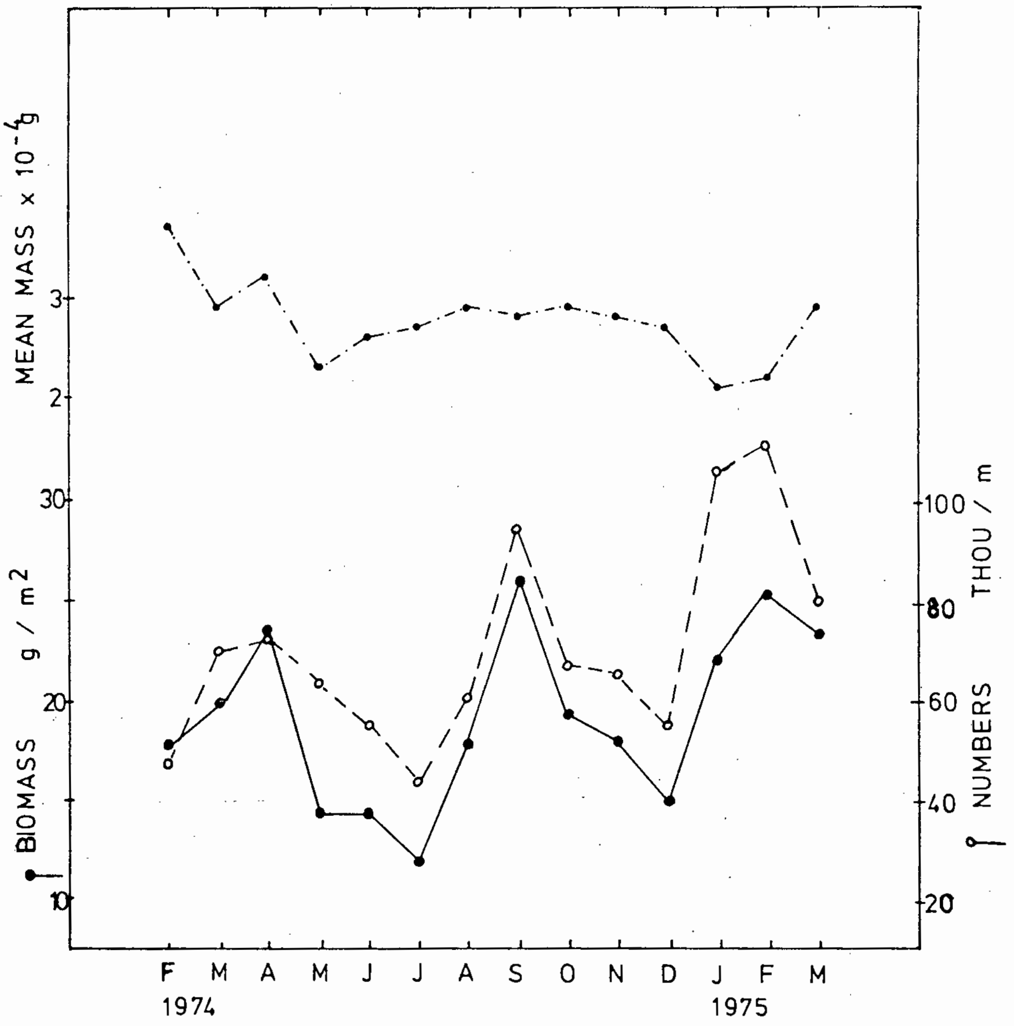

Fig. 7. Mean numbers and biomass (bottom) and mean mass (top) of *Assiminea globulus*. Mean annual biomass was 19,55 ± 1,23 g/m^2 (± S.E.) and numbers 70 524 ± 5 634,5/m^2 (± S.E.).

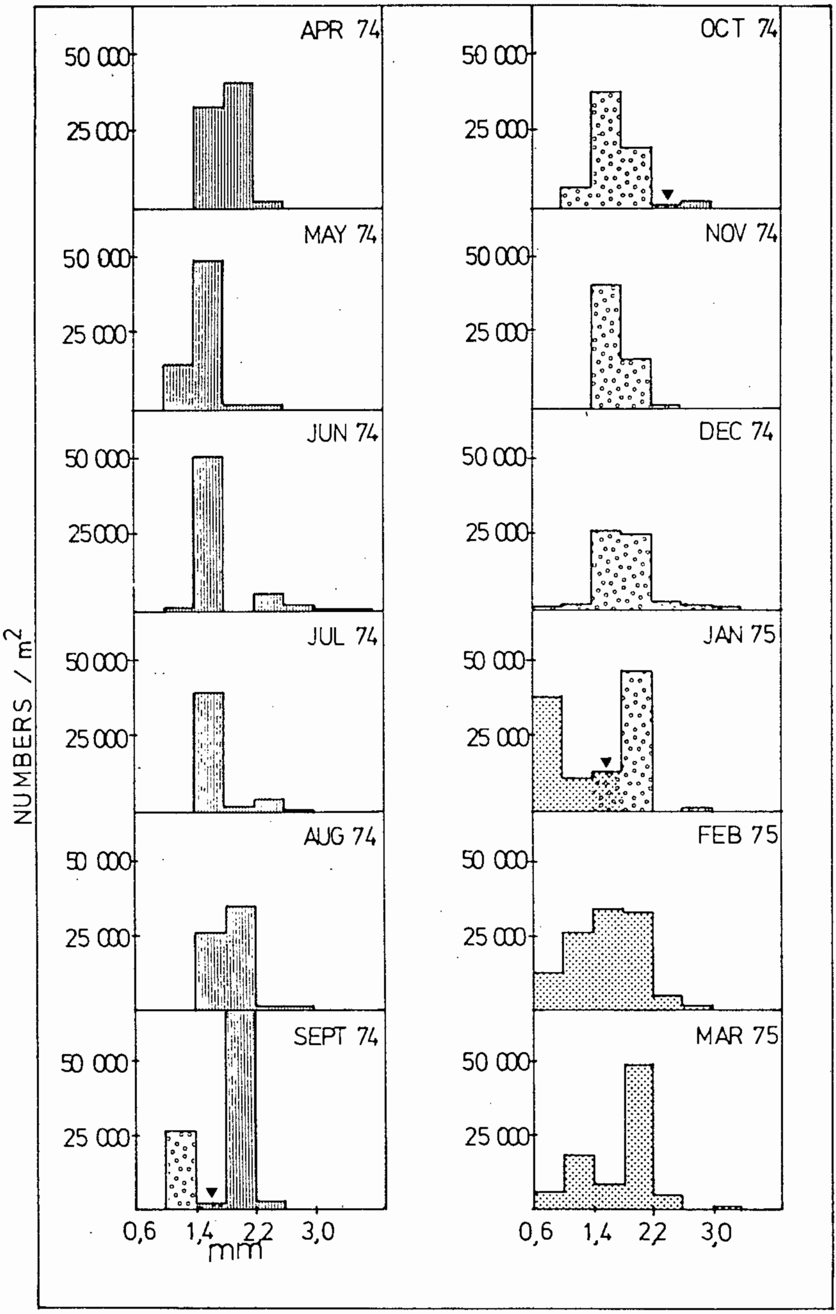

Fig. 8. Size-frequency histograms showing the age distribution of *Assiminea globulus*.

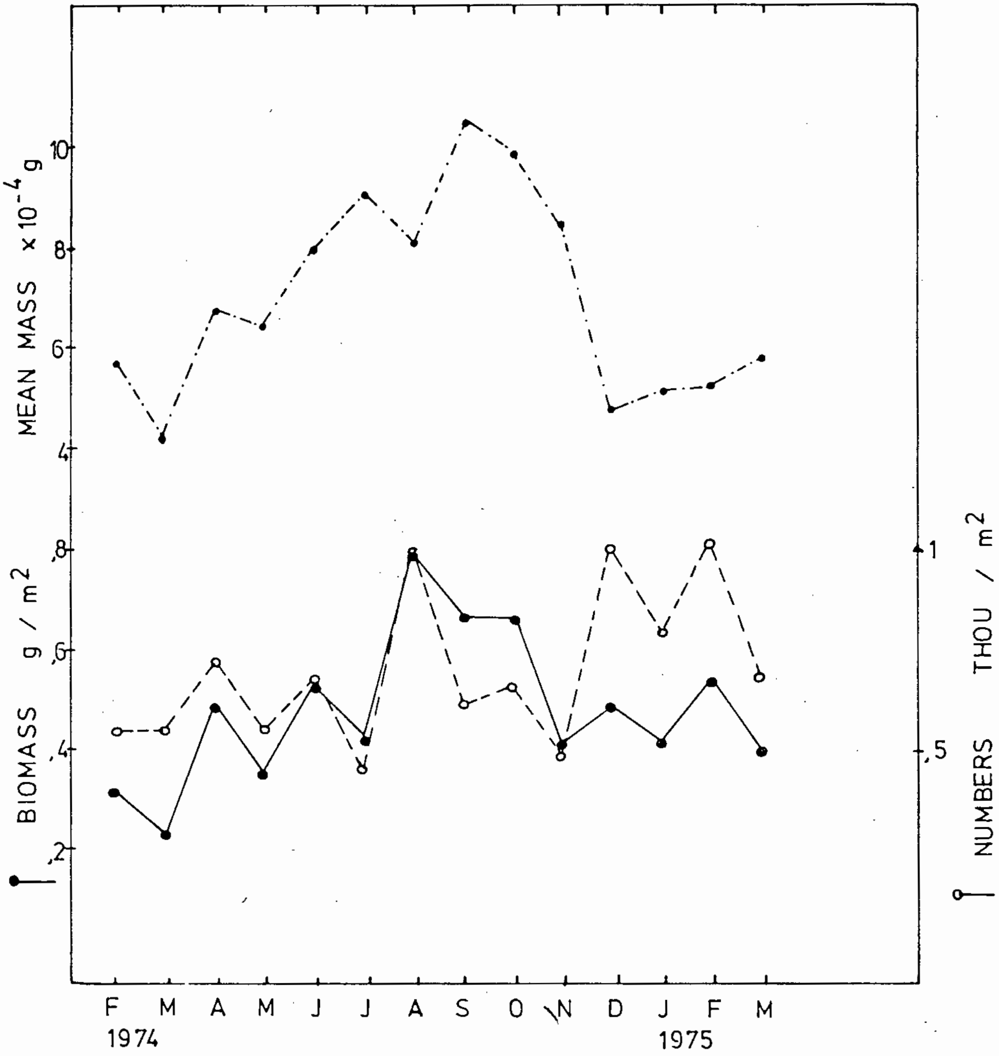

Fig. 9. Mean numbers and biomass (bottom) and mean mass (top) of *Urothoe grimaldi*. Mean annual biomass was 0,51 ± 0,04 g/m² (± S.E.) and numbers 705,2 ± 51,1/m² (± S.E.).

as a result of samples having been taken only every second month. Bottelary and Schrywershoek had similar patterns of biomass fluctuation (Fig. 11), differing from Geelbek and Rietbaai which had midwinter (July) peaks declining in spring and summer. (A checklist of the fauna at the three sites and mean biomass and numbers of invertebrates present per month are given in Appendix 1. Biomass at individual stations is given in Appendix 3.)

The vertical distribution of the fauna was similar to that at Bottelary (Fig. 2).

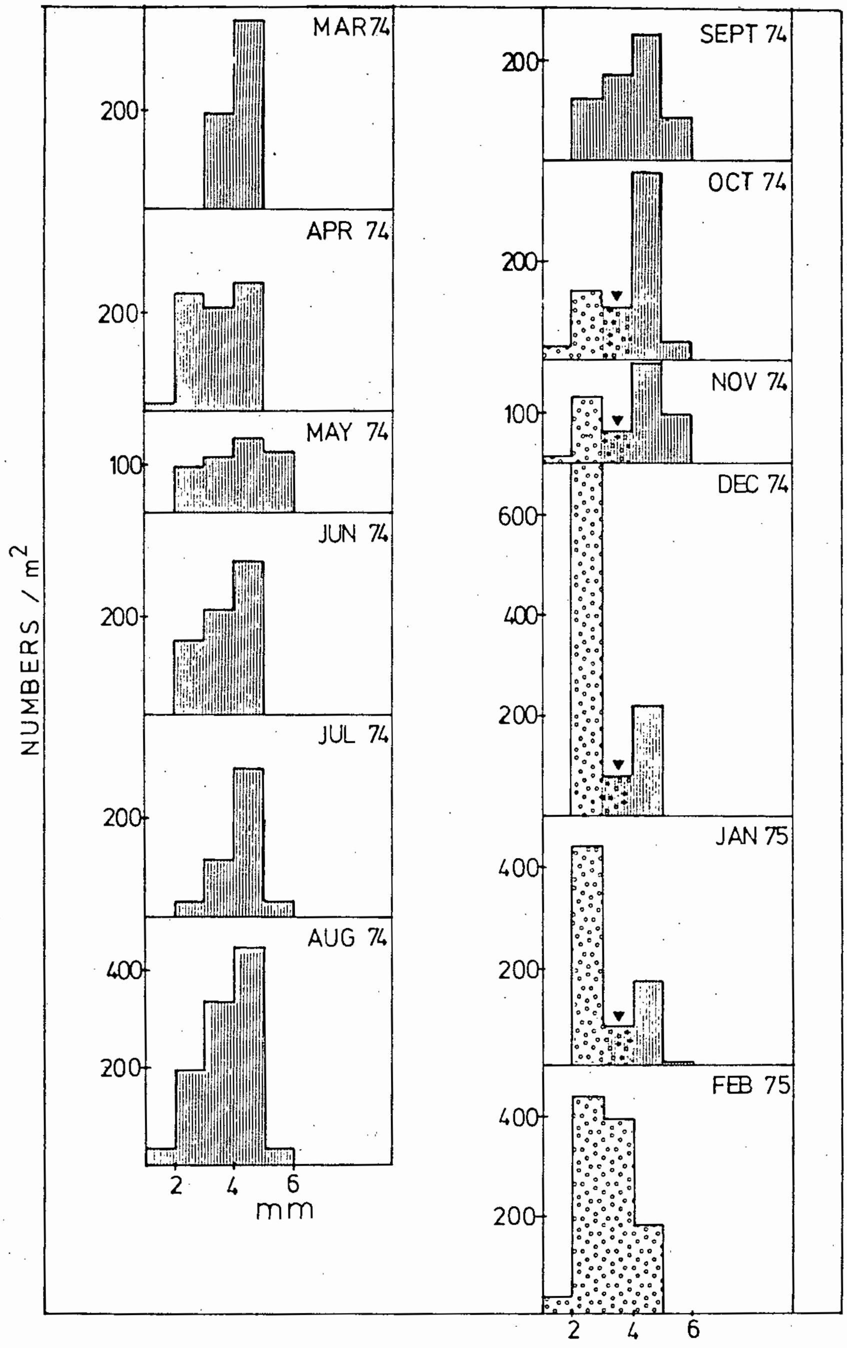

Fig. 10. Size-frequency histograms showing the age distribution of *Urothoë grimaldi.*

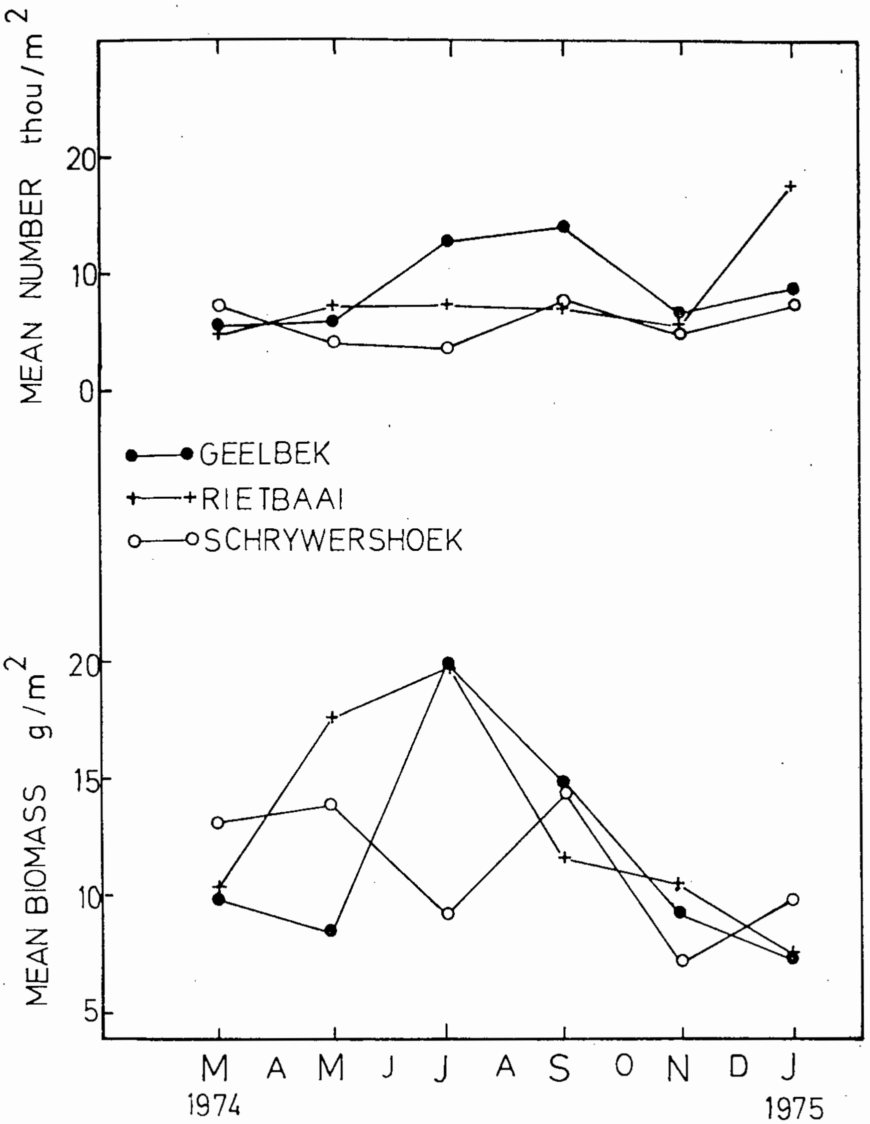

Fig. 11. Mean biomass and numbers of benthic organisms at Geelbek, Schrywershoek and Rietbaai.

Similarity analysis

Figure 12 shows that there were four groups of similar stations: stations on bare sand, with slightly different sediment parameters (Table 1), were similar at the 53 % level; stations with *Zostera* or *Spartina* were similar at the 54 and 58,5 % levels; and stations having *Assiminea* were similar at the 56,5 % level.

The points obtained for each sample by position vectors ordination were plotted along the first two vectors. Figure 13 shows that the stations divided into two groups:

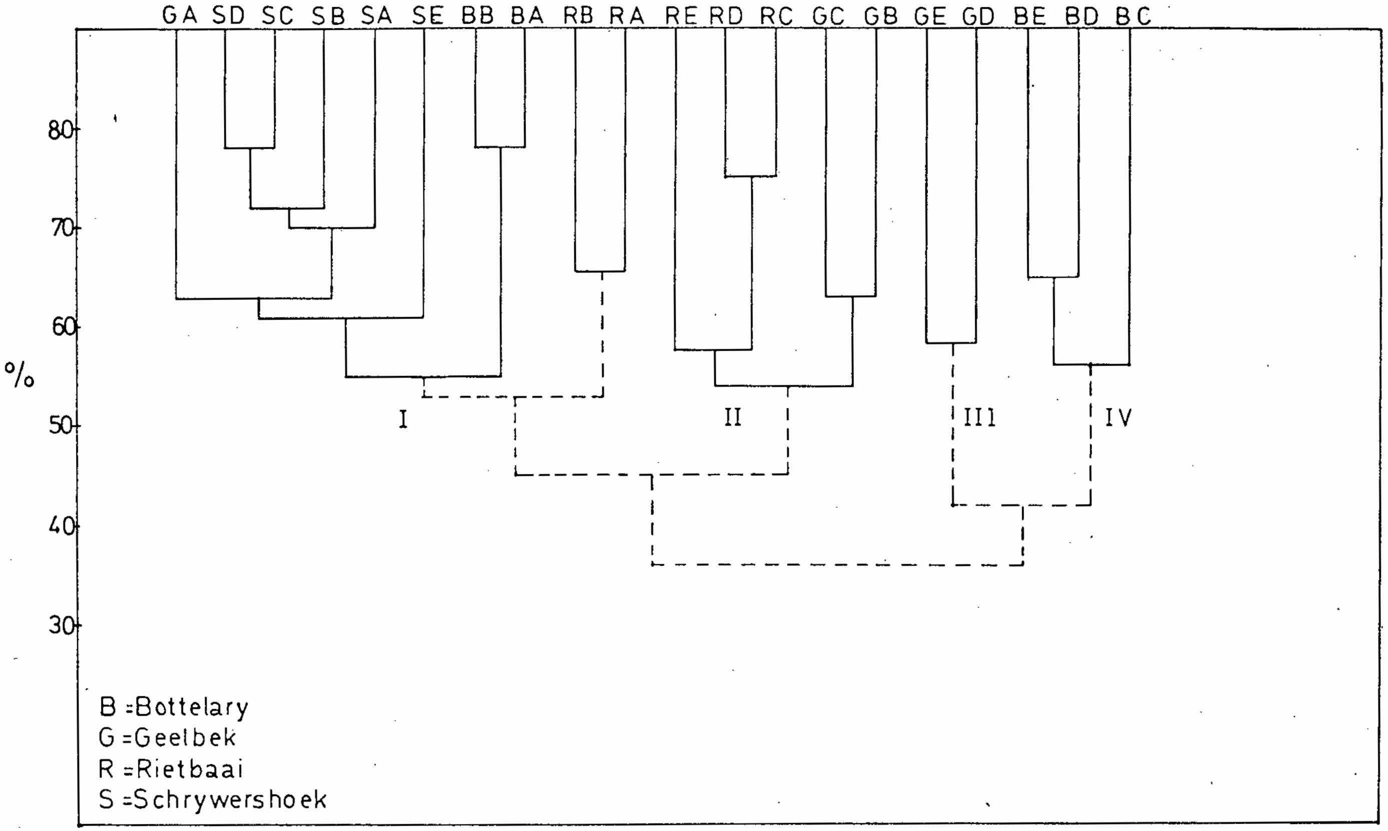

Fig. 12. Dendrogram showing similarity between all stations at all four transect sites. The axis shows percentage similarity obtained by the Czekanowski co-efficient using log-transformed mean abundances at each station with group-average sorting. The figures I–IV indicate the four main groups recognized. The broken lines indicate that the stations or groups of stations differ significantly at the 1 % level when tested using the information statistic.

Table 6

Regressions of mass (W) in grams against body length (L) in mm for some benthic organisms at Langebaan Lagoon

Species	Regression equation	r	N
Assiminea globulus			
April 1974	$\log W = 2,55 \log L + \log 0,0001$	0,99	11
September 1974	$\log W = 2,71 \log L + \log 0,00004$	0,91	27
March 1975	$\log W = 2,02 \log L + \log 0,00009$	0,98	11
Assiminea isosceles	$\log W = 2,18 \log L + \log 0,00005$	0,94	27
Marginella capensis	$\log W = 3,03 \log L + \log 0,00007$	0,88	30
Nassa kraussiana	$\log W = 2,99 \log L + \log 0,00003$	0,99	7
Nassa speciosa	$\log W = 2,13 \log L + \log 0,00009$	0,95	14
Tellimya sp.	$\log W = 5,17 \log L + \log 0,000001$	0,76	10
Nucula sp.	$\log W = 2,8 \log L + \log 0,00006$	0,89	23
Carditella rugosa	$\log W = 2,85 \log L + \log 0,00002$	0,91	41
Cylindroleberis ?galathea	$\log W = 2,98 \log L + \log 0,00008$	0,98	13
Exosphaeroma hyloecetes	$\log W = 2,14 \log L + \log 0,00007$	0,91	29
Hymenosoma orbiculare	$\log W = 3,24 \log L + \log 0,00004$	0,94	21
Cleistostoma edwardsii	$\log W = 3,46 \log L + \log 0,00013$	0,95	18
Urothoe grimaldi	$\log W = 2,22 \log L + \log 0,00003$	0,84	28
Austrochiltonia capensis	$\log W = 1,48 \log L + \log 0,00010$	0,91	19
Stratiomyid larvae	$\log W = 2,30 \log L + \log 0,00003$	0,95	15
Ampelisca palmata	$\log W = 2,16 \log L + \log 0,00003$	0,92	12
Jaw length/body mass			
Ceratonereis erythraensis	$\log W = 1,82 \log L + \log 0,0104$	0,88	43
Marphysa depressa	$\log W = 2,38 \log L + \log 0,0192$	0,87	15
Glycera convoluta	$\log W = 2,82 \log L + \log 0,0189$	0,96	40
G. convoluta (jaw strut/body mass)	$\log W = 3,09 \log L + \log 0,9932$	0,99	11
Stratiomyid larvae	$\log W = 2,54 \log L + \log 0,0016$	0,84	7
Chela length/body mass			
Cleistostoma edwardsii	$\log W = 2,25 \log L + \log 0,0027$	0,96	16
Hymenosoma orbiculare	$\log W = 5,23 \log L + \log 0,0012$	0,97	4

those with macrophytes and/or *Assiminea* on the right and those without these two elements, i.e. sandy-zone stations, on the left. Rietbaai B and A were included in Group 1 stations (Fig. 12), because of their similarity shown in Figure 13.

Significant differences between sediment parameters occurred at all sampling sites, especially in the silt and clay fraction and in the percentage of organics present (Table 7). Significant differences occurred in various sediment parameters between Group 1 and the other three groups of stations. Also, the sediments at stations with macrophytes had a significantly greater silt and clay fraction and a higher percentage of organics than those without these elements. Almost all the stations without macrophytes (Groups 2 and 3) had winter peaks in biomass (Table 8), whereas those without, except Rietbaai A, had spring and/or autumn peaks.

Marsh

The biomass of invertebrates in *Arthrocnemum* fluctuated seasonally. Biomass peaked in midwinter (July) and in midsummer (January) at Geelbek (Fig. 14). This trend was not as clear at Bottelary (Fig. 14). Mean biomass was relatively higher at Geelbek, because the animals there were significantly bigger ($p < 0,001$).

Assiminea accounted for 70 % of the marsh-fauna biomass (Fig. 15). Crustacea (mainly amphipods and crabs) were most abundant in winter. Stratiomyid larvae were present throughout the year but especially in autumn and winter. Insects comprised a small percentage of the total biomass, although they were present in fairly high numbers. They constituted 12,8 % of the total number of animals at Geelbek. Stratiomyid larvae accounted for most of the insect biomass and were an important food item for curlew sandpipers (Puttick in prep.). Figure 16 indicates that recruitment of stratiomyid larvae (Geelbek and Bottelary samples pooled) occurred in April, June and possibly December, based on size distribution, mean mass of individuals and numbers of 'juveniles'. The duration of the larval stage is not known. No pupae nor adults were ever found.

The mean percentage by mass of the organisms comprising the epifauna was high

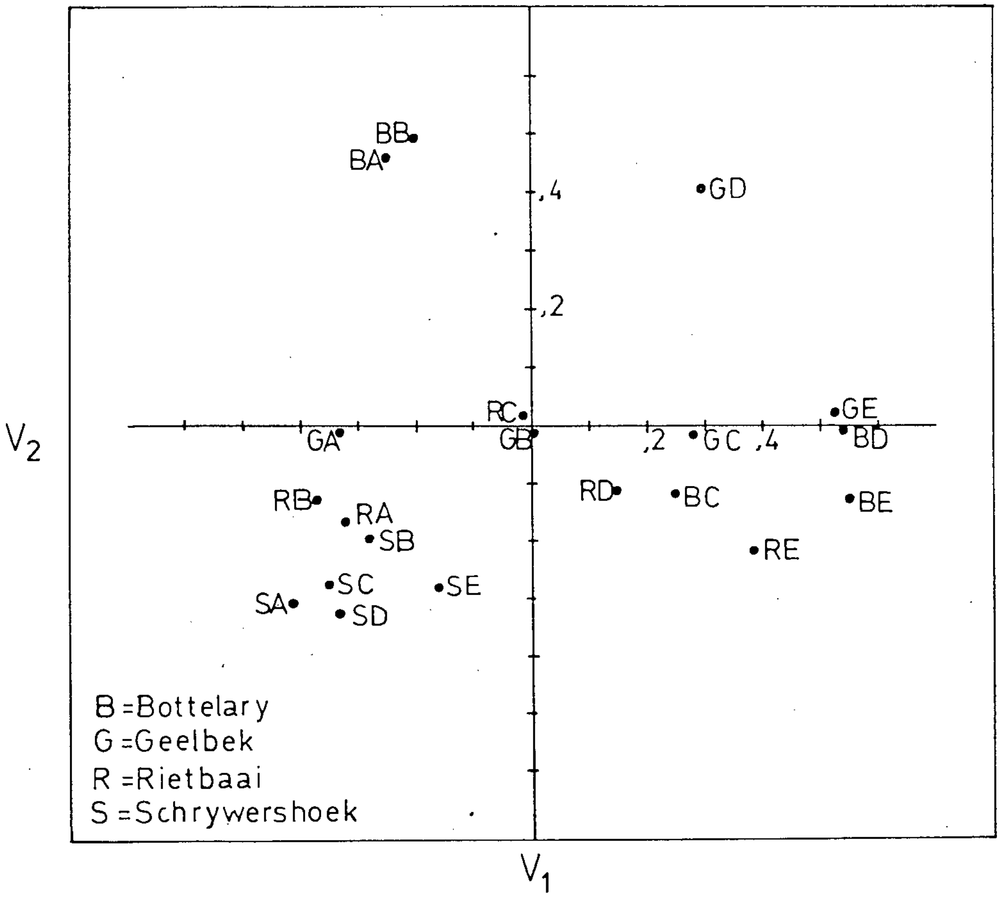

Fig. 13. Position vectors analysis of log-transformed data of samples from all 20 stations. The samples (lettered) are plotted as points with co-ordinates given by the first two vectors (V_1 and V_2). The vector scales are ratios related to values of the weighted similarity co-efficient.

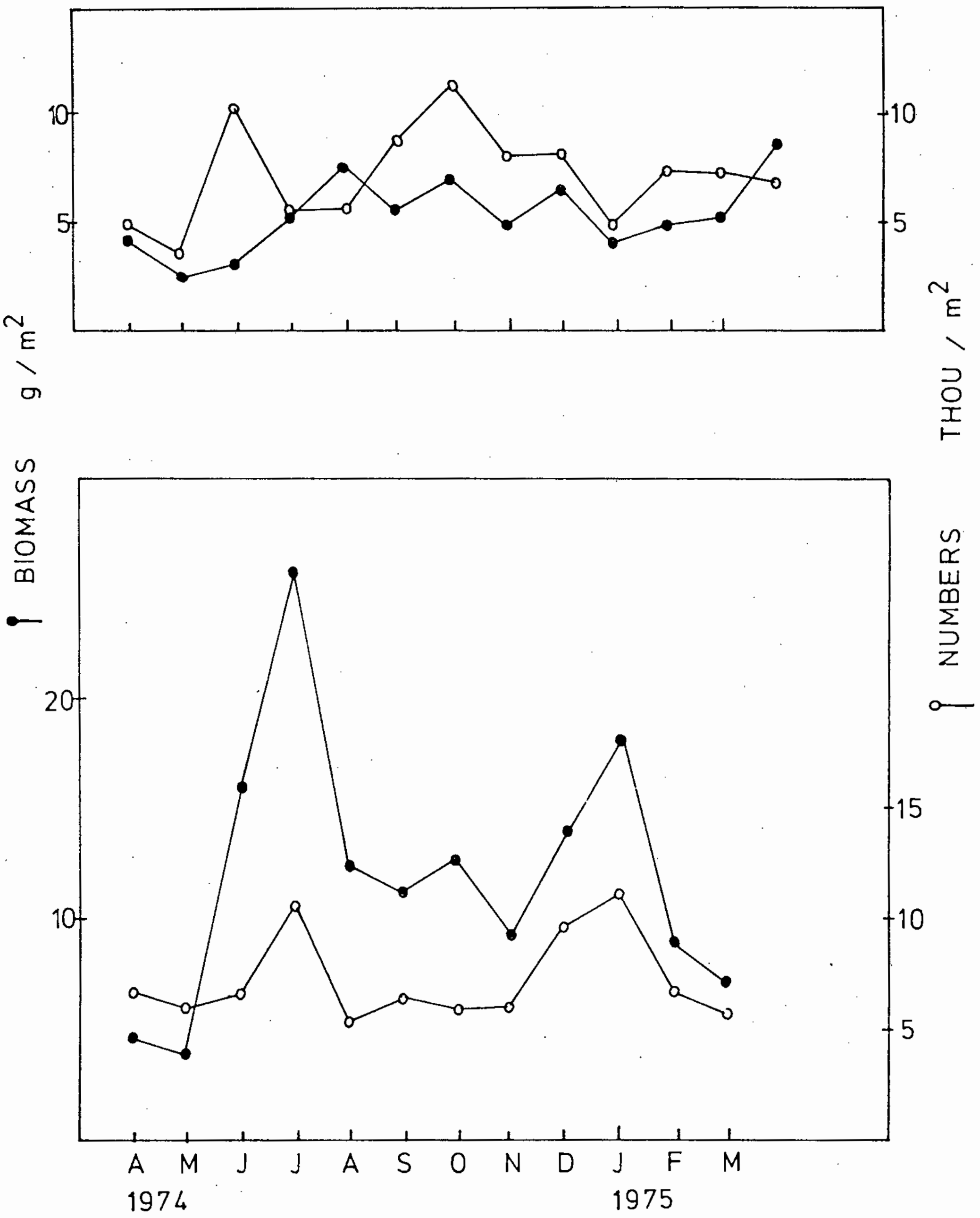

Fig. 14. Mean biomass and numbers at the marsh sampling stations at Bottelary (top) and Geelbek (bottom). Mean annual biomass and numbers at Geelbek were 12,13 ± 1,76 g/m^2 and 7 360,6 ± 597,11 (± S.E.). At Bottelary they were 5,34 ± 0,51 g/m^2 and 7 211,2± 616,62/m^2 (±S.E.). Mean mass therefore was 0,0016 ± 0,0006 at Geelbek and 0,0007 ± 0,0003 at Bottelary.

in the marsh (91,68 ± 2,81 % (± S.E.) at Bottelary and 92,81 ± 2,94 % (± S.E.) at Geelbek).

Biomass and numbers of animals in pools showed high values at the beginning of winter (May–June), and there was also a peak in September (Fig. 17). The net catches showed no clear trend, though biomass and numbers peaked in autumn (Fig. 17). Spring and summer levels were slightly higher than winter levels.

Table 7

Sediment characteristics which differ significantly between groups of stations (stns) using the Mann–Whitney U-test

Groups of stations	Sediment characteristic	Probability
Bottelary < Schrywershoek	Silt and clay	0,05
	Coarse fraction	0,01
	% organics	0,05
Bottelary < Rietbaai	Silt and clay	0,02
	Coarse fraction	0,01
	% organics	0,02
Bottelary < Geelbek	Silt and clay	0,005
	% organics	0,005
Stns with macrophytes < stns without macrophytes	Silt and clay	0,005
	% organics	0,01
Dendrogram Group 1 < Dendrogram Group 2	Silt and clay	0,005
	% organics	0,025
	Very fine fraction	0,025
Dendrogram Groups 3 + 4 < Dendrogram Group 1	Mdϕ	0,025

Table 8

Occurrence of biomass peaks related to dendrogram grouping of stations and to presence of macrophytes

Dendrogram Group	Stations	Biomass peak	Macrophytes
I	Rietbaai A	Winter	Absent
	Rietbaai B	Spring and autumn	Absent
	Schrywershoek A	Spring and autumn	Absent
	Schrywershoek B	Spring and autumn	Absent
	Schrywershoek C	Spring and autumn	Absent
	Schrywershoek D	Spring and autumn	Absent
	Schrywershoek E	Spring and autumn	Absent
	Geelbek A	Spring and autumn	Absent
	Bottelary A	Autumn	Absent
	Bottelary B	Autumn	Absent
II	Rietbaai E	Winter	*Spartina*
	Rietbaai D	?	*Zostera*
	Rietbaai C	Winter	*Zostera*
	Geelbek B	?	*Zostera*
	Geelbek C	Winter	*Zostera*
III	Geelbek D	Winter	*Zostera*
	Geelbek E	Winter	*Spartina* and *Zostera*
IV	Bottelary E	Spring and autumn	Absent
	Bottelary D	Spring and autumn	Absent
	Bottelary C	Late summer	Absent
Marsh	Bottelary	Winter	*Arthrocnemum*
Marsh	Geelbek	Winter	*Arthrocnemum*

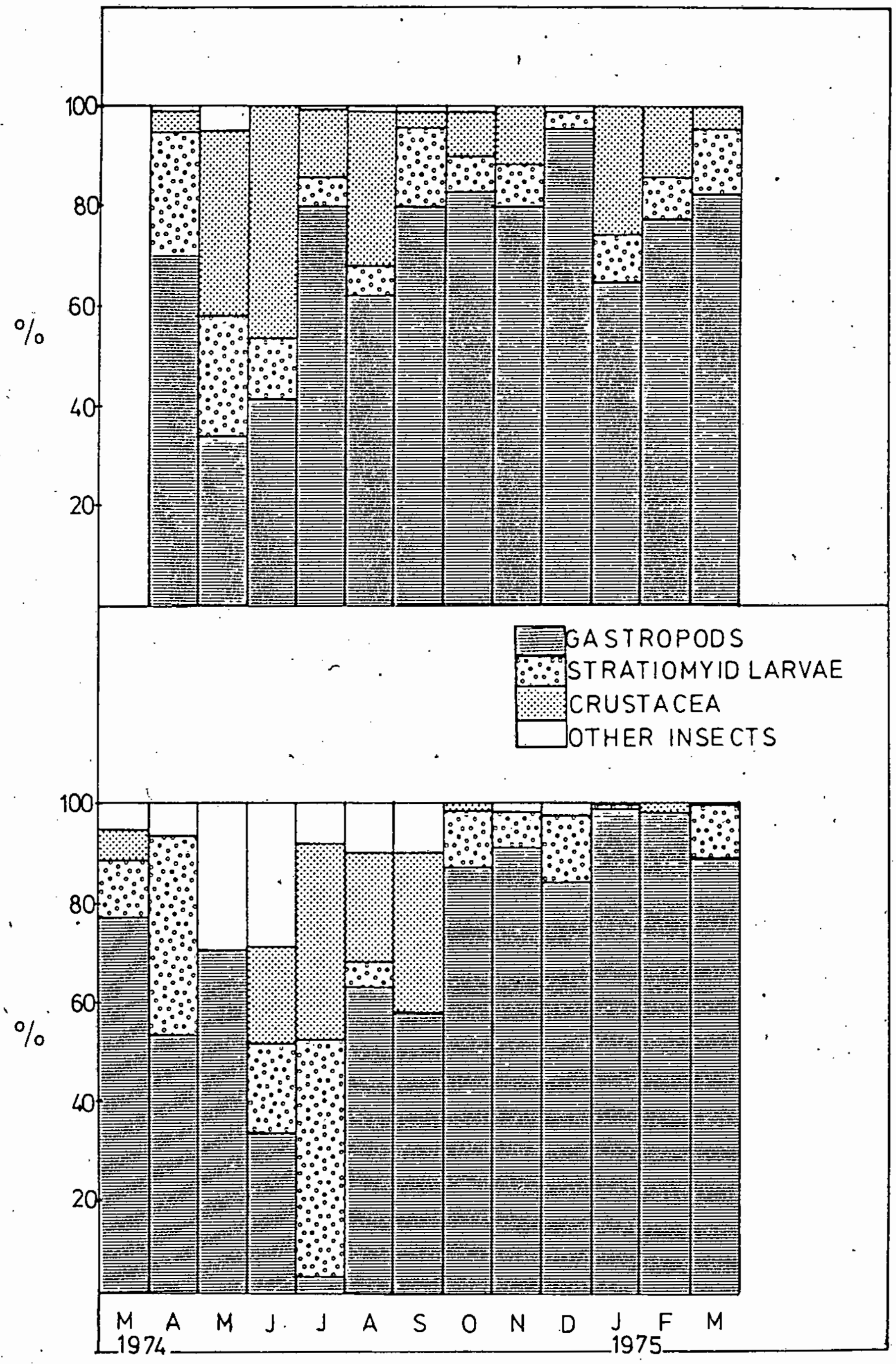

Fig. 15. Percentage occurrence of major categories of marsh organisms based on total biomass at Geelbek (top) and Bottelary (bottom).

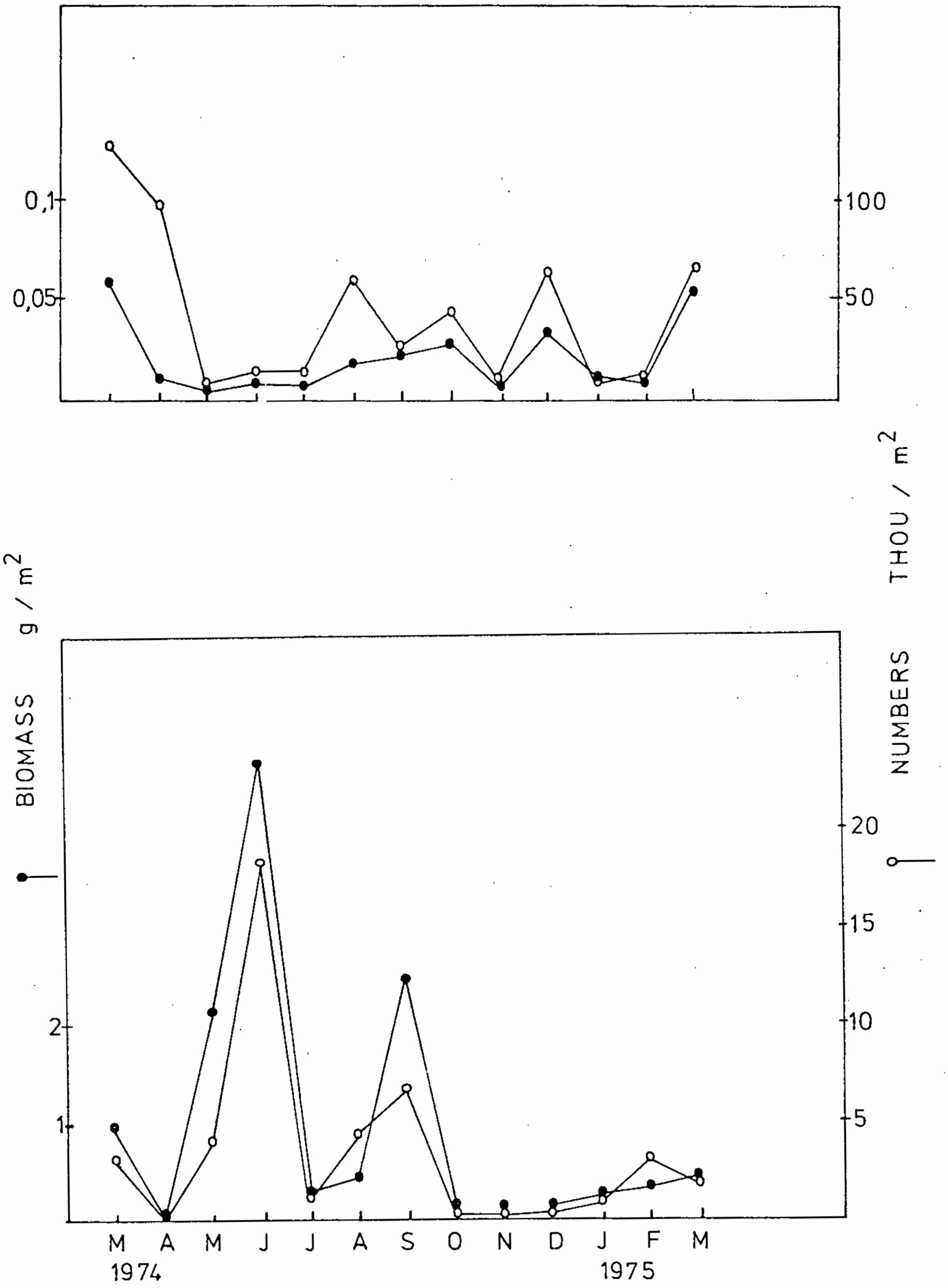

Fig. 17. Mean numbers and biomass of organisms sampled by net above marsh pools (top) and in marsh pools (bottom) at Bottelary.

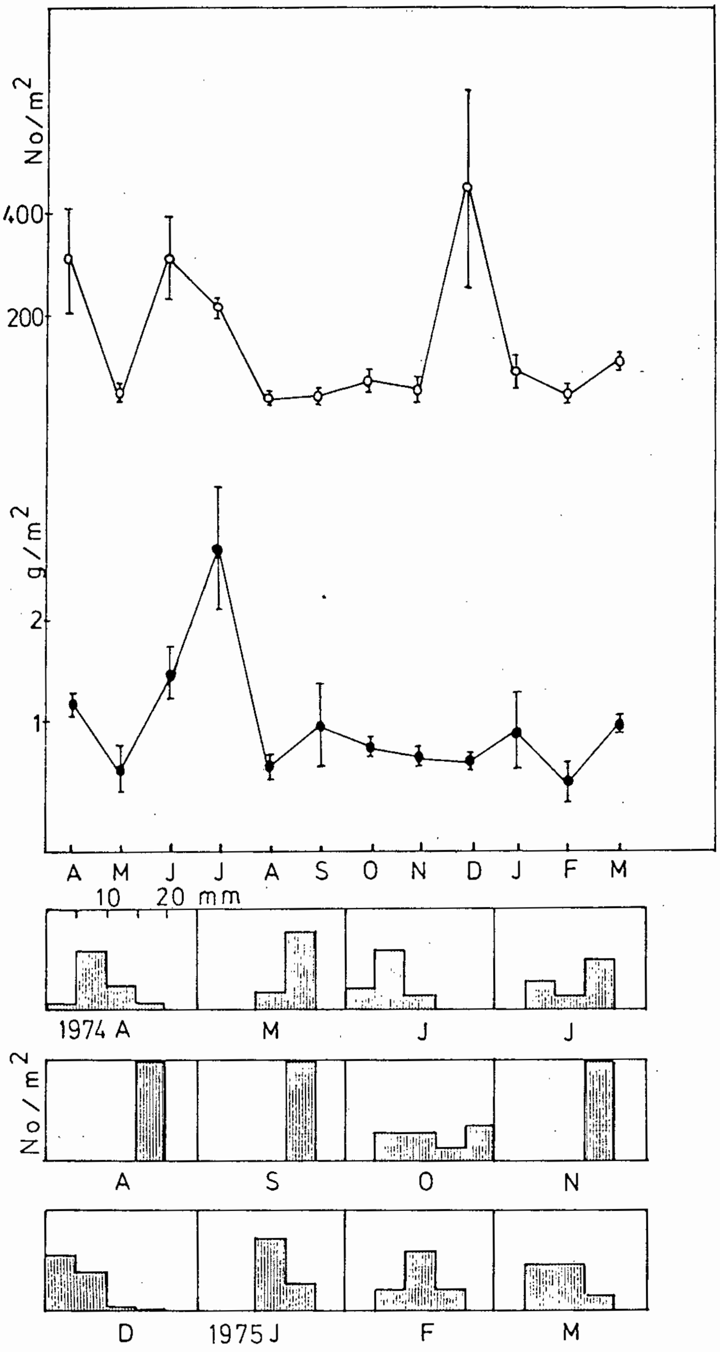

Fig. 16. Mean number ± S.E. (top) and mean biomass ± S.E. (middle) of stratiomyid (dipteran) larvae. Mean annual number was 143 ± 41,24/m^2 and biomass 0,93 ± 0,18 g/m^2 (± S.E.). Size-frequency histograms are shown (bottom).

DISCUSSION

Biomass fluctuations

There is very little published information on seasonal changes in density and biomass of sandy and/or muddy-shore benthos. Data are available for individual species in the Northern Hemisphere (Brafield & Chapman 1967; Chambers & Milne 1975*b*; George 1964; Hughes 1970; Rees 1975), and in South Africa McLachlan (1974). Anderson (1972) describes changes in numbers only of organisms occurring in Morecambe Bay during 1968–9, but sampling was erratic and no clear seasonal fluctuations were observed. Burke & Mann (1974) estimated P: B ratios for *Mya arenaria, Macoma balthica* and *Littorina saxatilis* which are dominant inter-tidal herbivores at Petpeswick Inlet, Nova Scotia. Warwick & Price (1975) give estimates of production for six major species of an estuarine inter-tidal *Macoma* community near the River Tamar, Cornwall, and they point out that production of total macrofauna has not been estimated anywhere.

Beukema (1974) reports on seasonal fluctuations in total inter-tidal faunal biomass in the Dutch Wadden Sea. He records a drop in autumn, a rise in spring, and a distinct summer level almost twice that of the winter level. The biomass drop in autumn and winter was brought about by a decline in both numbers of individuals and their masses; the severity of the European winter accounting for the decline. The increase in spring was predominantly due to growth of animals already present in winter. Recruitment and immigration were found to be important factors only if the preceding winter had been very severe.

The pattern of biomass fluctuation at Bottelary was similar to that at the Wadden Sea, except that the winter and summer levels had mean values which were not significantly different ($p > 0{,}01$). Although total biomass and numbers dropped during March–August 1974, the masses of individual animals increased (Fig. 4), i.e. growth occurred in autumn and winter. Total numbers also increased in August. This may have been due to recruitment or to immigration, but it is not possible to say which of these occurred. The increase in biomass due to growth of existing animals obscures any other trends which may have been present (e.g. a drop in individual mass which would indicate that recruitment and not immigration had taken place). The relatively low individual mass and the large increase in total numbers of individuals in September 1974 indicate that recruitment may have occurred then. Recruitment definitely occurred in January and February 1975, when the figures for individual mass were much lower concomitant with a large increase in total numbers of individuals. Many polychaetes, amphipods and decapods were observed carrying eggs during March–October; and the young could have entered the adult populations by February of the following year. Small nereids and orbiniids were observed in February and March, and masses of individual *Assiminea* and *Urothoe* were lowest in late summer–early autumn.

Distribution

Species diversity increases toward low water where the environment is less harsh and where habitat diversity is greater (Newell 1970; Eltringham 1971). At Bottelary, few species colonized the upper-shore levels (Fig. 2) but numbers and biomass at stations D and E were higher than at any of the lower-shore stations (Fig. 5). This was almost entirely due to the small hydrobiid gastropod *Assiminea*, which on one occasion (26 September 1974) had a density of 145 700 individuals per m². Boltt (1975) found varying densities of *Assiminea bifasciata* at Lake St Lucia in July 1972 and January 1973, the mean value being 119 600/m². *Hydrobia ulvae*, a similar Northern Hemisphere species, occurs at the Ythan estuary in densities between 60 000 and 110 000/m² (Milne & Dunnet 1972). The amphipod *Urothoe grimaldi* was numerically the most important crustacean at Bottelary. Densities of the similar Northern Hemisphere *Corophium volutator* varied widely between 22 and 4 397 per m² in various British estuaries (Barnes 1974); bivalves and polychaetes generally dominating the lower inter-tidal regions on sandy shores (Eltringham 1971). Day (1951), however, notes that bivalves are generally scarce in South African estuaries. Only *Carditella rugosa* and *Tellimya* sp. were found at Bottelary where they occurred sparingly; they ranged in size between 0,8 and 4,0 mm.

Production and P : B of Assiminea globulus *and* Urothoe grimaldi

Assiminea globulus may breed more than once a year at Langebaan, and *A. bifasciata* at Lake St Lucia may breed several times a year (Boltt 1975). *Hydrobia ulvae* breeds twice a year in May–June and February–March in the Clyde estuary (Hunter & Hunter 1962, in Green 1968). The species had two peaks of spawning activity in April–May and August–September in the Dovey estuary (Fish & Fish 1974). The P : B ratio for *Assiminea* at Langebaan is within the range found for other benthic marine organisms with a short life cycle (Burke & Mann 1974).

Apart from the December recruitment peak, *Urothoe grimaldi* probably reproduces at a low level during most of the year. Small numbers of juveniles entered the Langebaan population in April, August, October and February. Also, ovigerous females were observed in all months during April–November. The P : B ratio for *Urothoe* at Langebaan is low for an annual form and is closer to values obtained for animals living for two years or longer (Burke & Mann 1974). However, the value for production (Table 4) may be too low due to inadequate sampling.

Similarity analysis

Sediment characteristics appear to underlie the different faunistic groups shown here by classification and ordination (Figs 12 & 13). Benthic communities change in accordance with change in particle size and associated factors, particularly organic content which increases logarithmically with decrease in particle size (Newell 1970). This pattern is followed by the inter-tidal benthic communities at Langebaan. Table 10 shows that there were significant differences between sediment characteristics, especially the silt and clay fraction and the organic content, associated both with locality and with the stations grouped in the dendrogram.

The relatively high silt and clay fraction and organic content at stations with macrophytes presumably are a result of the sediment-trapping action of the macrophytes (Barnes 1974; Newell 1970). Driscoll (1975) found that the organic content of the sediment varied seasonally at Buzzard's Bay, in Massachusetts, and that this was related to temperature-dependent variation in the biomass of micro-organisms. Conceivably, micro-organism biomass is related to the amount of nutrients available. Dependent on all these factors would be the benthic biomass and that of deposit feeders in particular. The high proportion (nearly 90 %) of deposit feeders at Bottelary indicates the importance of detrital food sources to the benthic community and hence to higher trophic levels, especially fish and birds.

Marsh

The salt marshes at Langebaan cover an area of 13 km^2. *Arthrocnemum* covers 70 % of the total marsh area. The marsh supports a varied community of invertebrates including *Assiminea*, some Crustacea and insects whose mean biomass (Fig. 12) equals that of tidal-flat areas such as Schrywershoek. However, I used relatively crude collecting techniques (with respect to insects particularly), and insect biomass especially that of adults may be underestimated.

A feature of the marsh fauna, compared with that of the tidal flats, is its high content of epifauna. A few ephydrid pupae, amphipods and polychaetes were found in the substrate. The rest of the fauna is a very mobile surface-dwelling community. Paviour-Smith (1956) found that 94 % of the total number of animals sampled in a New Zealand salt marsh occurred within the top 10 mm of substrate.

Biomass peaks at Geelbek were mainly due to increased numbers of *Assiminea* and *Cleistostoma*. Increased numbers of *Assiminea* may have been due to recruitment or to immigration. The fact that very small (< 1 mm) snails were never found in the marshes, but only on the flats, suggests that movement into the marsh does take place as the animals become bigger and therefore better able to tolerate increased temperatures and exposure. The winter biomass peak at Bottelary marsh is due to increases in numbers of the amphipod *Orchestia capensis*; recruitment occurs during June–September.

The difference in mean biomass between Bottelary and Geelbek marshes is apparently due to the significantly smaller size of individual animals at Bottelary. This may be because the substrate at Geelbek is much finer and has a far higher organic content. The Bottelary substrate is composed of fairly clean, coarse sand. A second factor may be that Bottelary marsh is frequently disturbed by vehicles, sheep and cattle whose tracks destroy the *Arthrocnemum*. However, more representative and extensive sampling might show that marsh animals tend generally to be larger towards the head of the lagoon, where nitrates and phosphates are relatively high (Christie pers. comm.).

Biomass and numbers of invertebrates in pools of water in the marshes were relatively low. Species diversity was low; on average only three species occurred in each monthly sample (the amphipod *Orchestia capensis* and two dipteran larvae). The pool fauna is subjected to salinities as high as 84 ‰ (Herholdt 1975). Pools seldom were deeper than 12 cm, except at HWS. Temperatures of 29 °C were recorded. The combination of high temperature and salinity may stress the fauna during neap tides when pools remain stagnant for several consecutive days.

Adult dipterans were difficult to sample. However, fluctuations in biomass and numbers were correlated with the appearance of different species at different times. The autumn peak was linked with the appearance of ephydrids and agromyzids, the peak in spring with dolichopodids, and the summer peak with the same ephydrid species. In North Carolina, Davis & Gray (1966) found that several species of dolichopodids and ephydrids were abundant in spring and present in summer and autumn; they were erratic in occurrence and probably emerged in short-lived broods.

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Ms Gillian M. Puttick, Zoology Department, University of Cape Town, Rondebosch 7700.

Appendix 1

Checklist of benthic organisms including mean monthly biomass and numbers at Langebaan Lagoon

BOTTELARY	March 1974	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan. 1975	Feb.	March
Scoloplos johnstonei Day .	*1 381*	*2 755*	*1 907*	*1 507*	*1 012*	*1 095*	*2 072*	*1 130*	*1 578*	*1 625*	*910*	*1 389*	*1 601*
	2,34	7,76	5,89	5,92	4,05	4,40	10,45	3,05	5,77	5,83	1,56	5,78	14,83
Orbinia angrapequensis (Aug.)	*188*	*188*	*353*	*659*	*271*	*318*	*471*	*235*	*126*	*94*	*94*	*141*	*110*
	1,26	1,92	5,72	10,16	2,52	3,99	4,52	1,32	0,78	0,25	0,85	1,43	1,04
Glycera convoluta Kef. .		*47*	*71*	*47*	*70*	*50*	*94*	*70*	*70*	*70*	*141*	*96*	
		0,05	0,27	0,10	0,69	0,54	0,39	0,39	0,31	0,05	0,16	0,71	
Marphysa depressa (Schm.)	*140*	*95*	*70*	*94*							*45*	*140*	*70*
	2,36	1,90	0,52	0,73							0,01	0,10	0,04
Ceratonereis erythraensis	*870*	*220*	*801*	*283*	*675*	*530*	*140*	*424*	*122*	*165*	*188*	*235*	*204*
Fauvel	2,02	0,44	1,75	0,53	1,40	1,50	0,55	1,30	0,27	1,09	0,23	1,02	0,57
Prionospio sexoculata Aug.						*45*				*70*	*45*	*48*	
						0,01				0,02	0,04	0,02	
Lumbrinereis tetraura (Schm.)		*612*								*47*	*95*		
		0,33								0,02	0,01		
Telothelepus capensis Day .	*188*	*47*		*48*	*48*	*48*		*47*				*313*	*94*
	1,57	0,07		0,86	0,01	0,44		2,10				2,80	1,14
Cirriformia tentaculata		*212*	*71*	*79*	*188*	*126*	*94*	*157*	*48*	*188*	*140*	*306*	*140*
(Montagu) . . .		0,91	0,11	0,01	0,52	1,36	0,88	1,73	0,50	1,08	0,29	0,92	1,15
Notomastus laticereus Sars.	*518*	*436*	*188*	*267*	*165*	*106*	*110*	*165*	*188*	*306*	*140*	*377*	*70*
	0,40	0,90	0,12	0,23	0,10	0,22	0,22	0,31	0,84	0,96	0,09	0,28	0,04
Perinereis nuntia v. *vallata* Gr.	*188*											*377*	*140*
	0,22											2,77	0,84
Clymene sp.		*50*	*50*			*50*				*50*	*95*		
		0,05	0,47			0,14				0,09	0,40		
Paraonidae			*659*	*479*	*47*	*235*	*48*			*70*	*48*	*48*	
			0,63	0,56	0,01	0,09	0,02			0,02	0,04	0,02	
Turbonilla kraussi Clessin .											*47*		*47*
											0,08		0,10
Nassa speciosa Adams .	*47*										*50*		*50*
	0,11										0,14		0,17
Nassa kraussiana (Dunker)				*48*	*140*						*50*		*50*
				0,15	0,90						0,20		0,01
Coriandria cf. *gisia* . .	*2 778*			*48*							*2 166*	*1 083*	*1 270*
	0,28			0,01							0,22	0,11	0,13
Turritella capensis Krauss .	*47*	*140*	*140*	*188*	*140*	*283*	*48*			*94*		*48*	
	0,01	0,03	0,04	0,01	0,04	0,07	0,01			0,02		0,01	
Marginella capensis Krauss	*94*	*140*	*48*	*48*		*48*	*48*	*48*	*48*	*188*	*94*	*94*	*140*
	0,13	0,23	0,05	0,02		0,02	0,03	0,17	0,15	0,18	0,02	0,14	0,11

Littorina knysnaensis Philippi						*95*		*95*	*95*	*283*	*377*	*1 036*	*2 213*
						0,12		0,12	0,12	0,37	0,49	1,35	2,88
Assiminea globulus (Connolly)	*70 227*	*72 428*	*63 556*	*55 000*	*43 510*	*60 276*	*94 070*	*66 726*	*64 686*	*54 687*	*104 854*	*110 332*	*79 645*
	20,08	23,50	14,28	14,23	11,73	17,77	26,04	19,49	17,95	14,93	22,06	25,26	23,25
Siphonaria compressa n. sp. Allanson											*94*	*140*	*180*
											0,04	0,04	0,06
Tellimya sp.						*47*		*47*					
						0,16		0,01					
Nucula sp.	*140*					*47*		*94*					
	0,01					0,02		0,01					
Carditella rugosa Sow.	*330*	*188*	*330*	*94*	*424*	*377*	*377*	*320*	*235*	*565*	*235*	*471*	*1 271*
	0,04	0,02	0,09	0,01	0,16	0,15	0,13	0,08	0,06	0,16	0,07	0,12	0,34
Cylindroleberis ?galathea		*50*	*50*	*50*	*50*			*50*				*95*	
		0,05	0,01	0,01	0,02			0,05				0,12	
Gastrosaccus sp.			*140*	*235*	*95*		*353*						*50*
			0,17	0,13	0,16		0,10						0,04
Upogebia africana (Ortm.)		*50*	*50*	*50*	*50*		*71*	*78*	*50*	*59*	*50*	*50*	*50*
		0,94	2,11	0,11	0,55		0,40	0,33	0,20	0,46	0,06	1,20	0,41
Callianassa kraussi Steb.										*50*		*50*	
										0,24		0,17	
Cirolana hirtipes M. Edw.								*126*				*50*	*50*
								0,21				0,07	0,13
Exosphaeroma hyloecetes Brnrd.		*95*	*50*	*140*	*50*		*895*						
		0,17	0,06	0,44	0,18		1,23						
Paridotea ungulata (Pallas)								*50*		*50*			
								0,01		0,01			
Cymadusa filosa Sav.												*95*	
												0,08	
Paramoera capensis (Dana.)			*95*			*95*	*283*	*188*	*110*	*118*	*118*	*118*	*140*
			0,02			0,01	0,19	0,11	0,05	0,06	0,04	0,05	0,08
Ampelisca palmata Brnrd.				*50*				*50*			*50*		
				0,04				0,01			0,01		
Urothoe grimaldi Chevr.	*565*	*722*	*549*	*671*	*459*	*1 005*	*628*	*683*	*494*	*1 005*	*800*	*1 036*	*691*
	0,24	0,49	0,35	0,54	0,42	0,80	0,67	0,67	0,42	0,49	0,43	0,55	0,40
Cleistostoma edwardsii McLeay	*165*	*173*	*47*	*188*	*47*	*94*	*47*	*94*	*188*	*48*	*71*	*48*	*95*
	1,29	0,73	0,13	0,48	0,15	0,10	0,10	0,05	0,35	0,19	0,30	0,01	0,19
Hymenosoma orbiculare Desm.	*48*	*48*	*118*	*110*		*153*	*118*	*113*	*70*	*48*	*94*	*140*	*48*
	1,39	0,07	0,09	0,04		0,14	0,15	0,06	0,56	1,30	0,07	0,10	0,12
Cerebratulus fuscus McIntosh			*50*					*50*	*50*			*50*	*50*
			0,04					0,04	0,01				
Dolichopodid larvae					*235*							*50*	*50*
					0,08							0,03	0,09

Appendix 1 (*cont.*)

Checklist of benthic organisms including mean monthly biomass and numbers at Langebaan Lagoon

GEELBEK	March 1974	May	July	Sept.	Nov.	Jan. 1975
Scoloplos johnstonei Day	*95*	*283*			*140*	
	0,14	0,22			0,07	
Orbinia angrapequensis (Aug.)	*400*	*683*	*298*	*518*	*612*	*565*
	1,30	3,14	1,98	3,56	4,56	3,38
Glycera convoluta Kef.		*50*	*50*			
		0,34	0,60			
Marphysa depressa (Schm.)			*50*		*71*	*50*
			0,65		0,23	0,10
Ceratonereis erythraensis Fauvel	*259*	*267*	*1 412*	*600*	*800*	*283*
	0,55	2,76	3,04	1,45	1,98	0,28
Prionospio sexoculata Aug.					*71*	*188*
					0,01	0,04
Lumbrinereis tetraura (Schm.)	*3 296*	*2 096*	*377*	*188*	*424*	*283*
	0,56	1,56	0,19	0,08	0,12	0,09
Telothelepus capensis Day	*345*		*50*			
	5,20		0,02			
Cirriformia tentaculata (Montagu)		*400*	*2 378*	*1 354*	*1 507*	*706*
		2,12	19,55	5,80	6,51	1,13
Notomastus laticereus Sars	*377*	*259*	*6 247*	*2 272*	*377*	*706*
	0,23	0,08	3,10	1,32	0,10	0,11
Nephthys capensis Day					*140*	*90*
					0,14	0,03
Clymene sp.				*50*		
				0,40		
Cerebratulus fuscus McIntosh				*140*		
				0,31		
Turbonilla kraussi Clessin					*50*	
					0,03	
Littorina knysnaensis Philippi			*94*	*50*		
			0,12	0,03		
Nassa kraussiana (Dunker)			*94*	*235*	*50*	
			0,06	0,16	0,14	
Nassa speciosa Adams	*235*	*50*	*50*	*50*	*188*	*155*
	0,19	0,05	0,05	0,09	0,04	0,04
Turritella capensis Krauss	*95*		*94*	*50*		*50*
	0,03		0,02	0,02		0,01
Marginella capensis Krauss	*95*	*95*			*188*	
	0,05	0,07			0,03	
Assiminea spp.	*1 366*	*6 593*	*9 399*	*9 505*	*10 736*	*8 947*
	0,46	3,51	8,17	7,56	6,51	3,74
Siphonaria compressa n. sp. Allanson				*989*		
				1,30		
Nucula sp.	*408*	*235*	*800*	*283*	*1 844*	*2 435*
	0,09	0,14	0,30	0,41	0,33	0,62
Carditella rugosa Sow.	*314*	*188*			*188*	*612*
	0,05	0,13			0,14	0,23
Cylindroleberis ?galathea		*50*	*50*	*424*	*377*	*283*
		0,10	0,17	0,54	0,50	0,31
Upogebia africana (Ortm.)				*50*	*50*	
				0,01	0,05	
Hymenosoma orbiculare Desm.	*95*	*188*	*130*	*153*	*94*	*50*
	0,21	0,18	0,35	0,56	0,39	0,16

Cleistostoma edwardsii McLeay . . .	*220*	*188*	*122*	*71*	*471*	*82*
	2,54	1,81	1,65	1,46	2,82	0,94
Paramoera capensis (Dana.)		*50*	*408*	*118*	*330*	*50*
		0,01	0,11	0,03	0,03	0,01
Melita zeylanica Stebb.			*140*	*800*	*283*	*188*
			0,12	0,80	0,23	0,08
Ampelisca palmata Brnrd.	*4 897*	*283*	*690*	*2 613*	*377*	*71*
	1,73	0,12	0,28	1,53	0,85	0,03
Urothoe grimaldi Chevr.			*95*	*377*		*50*
			0,05	0,09		0,02
Exosphaeroma hyloecetes Brnrd. . . .		*95*	*140*	*247*	*589*	*424*
		0,01	0,66	0,68	0,47	1,05
Chironomid larvae			*424*		*140*	*140*
			0,20		0,10	0,02
Dolichopodid larvae			*140*	*235*		*50*
			0,31	0,14		0,02
SCHRYWERSHOEK						
Scoloplos johnstonei Day	*2 166*	*763*	*1 149*	*2 166*	*1 698*	*1 912*
	1,89	2,50	3,52	5,99	3,02	4,09
Orbinia angrapequensis (Aug.)	*358*	*494*	*200*	*235*	*106*	*574*
	2,05	4,93	2,75	0,59	0,47	3,15
Glycera convoluta Kef.	*94*		*50*		*50*	*45*
	0,04		0,03		0,25	0,30
Marphysa depressa (Schm.)				*50*		*45*
				0,09		0,08
Ceratonereis erythraensis Fauvel . . .	*1 035*	*235*	*173*	*365*	*113*	*485*
	0,53	0,59	0,31	1,26	0,42	0.38
Lumbrinereis tetraura (Schm.)	*2 425*	*1 271*	*424*	*1 680*	*1 613*	*1 200*
	0,98	0,61	0,22	0,78	0,08	0,45
Teleothelepus capensis Day	*94*			*50*		
	0,01			0,31		
Cirriformia tentaculata (Montagu) . . .		*2 119*	*50*	*1 742*	*220*	*212*
		6,28	0,20	6,04	0,45	0,28
Notomastus laticereus Sars	*659*	*848*	*753*	*584*	*306*	*812*
	0,28	1,24	1,28	1,32	0,42	0,34
Nephthys capensis Day				*50*		
				0,30		
Perinereis nuntia v. *vallata*						*78*
						0,20
Clymene sp.	*188*	*79*	*188*	*283*	*118*	*71*
	0,24	0,66	1,10	0,38	0,66	0,24
Paraonidae			*518*			*267*
			0,24			0,04
Cerebratulus fuscus McIntosh			*188*			*283*
			0,03			0,18
Balanoglossus capensis Gilchrist . . .	*377*	*1 695*	*165*	*50*	*118*	*283*
	2,53	9,05	0,50	0,32	1,23	1,99
Marginella capensis Krauss	*94*		*50*		*50*	*82*
	0,09		0,06		0,03	0,08
Turritella capensis Krauss		*50*				
		0,03				
Nassa kraussiana (Dunker)		*50*	*50*	*50*		*45*
		0,16	0,09	0,04		0,04
Nucula sp.	*989*	*499*	*965*	*2 637*	*1 130*	*1 516*
	0,31	0,14	0,36	0,64	0,28	0,35
Tellimya sp.				*71*	*45*	*95*
				0,01	0,01	0,03
Carditella rugosa Sow.	*188*		*330*	*235*	*59*	*188*
	0,20		0,09	0,07	0,03	0,11

Appendix 1 (*cont.*)

Checklist of benthic organisms including mean monthly biomass and numbers at Langebaan Lagoon

	March 1974	May	July	Sept.	Nov.	Jan. 1975
Cylindroleberis ?galathea		*188* 0,59	*188* 0,39	*94* 0,10	*94* 0,11	*165* 0,07
Gastrosaccus sp.		*140* 0,16	*95* 0,17			*48* 0,08
Upogebia africana (Ortm.)	*94* 0,42			*94* 0,02	*50* 0,02	*45* 0,02
Exosphaeroma hyloecetes Brnrd.		*235* 1,01	*95* 0,11		*565* 0,40	*50* 0,04
Leptanthura laevigata (Stimps.)				*50* 0,04	*50* 0,05	
Palaemon pacificus (Stimps.)					*50* 0,03	
Hymenosoma orbiculare Desm.		*50* 0,01	*118* 0,18	*118* 0,25	*48* 0,11	*78* 0,14
Cleistostoma edwardsii McLeay	*94* 0,39	*71* 0,60	*94* 1,78	*188* 0,40	*235* 0,26	*45* 0,17
Paramoera capensis (Dana.)	*424* 0,15	*306* 0,05		*71* 0,07	*471* 0,11	*61* 0,01
Ampelisca palmata Brnrd.		*565* 0,27	*235* 0,14	*50* 0,02		
Lysianassa ceratina (Wlkr.)						*94* 0,01
Urothoe grimaldi Chevr.			*330* 0,14	*848* 0,29	*283* 0,08	*283* 0,04
Pycnogonida					*50* 0,04	
RIETBAAI						
Scoloplos johnstonei Day	*188* 0,18	*190* 0,13	*50* 0,23	*659* 1,75	*141* 0,41	
Orbinia angrapequensis (Aug.)	*424* 1,86	*184* 2,10	*235* 2,35	*292* 3,40	*593* 2,73	*259* 1,15
Glycera convoluta Kef.	*95* 0,18	*80* 0,57	*50* 2,64	*79* 0,49	*82* 0,15	*71* 0,08
Ceratonereis erythraensis Fauvel	*612* 1,42	*294* 2,04	*318* 2,02	*173* 0,54	*251* 0,34	*2 227* 2,27
Prionospio sexoculata Aug.					*129* 0,06	*188* 0,04
Lumbrinereis tetraura (Schm.)	*188* 0,07		*94* 0,29			
Telothelepus capensis Day	*95* 1,39	*59* 1,39	*50* 0,08		*71* 2,59	
Cirriformia tentaculata (Montagu)		*90* 0,44	*283* 1,76	*188* 0,51	*165* 0,64	*730* 1,45
Notomastus laticereus Sars	*283* 0,02	*110* 0,03	*188* 0,06	*212* 0,06	*353* 0,13	*659* 0,18
Clymene sp.	*95* 1,48	*118* 0,38	*94* 0,17	*129* 0,30	*82* 0,21	*50* 0,12
Paraonidae			*330* 0,38			
Ochaetostoma capense Stephen					*50* 0,09	
Balanoglossus capensis Gilchrist		*2 778* 21,58	*2 967* 24,38	*50* 0,02	*989* 11,12	*212* 2,09

Turritella capensis Krauss	*140*	*71*	*50*		*50*	
	0,10	0,06	0,01		0,01	
Assiminea isosceles (Connelly)	*2 998*	*14 080*	*8 005*	*11 443*	*7 464*	*31 268*
	1,05	5,22	4,43	6,19	4,50	5,95
Marginella capensis Krauss	*95*	*88*	*169*	*132*	*335*	*235*
	0,07	0,04	0,32	0,08	0,09	0,19
Littorina knysnaensis Philippi				*118*		
				0,05		
Nassa kraussiana (Dunker)			*50*	*50*		
			0,05	0,04		
Nassa speciosa Adams			*50*		*50*	*50*
			0,06		0,04	0,04
Siphonaria compressa n. sp. Allanson						*95*
						0,02
Nucula sp.	*848*	*424*	*541*	*1 248*	*470*	*695*
	0,57	0,18	0,20	0,19	0,24	0,24
Tellimya sp.	*330*		*800*	*447*	*94*	*565*
	0,18		0,51	0,12	0,03	0,12
Carditella rugosa Sow.	*95*	*140*	*94*	*79*	*95*	
	0,06	0,08	0,05	0,13	0,05	
Cylindroleberis ?galathea			*188*	*188*	*108*	*71*
			0,37	0,38	0,24	0,10
Upogebia africana (Ortm.)				*94*		
				0,02		
Nebalia capensis Brnrd.		*141*	*377*	*50*	*50*	
		0,08	0,11	0,01	0,14	
Paridotea ungulata (Pallas)			*50*			
			0,35			
Cirolana hirtipes M. Edw.				*71*	*50*	*94*
				0,15	0,25	0,12
Ampelisca palmata Brnrd.	*95*	*71*	*235*		*94*	
	0,01	0,06	0,21		0,02	
Urothoe grimaldi Chevr.	*659*	*188*	*753*	*424*	*188*	*94*
	0,41	0,10	0,32	0,23	0,10	0,03
Cymadusa filosa Sav.						*188*
						0,42
Paramoera capensis (Dana.)					*155*	*50*
					0,05	0,02
Cleistostoma edwardsii McLeay	*235*	*110*	*267*	*259*	*165*	*283*
	0,42	1,46	4,18	1,13	1,00	0,77
Hymenosoma orbiculare Desm.		*50*	*224*	*71*	*50*	*71*
		0,01	1,13	0,49	0,38	0,07
Dolichopodid larvae		*188*	*306*		*95*	*126*
		0,50	0,20		0,23	0,05

Appendix 2

Animals smaller than 1 mm in body length (all were *Assiminea globulus*) as a proportion of the total inter-tidal benthos at Bottelary. All figures are percentages

Month	Total number of *Assiminea* at Stns C, D and E	Total mass of *Assiminea* at Stns C, D and E	Total number of organisms sampled	Total mass of organisms sampled
September	—	—	0	—
October	—	—	0	—
November	0,29	0,004	0,28	0,004
December	0,75	0,005	0,69	0,004
January	34,1	0,02	32,37	0,021
February	26,2	0,017	25,04	0,013
March	19,1	0,02	17,67	0,012

Appendix 3

Biomass (g/m²) of invertebrates at individual stations at Geelbek, Rietbaai and Schrywershoek

Station		March 1974	May	July	Sept.	Nov.	Jan. 1975
Geelbek	A	8,56	6,69	6,79	17,11	6,89	9,48
	B	7,73	6,29	4,34	3,38	7,12	4,93
	C	6,93	6,01	17,49	13,25	6,36	2,82
	D	22,75	17,73	58,74	33,18	17,40	10,10
	E	3,34	4,90	13,45	7,42	7,49	8,30
Rietbaai	A	8,49	25,93	36,40	9,29	15,61	2,95
	B	4,75	23,92	5,04	10,97	5,53	7,17
	C	11,59	6,55	16,73	6,17	10,55	6,93
	D	19,21	9,88	8,42	8,72	7,42	5,47
	E	6,62	22,58	33,75	21,83	12,80	13,55
Schrywershoek	A	25,89	13,50	8,56	12,56	11,47	7,12
	B	13,14	3,32	8,08	12,46	4,70	10,15
	C	9,82	13,51	6,92	8,88	4,81	4,77
	D	9,49	17,28	5,45	8,64	6,58	11,80
	E	7,82	23,48	16,67	32,04	6,63	14,85

PART 2

The diet of the curlew sandpiper at Langebaan Lagoon, South Africa

THE DIET OF THE CURLEW SANDPIPER AT LANGEBAAN LAGOON, SOUTH AFRICA

GILLIAN M. PUTTICK

Received April 1978

SUMMARY

PUTTICK, G. M. 1978. The diet of the Curlew Sandpiper at Langebaan Lagoon, South Africa. *Ostrich* 49:158–167.
Nereid worms (mainly *Ceratonereis erythraensis*) and the hydrobiid gastropod *Assiminea globulus* were the most important prey items throughout the year for Curlew Sandpipers *Calidris ferruginea* feeding at Langebaan Lagoon. Other important items were the amphipod *Urothoe grimaldi*, the crabs *Hymenosoma orbiculare* and *Cleistostoma edwardsii* and dipteran larvae (Stratiomyidae). Immature Curlew Sandpipers took smaller prey items than adult birds. The diet of male and female birds differed in the proportion, size and range of prey items taken.

INTRODUCTION

The Curlew Sandpiper *Calidris ferruginea* is the most abundant Palaearctic migrant at Langebaan Lagoon (33S; 18E) (Pringle & Cooper 1975). The food potentially available to Curlew Sandpipers at Langebaan has been described (Puttick 1977). This paper describes seasonal changes in the diet of Curlew Sandpipers feeding in the intertidal sandflats and marshes at Langebaan, and includes a comparison of food taken by male and female, and immature and adult birds.

MATERIALS AND METHODS

Data collection

At least 20 Curlew Sandpipers were shot at Bottelary (Fig. 1) each month from February 1974 to March 1975. Totals of 57 and 191 birds were shot while feeding in the marshes and on the sandflats respectively. I considered a sample size of 20 birds per month to be adequate, since increasing it to 40 birds increased the number of new prey items represented by only five items.

The birds were weighed immediately after being shot. The oesophagus and stomach of each bird were injected with 1 ml of 10% formalin to halt digestion, and the birds were deep frozen. In the laboratory, the sex and moult of each bird were recorded. The contents of the stomach and oesophagus were removed and preserved separately in 70% alcohol. Whole food organisms excluding insects were identified to species level. Insects were identified to family level, based on Usinger (1956). The size of prey organisms was determined (Table 1). The body lengths of all remaining prey organisms in each sample were determined from identified fragments whose size relationship to body length had been separately determined from whole items. All organisms were counted except for unrecognizable material which generally comprised less than 5% by mass of the total food sample. The mass of each food organism was determined from length-mass regression equations (Puttick 1977). A portion of each food sample was examined microscopically under phase contrast to determine whether the setae of orbiniid worms were present since these worms did not leave any macroscopic remains, and they are the most abundant polychaetes in the substrate (Puttick 1977).

Spring was taken as September, October, November; summer as December, January, February; autumn as March, April, May; and winter as June, July, August.

Data analysis

Ashmole & Ashmole (1967) review desirable methods of analyzing the food of birds. In the present study, the stomach and oesophagus contents were analyzed separately by number, mass and frequency of occurrence. Mass and number of each food item in each food sample were expressed as percentages of the total mass and number of items. Frequency of occurrence was expressed as the percentage of food samples in which the item was recorded. The size frequency distribution of the commonest food items was determined. Gravimetric analysis gives an indication of the size of food items and is perhaps the most important method (Ashmole & Ashmole 1967) since it provides a basis for estimating absolute quantities of energy ingested by the birds. Numerical analysis

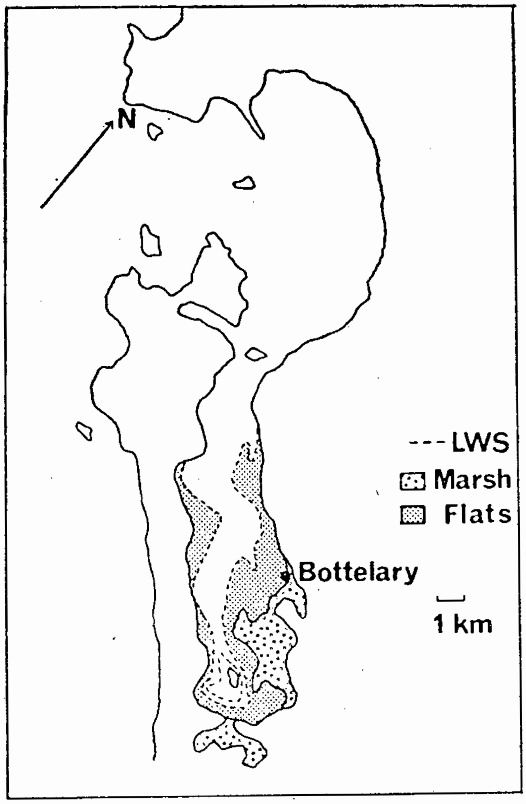

FIGURE 1.
Langebaan Lagoon, showing study area.

TABLE 1

MEASUREMENTS USED FOR DETERMINATION OF PREY SIZE FROM FOOD ITEMS FOUND IN CURLEW SANDPIPER STOMACH AND OESOPHAGUS SAMPLES

Prey item	Measurement
Gastropods	Base to tip of whorl
Amphipods	Base of first antenna to tip of telson
Crabs	Rostrum to posterior edge of cephalothorax
Bivalves	Across shortest length of valve from hinge line
Polychaetes	Jaw length

gives an indication of the abundance of food objects but it also tends to emphasize those items with hard parts resistant to digestion (polychaete jaws, mollusc shells). Frequency of occurrence gives the proportion of food samples in which each food item is present and therefore indicates the availability of food items and their degree of selection by the birds.

There are many uncontrollable variables inherent in food studies. King & Ikehara (1956) point out that the results of food studies are generally not suitable for statistical analysis. However, some of the data reported here lend themselves to non-parametric statistical tests in which underlying assumptions are less rigorous (Siegel 1956).

RESULTS

Seasonal differences in diet

Nereid worms (mainly *Ceratonereis erythraensis*), the gastropod *Assiminea globulus*, the amphipod *Urothoe grimaldi* and the crabs *Cleistostoma edwardsii* and *Hymenosoma orbiculare* were the main prey items in the diet of Curlew Sandpipers feeding on the sandflats. The worms and gastropods were important items throughout the year according to all three methods of analysis (Fig. 2). The importance of Crustacea was emphasized by frequency of occurrence. The category "other" comprised the undigested remains of marsh organisms presumably from a previous "meal" and

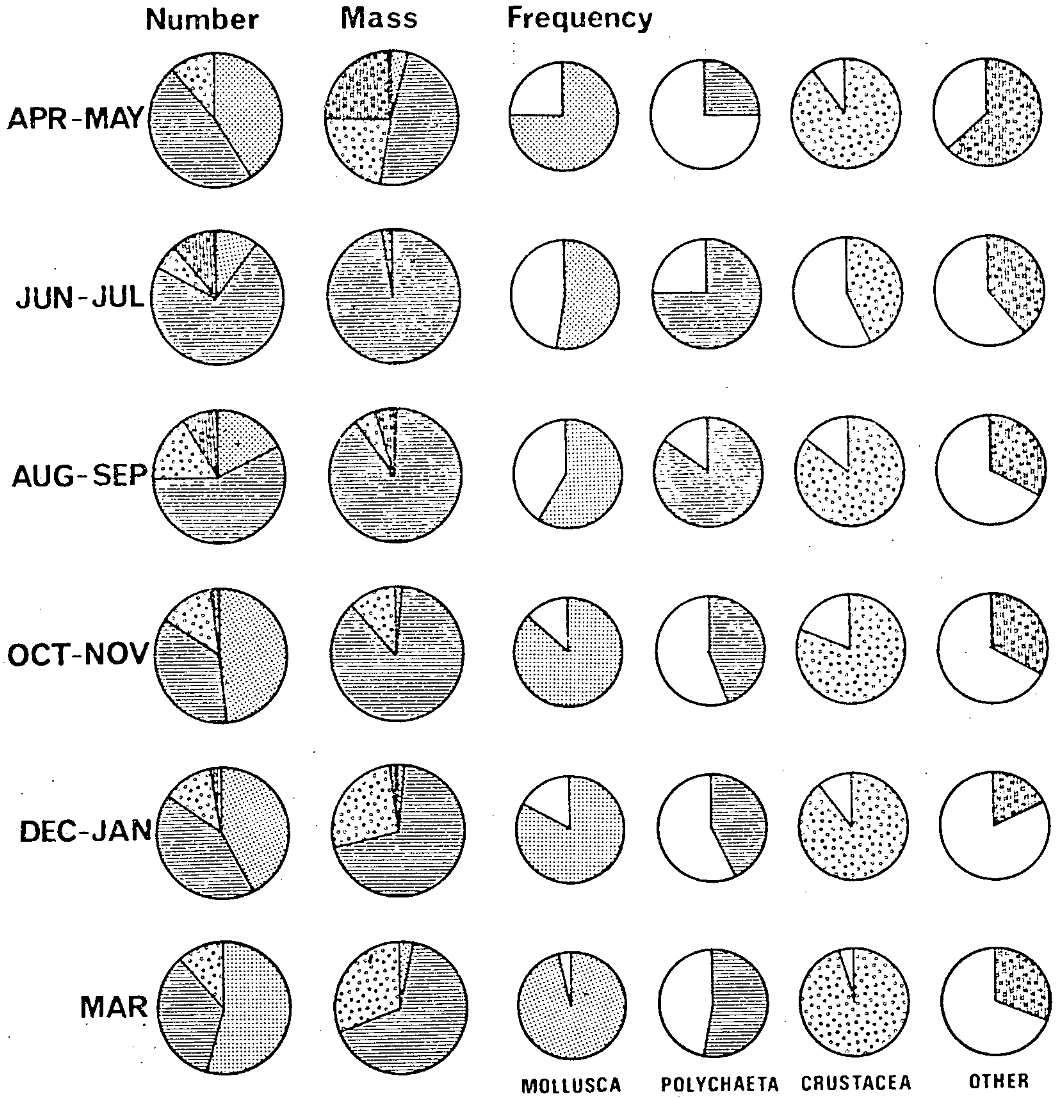

FIGURE 2

Seasonal change in the diet of Curlew Sandpipers collected while feeding on sandflats. Major prey categories are represented as per cent by number, mass and frequency of occurrence. A full circle represents 100%.

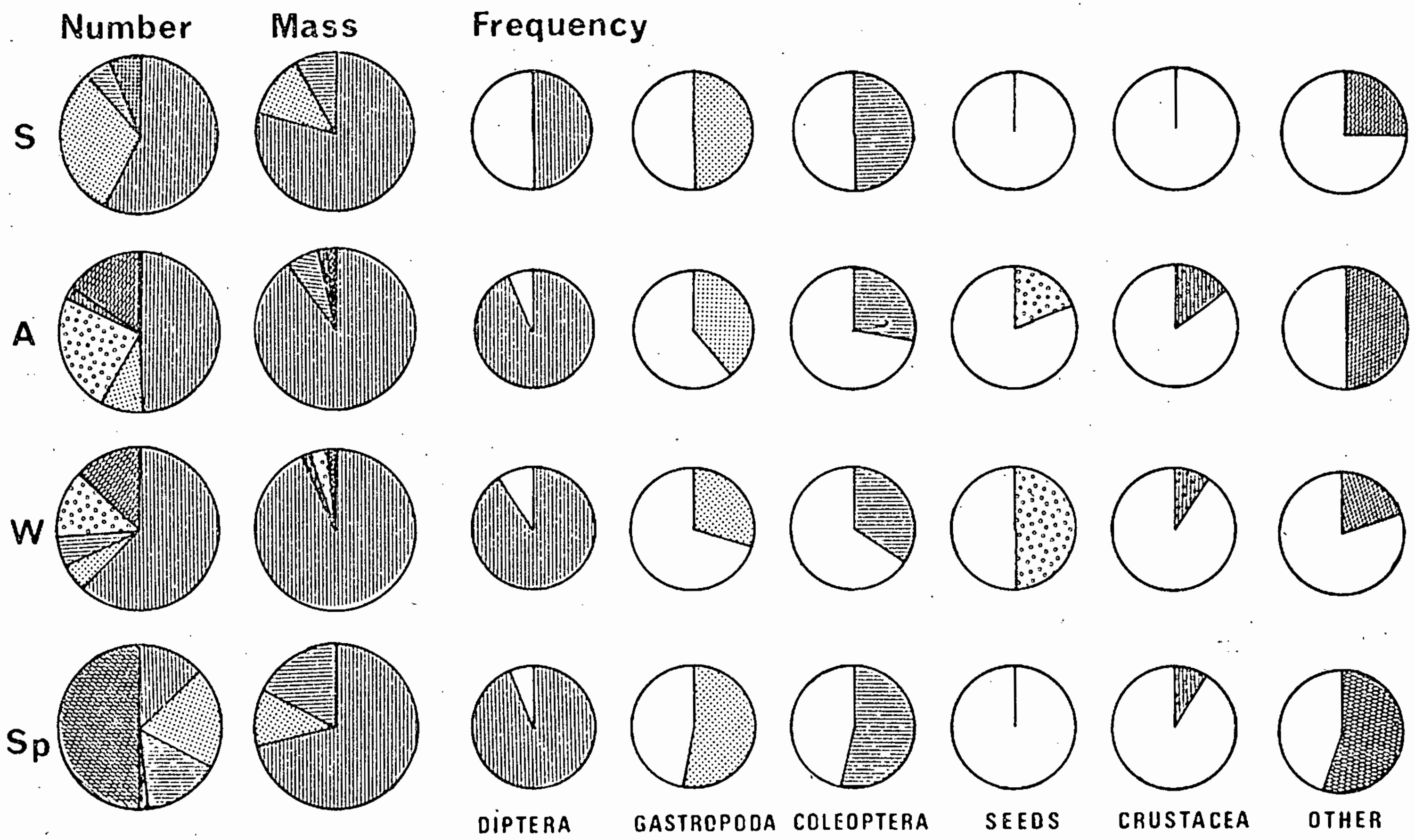

FIGURE 3

Seasonal change in the diet of Curlew Sandpipers collected while feeding in marshes. Major prey categories are represented as per cent by number, mass and frequency of occurrence. A full circle represents 100%. S = summer, A = autumn, W = winter, Sp = spring.

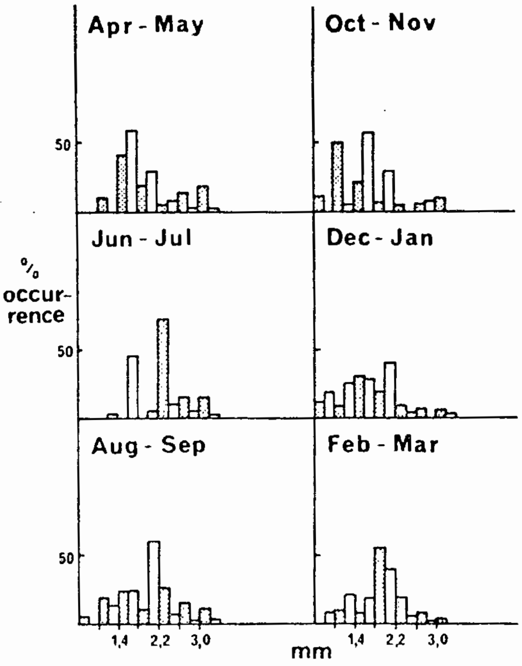

FIGURE 4

Comparison of sizes of *Assiminea* taken by Curlew Sandpipers (shaded) and those available (unshaded) during April 1974 – March 1975.

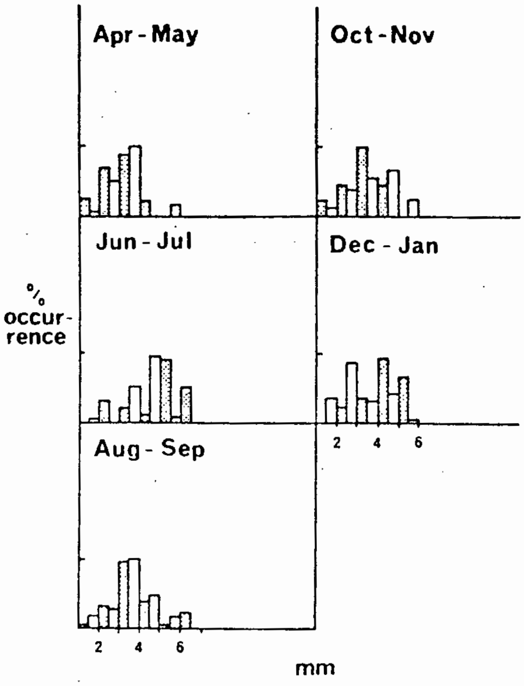

FIGURE 5

Comparison of sizes of *Urothoe* taken by Curlew Sandpipers (shaded) and those available (unshaded) during April 1974 – March 1975.

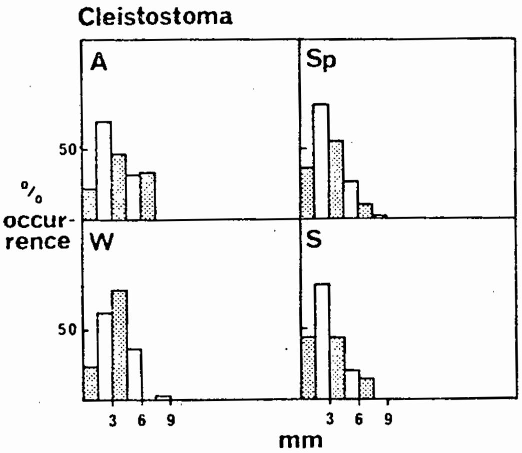

FIGURE 6

Comparison of sizes of *Cleistostoma* taken by Curlew Sandpipers (shaded) and those available (unshaded) during autumn (A) winter (W) spring (Sp) and summer (S).

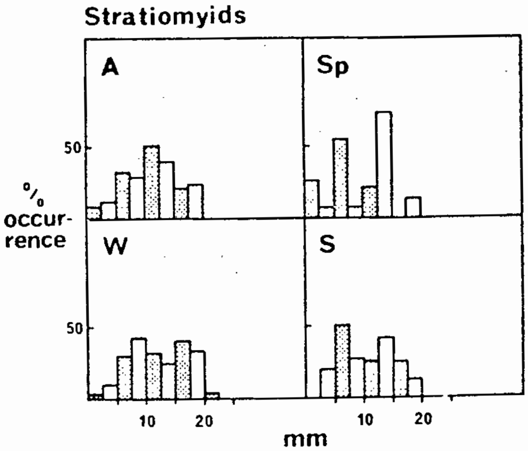

FIGURE 7

Comparison of sizes of stratiomyid larvae taken by Curlew Sandpipers (shaded) and those available (unshaded) during autumn (A) winter (W) spring (Sp) and summer (S).

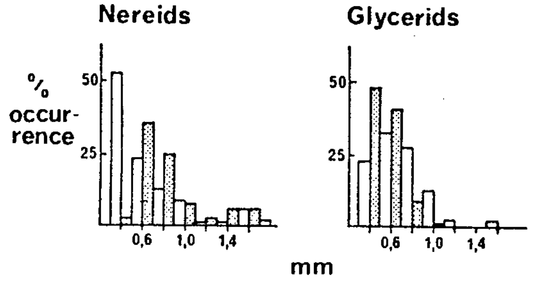

FIGURE 8

Comparison of sizes of nereids and glycerids taken by Curlew Sandpipers (shaded) and those available (unshaded) during January – December 1974.

hence did not feature prominently in number and mass. The proportion of polychaetes in the diet rose in winter and spring while that of molluscs dropped. The proportion of crustaceans increased in spring and early summer (Fig. 2). Together, polychaetes, gastropods and crustaceans comprised over 60% of the diet in gravimetric and numerical analyses. However, the remaining 40% of the diet was highly heterogeneous.

Dipterans (mainly stratiomyid larvae) and hydrobiid gastropods were the most important food categories taken by birds feeding on the marshes throughout the year (Fig. 3). *Salicornia* seeds apparently formed a supplement to the diet in autumn and winter.

Chi-square contingency tables showed that the seasonal changes in the proportion of objects present in each food category were significant ($p < 0,001$) both in the flats and marsh samples, while the frequency of occurrence analysis did not show statistically significant differences. Mass was not analyzed in the same way because the *chi*-square test can be used only for comparing frequencies.

The sizes of food items taken by the birds, except for those of stratiomyids, differed significantly ($p < 0,001$) from those potentially available (Figs 4–8). The birds selected bigger *Assiminea* and *Urothoe* in winter and bigger *Cleistostoma*, nereids and glycerids throughout the year. However, they appear to have taken whatever size stratiomyid larvae were available. About 80% of all prey objects taken were bigger than 1,5 mm (except *Assiminea* in spring when most available were small (Puttick 1977)).

Comparison of oesophagus and stomach samples

A comparison of oesophagus and stomach contents showed that crustaceans (mainly *Urothoe grimaldi*) were under-represented in stomach samples in the numerical analysis but not in frequency of occurrence (Fig. 9), while molluscs and polychaetes were over-represented. Crustacea (mainly

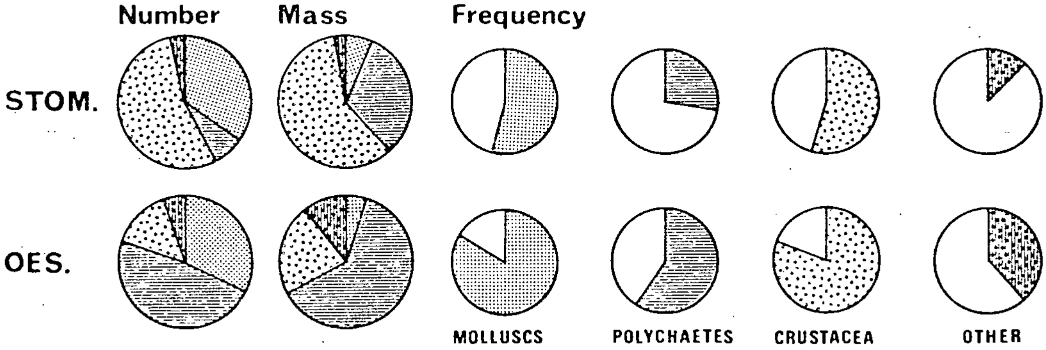

FIGURE 9

Proportion of food categories in the stomachs and oesophagi of adult and male and female Curlew Sandpipers collected while feeding on sandflats, represented as per cent by number, mass and frequency of occurrence. A full circle represents 100%.

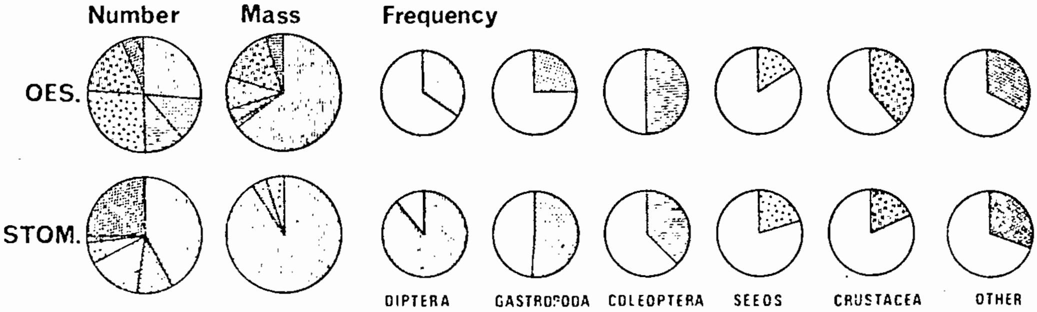

FIGURE 10

Proportion of food categories in the stomachs and oesophagi of adult male and female Curlew Sandpipers collected while feeding in marshes, represented as per cent by number, mass and frequency of occurrence. A full circle represents 100%.

Austrochiltonia capensis) were also under-represented in the stomach contents of birds shot while feeding on the marshes (Fig. 10).

Diet of immature and adult Curlew Sandpipers

The diet of first-year, second-year and adult birds did not differ significantly in the proportion of food objects taken on the flats (Fig. 11). However, immatures (first-year and second-year birds combined) selected a slightly higher proportion of smaller *Assiminea*, *Nucula* and *Urothoe* (Fig. 12).

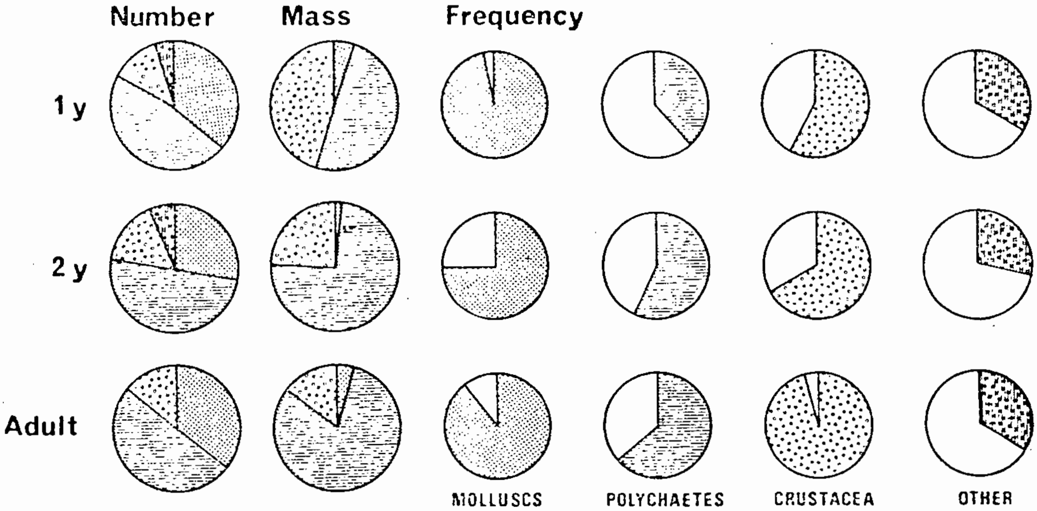

FIGURE 11

Proportion of food categories in the diet of first-year, second-year and adult birds collected while feeding on sandflats, represented as per cent by number, mass and frequency of occurrence. A full circle represents 100%.

Diet of male and female Curlew Sandpipers

The diet of male and female birds differed significantly ($p < 0{,}001$) in the proportion of objects in each food category (Fig. 13). Males had almost double the number of gastropods and not as many of the other categories. The proportion of "other" items was smaller in the diet of females.

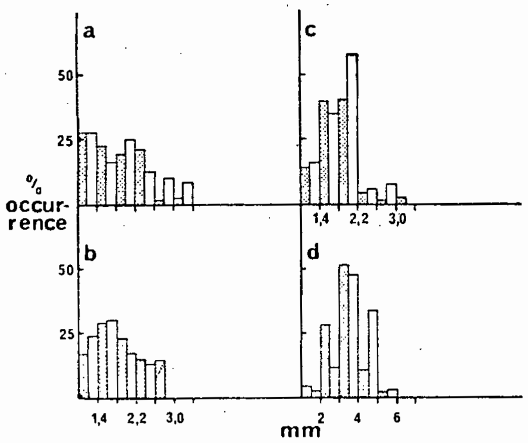

FIGURE 12

Comparison of sizes of (a) *Assiminea* (b) *Marginella* (c) *Nucula* and (d) *Urothoe* taken by immature (shaded) and adult (unshaded) Curlew Sandpipers.

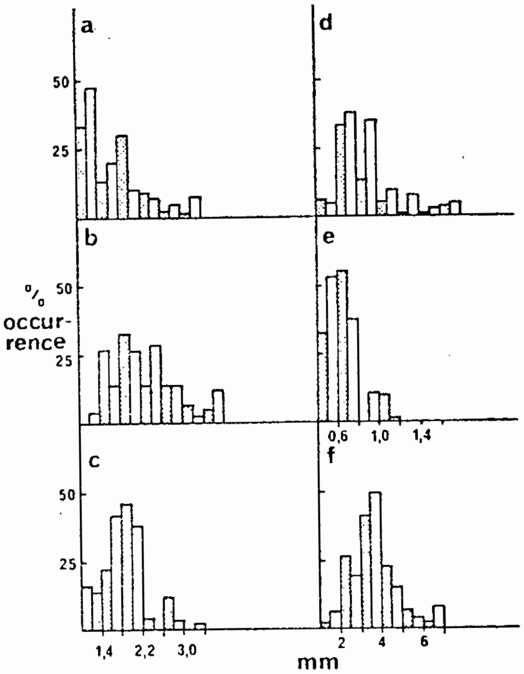

FIGURE 14

Comparison of sizes of (a) *Assiminea* (b) *Marginella* (c) *Nucula* (d) nereids (jaws) (e) glycerids (jaws) and (f) *Urothoe* taken by male (shaded) and female (unshaded) Curlew Sandpipers.

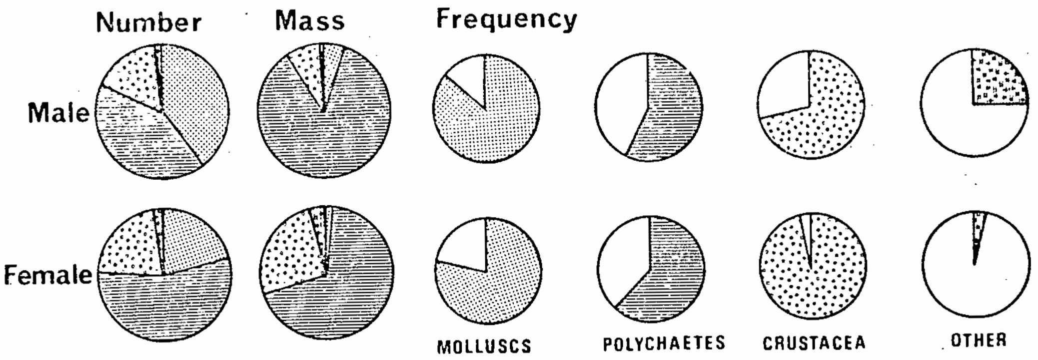

FIGURE 13

Proportion of food categories in the diet of male and female Curlew Sandpipers collected while feeding on sandflats, represented as per cent by number, mass and frequency of occurrence. A full circle represents 100%.

A comparison of individual prey items taken by males and females showed that they took significantly different proportions of *Assiminea*, *Marginella*, *Nucula*, nereids and glycerids, and *Urothoe* (p < 0,01) (Fig. 14). Males selected a slightly higher proportion of larger *Assiminea*, *Nucula*, nereids and glycerids. Females took a wider range of *Assiminea*, *Marginella*, *Nucula* and *Urothoe* (Fig. 14).

DISCUSSION

Seasonal differences in diet

Assiminea globulus occurred in large numbers in the upper region of the sandflats at Langebaan Lagoon and was available through nearly the whole tidal cycle (Puttick 1977). *Assiminea* was one of the most important food items in the diet of Curlew Sandpipers throughout the year. Orbiniids, then nereids, were the most abundant polychaete worms on the shore. I expected orbiniids to have been the most abundant polychaetes in the diet of the Curlew Sandpiper, on the basis of their abundance in the substrate, but apparently they were not available to the birds. Some information is available on the behaviour of intertidal benthic organisms in the northern hemisphere (Vader 1964; Goss-Custard 1969; Newell 1962), but very little is known about the behaviour of intertidal organisms occurring on sandy shores in southern Africa. Consequently, the effect that their behaviour may have on their availability to wading birds at Langebaan is unknown. The polychaetes taken by Curlew Sandpipers (nereids, glycerids and *Marphysa* sp.) are mostly predators. They may be more active in the substrate than the sedentary orbiniids and hence more "conspicuous". However, their chitinous jaws are resistant to digestion and this probably partly accounts for their relative abundance in the stomach samples. The crustaceans represented in the diet are also fairly mobile animals. Their lower abundance in the stomach samples can presumably be related to the fact that they have no resistant parts such as jaws or shells and so were quickly digested.

Temporal variation in the size and abundance of prey items affected the diet of the birds. The proportion of *Assiminea* taken by Curlew Sandpipers dropped in spring, while more polychaetes and crustaceans were taken. Although *Assiminea* was more abundant in spring, the snails available then were relatively small (Puttick 1977). Why do Curlew Sandpipers feed on larger organisms instead of many small ones? Although a burrowing worm may be more difficult to capture than a snail available on the surface, it is larger, has no indigestible shell and may represent a greater intake of energy per item taken. In winter, the birds may have required a higher return for energy expended because of increased energy demands and fewer hours available for feeding. This may be why the proportion of worms taken by Curlew Sandpipers in winter was higher and that of snails lower.

The incidence of dipteran larvae and *Assiminea* in the diet of birds feeding in the marshes is related to the availability of these items which were present throughout the year in the marsh (Puttick 1977). Also, seeds of *Salicornia* sp. were important dietary items in autumn and early winter when they were abundantly available (pers. obs.), and they may have been an important energy subsidy for birds increasing their pre-migratory fat load. Many insectivorous birds change from a protein-rich to a carbohydrate-rich diet before migration by selecting berries, fruits and seeds (Berthold 1975).

Curlew Sandpipers selected objects within a limited size range, regardless of relative fluctuations in sizes available. The upper size limit may be set by two factors. First, feeding morphology must limit the largest size of prey the bird can manipulate. Second, there must be a maximum handling time which an efficient predator will not exceed by trying to manipulate and swallow an item which is too large. The lower size limit of prey taken may be set by some minimum energy return. 96,6% of all *Corophium volutator* taken by Redshanks at Ythan were larger than 4 mm (Goss-Custard 1969). Curlew Sandpipers also avoid extremely small prey items, presumably because they are not worth the energy expended in capturing them. In most cases, they did not take the most abundant size classes available but selected the larger sizes although these were less abundant. Oystercatchers *Haematopus ostralegus* and Rock Pipits *Anthus spinoletta* take larger prey sizes than those most commonly available (Norton-Griffiths 1967; Gibb 1956). Oystercatchers take smaller cockles later in winter when cockle stocks are depleted (O'Connor & Brown 1977).

Diet related to age and sex

It is difficult to explain why immature Curlew Sandpipers took a higher proportion of smaller prey items than adult birds did. Adult Royal Terns *Sterna maxima*, Brown Pelicans *Pelecanus occidentalis*, and Blue Herons *Florida caerulea* feed more efficiently than immatures of the same species (Buckley & Buckley 1974; Orians 1969; Recher & Recher 1969). Qualitative differences exist in the diet of immature and adult Cattle Egrets *Ardeola ibis* (Siegfried 1972). The immatures take a slightly greater variety of food items. Immature Curlew Sandpipers may not yet have learnt to select larger prey items more consistently.

Female Curlew Sandpipers are bigger than males and have longer bills (Thomas & Dartnall 1971; Elliott *et al.* 1976). Sexual dimorphism in feeding apparatus reduces competition for food resources (Pianka 1974). Smith & Evans (1973) found that female Bartailed Godwits *Limosa lapponica* were more successful feeding in shallow water than the smaller males of that species. Females also took slightly larger size classes of prey than males. Female Curlew Sandpipers exploit a slightly different food spectrum from males by taking a wider range of prey sizes and a less diverse range of prey items. They may also improve their feeding efficiency by taking more crustaceans and worms, from which the energetic "reward" per item is higher.

ACKNOWLEDGMENTS

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Ms. G. M. Puttick, Percy Fitzpatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7700, South Africa.

PART 3

Foraging behaviour and activity budgets of curlew sandpipers

SUMMARY

The foraging and the daily and seasonal activity of curlew sandpipers _Calidris ferruginea_ at Langebaan Lagoon, South Africa, are described.

Curlew sandpipers spent 55-65% of daylight hours foraging in spring and summer, and up to 80% foraging in winter. They foraged on the intertidal sandflats when these were exposed. At high water in spring and summer they roosted on the adjacent marshes; in autumn and winter they fed there at high water. The birds foraged faster in autumn and winter than in spring and summer. Their foraging efficiency also increased in autumn, enabling them to accumulate fat reserves for migration in mid-April. Immature birds foraged more slowly and less successfully than adult birds. This possibly explains why immatures do not return to the breeding areas in their first year. The birds' foraging diversity was greatest in spring and winter, the former when prey density was relatively high and the latter when prey density was lower. Different foraging rates were associated with differences in microhabitat; this appeared to be a function of the foraging technique used. Foraging was faster but success rate lower on incoming tides. Foraging and success rates decreased progressively from the upper to the lower shore, related to the density and potential availability of prey.

INTRODUCTION

Langebaan Lagoon (33^{o}S, 18^{o}E) supports between 37 000 and 55 000 waders (Charadrii) during the austral summer (Pringle & Cooper 1975, Summers 1977). The curlew sandpiper *Calidris ferruginea* is the most abundant species, accounting for nearly two-thirds of the total wader population.

Very little information on the feeding ecology and daily and seasonal activity budgets of waders in southern Africa is available. Information on the food potentially available to curlew sandpipers at Langebaan, and their diet while feeding there, has been published elsewhere (Parts 1 and 2). This paper describes the foraging and the daily and seasonal activities of curlew sandpipers at Langebaan Lagoon. The study also provided information on the birds' use of microhabitat, foraging techniques and foraging related to shore level.

METHODS

Daily activity

The birds' daily activity was monitored for a total of 30 h each month on a 500 m stretch of the lagoon shore at Bottelary and on 500 m^2 of the *Arthrocnemum* marsh at Geelbek (Figure 1) over the period March 1974 - March 1975, by the

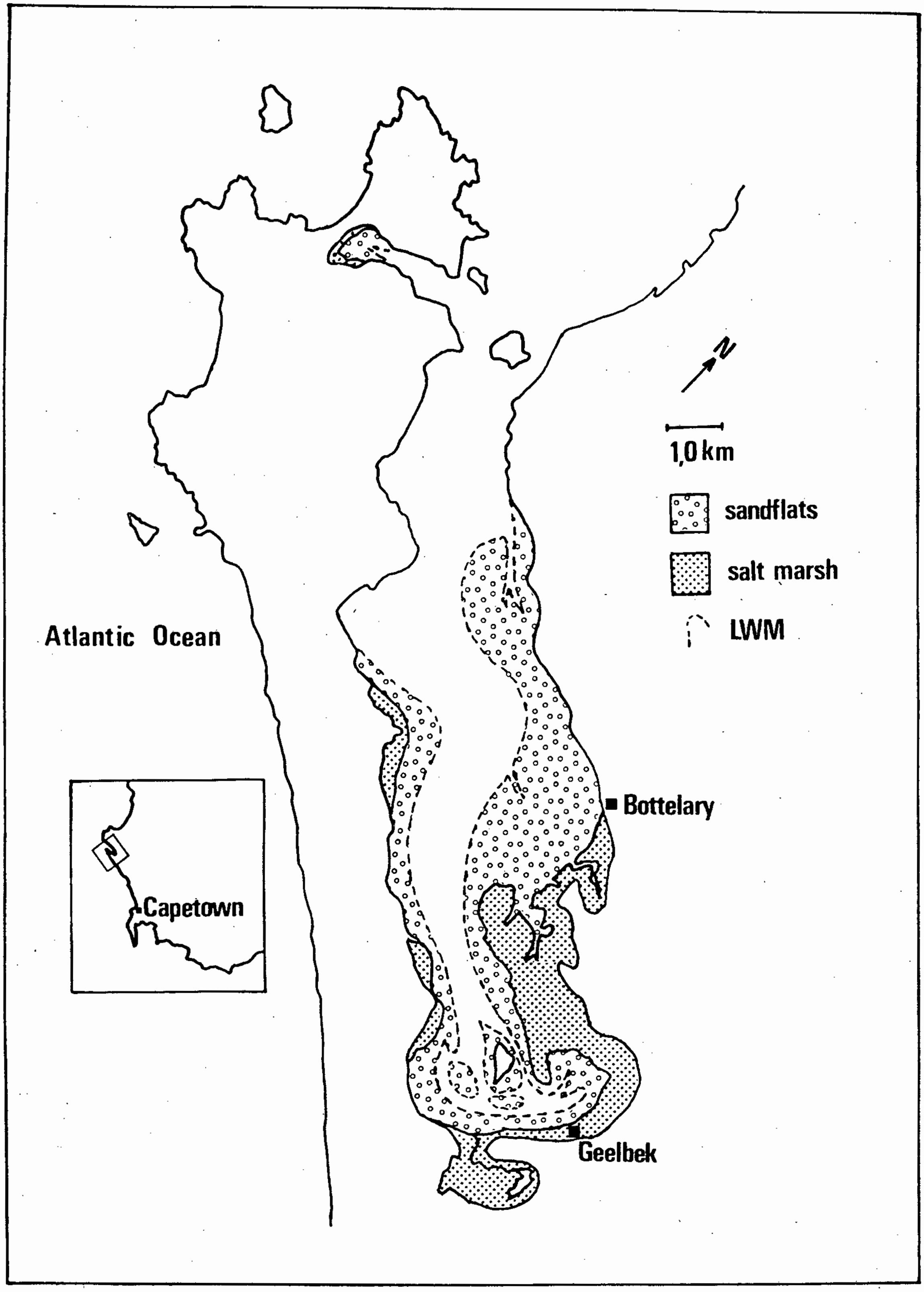

Figure 1. Map of Langebaan Lagoon showing study areas.

Instantaneous Scan method (Altmann1974). Observations were made at the sandflats when these were exposed by the tide, and at the marsh both at low and high tides. The birds were counted and their activity noted every 15 min , spaced over all daylight hours. Activity was classified into foraging, flying, standing (including preening) and roosting.

Foraging

The foraging behaviour of individual birds was observed through binoculars during March 1974 - March 1975, and through a 20x telescope during September 1974 - March 1975. Curlew sandpipers may stand (S), take single steps (St), walk (W) or run (R) while foraging. They may execute single pecks (P) or multiple pecks (MP) and probes (Pr) or multiple probes (MPr); the bird usually halts (H) before commencing a peck or probe. A peck was arbitrarily described as the insertion of the culmen up to a quarter of its length into the substrate. A probe was any deeper insertion. Curlew sandpipers use any combination of these strategies e.g. WHP, StMPr. They also use a technique known as 'stitching' (Burton 1971) where the culmen is inserted with a rapid succession of probes while the bird moves slowly forward. This appears to be a tactile search method. Foraging was observed both in the marsh and sandflat feeding areas at all stages of the tidal cycle. Individual birds were chosen from flocksat random for observation, care being taken to avoid observing the same bird more than once. Foraging rate was measured as the time taken for five foraging attempts involving any one of the activities described above. Swallowing movements indicated a successful foraging attempt (only observed after September 1974). The foraging behaviour, foraging rate and microhabitat being used were recorded. An average of 630 foraging bouts (of five foraging attempts each) was observed each month. Mature birds (i.e. second-year and adult birds) could be distinguished from first-year birds by the presence of breeding plumage in April 1974 and March 1975. The nonparametric statistical tests used in the analysis of data are described in Siegel (1956). The seasons were described as follows : spring, September-November; summer, December-February; autumn, March-May; and winter, June-August.

RESULTS

Daily activity

At spring tides, curlew sandpipers foraged over the sandflats as soon as these were exposed; they flew to roost in the marsh when the flats were submerged at high water (Figure 2). At neap tides, they remained roosting on sandspits at the high water mark at high tides. This may have been because low water neap occurs later in the day than low water springs does, and the birds gathered near the sandflats to wait for the foraging grounds to be uncovered. The birds vacated the sandflats altogether at high water neaps in September 1974 when there were two low tides in one day

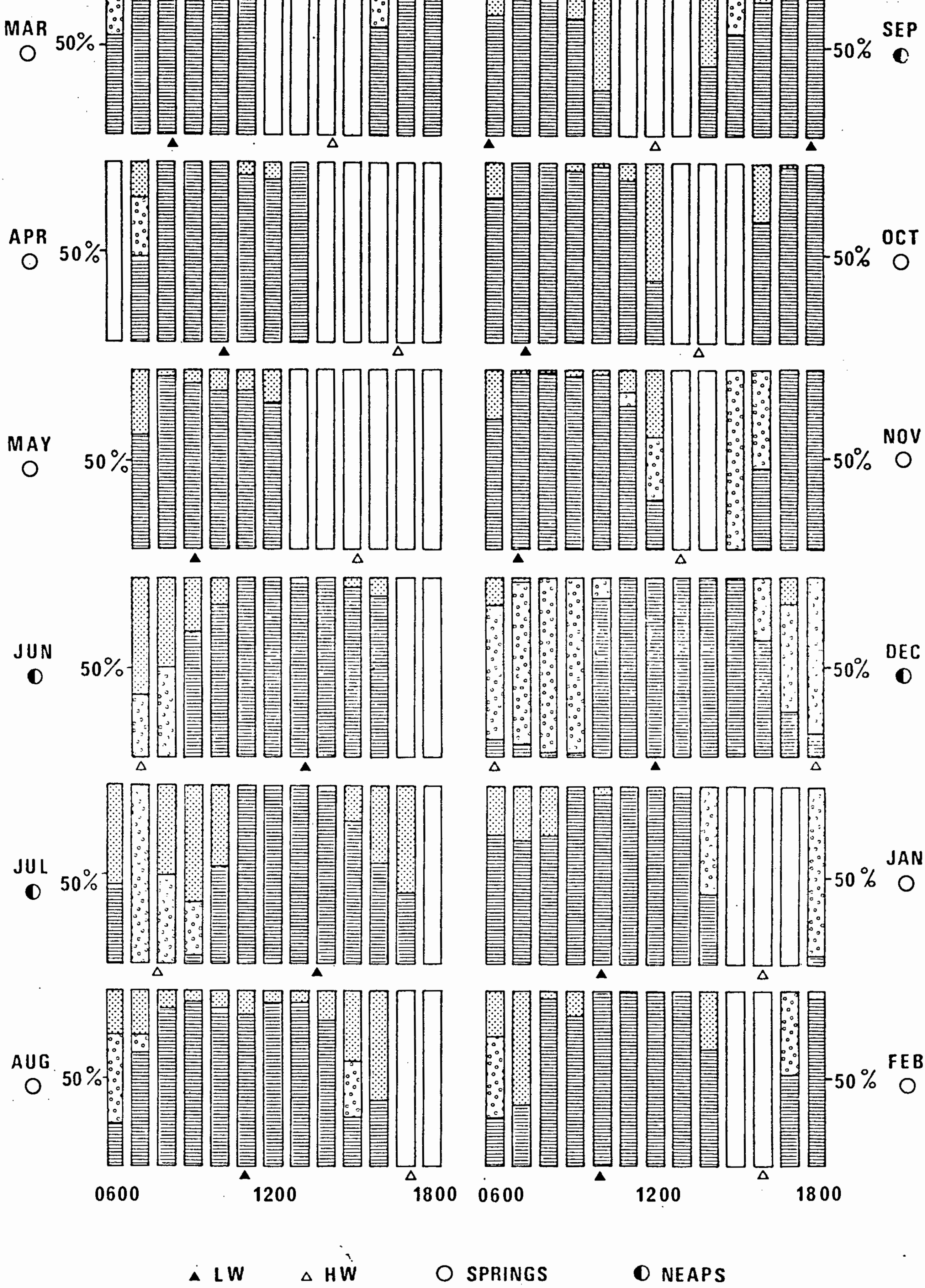

Figure 2. Variation in daily activity of curlew sandpipers (expressed as a percentage of total observed population engaged in each activity) on the intertidal sandflats at Bottelary from March 1974 to February 1975. Horizontal bars indicate foraging, open circles roosting, and dots 'other' (which included standing and preening). Blanks indicate that no birds were present. Histograms from May to August represent activity of immatures only.

(Figure 2).

The birds spent 55-65% of the diurnal period foraging in spring and summer, but in autumn and winter they foraged for about 80% of the day during both spring and neap tides (Figure 3). This meant that in autumn and winter they were foraging in the marshes at high tides (Figure 4). About a quarter of the total curlew sandpiper population foraged in the marshes at low water in all seasons (Appendices 1 and 2). The birds roosted for up to 25% of the daytime during the greater diurnal periods of spring and summer (Table 1). Activities other than foraging and roosting did not occupy more than about 20% of the daytime.

Seasonal changes in foraging rate and foraging success

Curlew sandpipers foraged faster in autumn and winter than in spring and summer both on the sandflats and on the marshes (Figures 5 and 6), although only the marsh foraging rates showed significant differences (Kruskal-Wallis one-way analysis of variance, $H = 24{,}69$, $df = 9$, $p < 0{,}01$). Variance was greater on the flats because more diverse foraging techniques were employed there (see below).

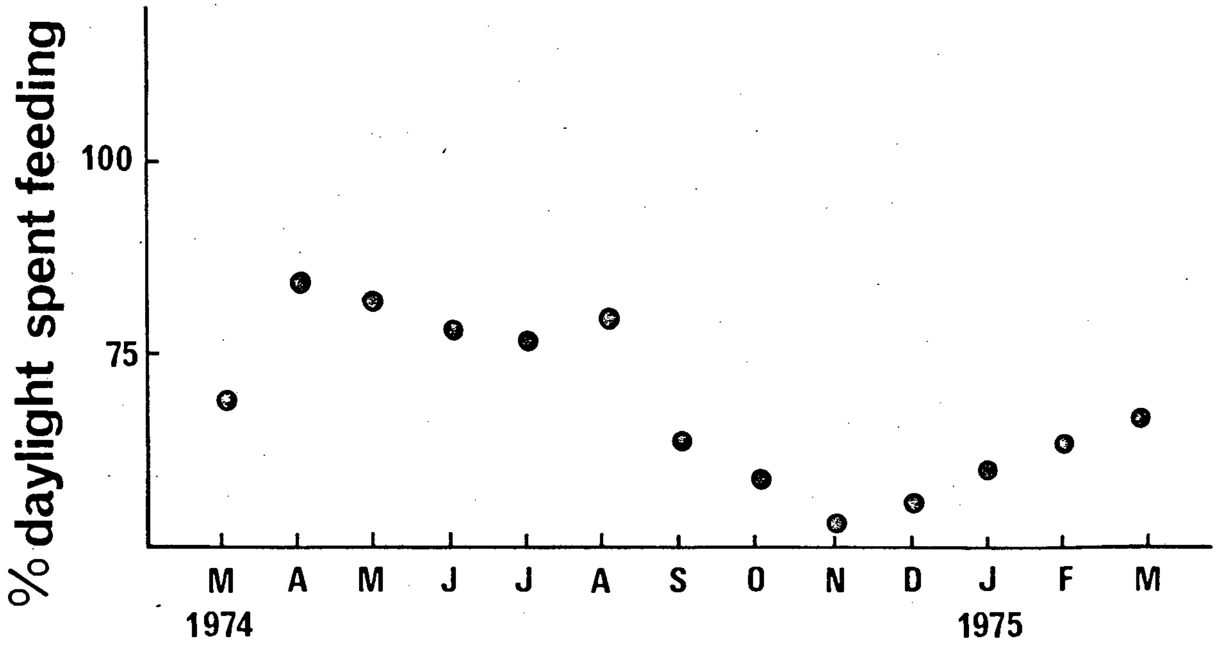

Figure 3. Monthly change in the percentage of daylight hours spent foraging by curlew sandpipers. Points from May to August represent foraging of immatures only.

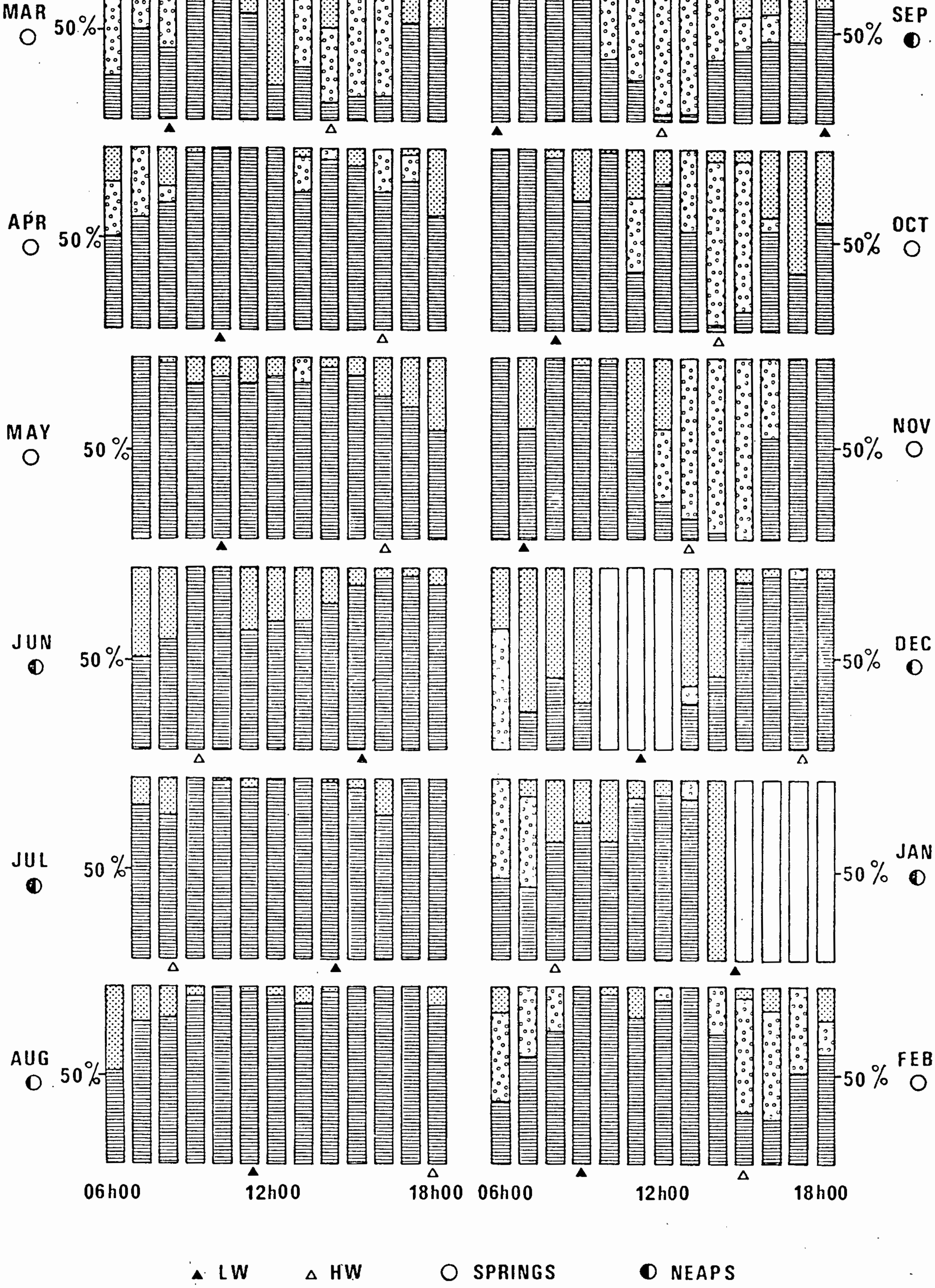

Figure 4. Variation in daily activity of curlew sandpipers (expressed as a percentage of total observed population engaged in each activity) on the marshes at Geelbek from March 1974 to February 1975. Horizontal bars indicate foraging, open circles roosting and dots 'other' (which included standing and preening). Blanks indicate that no birds were present. Histograms from May to August represent activity of immatures only.

TABLE 1 Mean daily (dawn to dusk) duration (min) of activities of adult and immature male and female curlew sandpipers at Langebaan during March 1974 to February 1975. Percentages are shown in parentheses.

MONTH	ACTIVITY				TOTAL DIURNAL PERIOD[b] (MIN)
	FORAGE	ROOST	FLY	OTHER[a]	
March 1974	525 (71)	105 (14)	36 (5)	74 (10)	740
April	570 (85)	34 (5)	46 (7)	25 (3)	675
May	515 (83)	20 (3)	28 (5)	57 (9)	620
June	472 (79)	25 (4)	66 (11)	37 (6)	600
July	465 (78)	45 (7)	56 (9)	34 (6)	600
August	512 (80)	32 (5)	43 (7)	53 (8)	640
September	448 (64)	180 (25)	57 (8)	20 (3)	705
October	456 (60)	141 (18)	74 (10)	89 (12)	760
November	437 (53)	211 (26)	53 (6)	119 (15)	820
December	480 (56)	240 (28)	49 (5)	91 (11)	860
January 1975	510 (60)	102 (12)	59 (7)	179 (21)	850
February	510 (64)	104 (13)	72 (9)	114 (14)	800

a Includes standing and preening

b Calculated for the middle day of each month

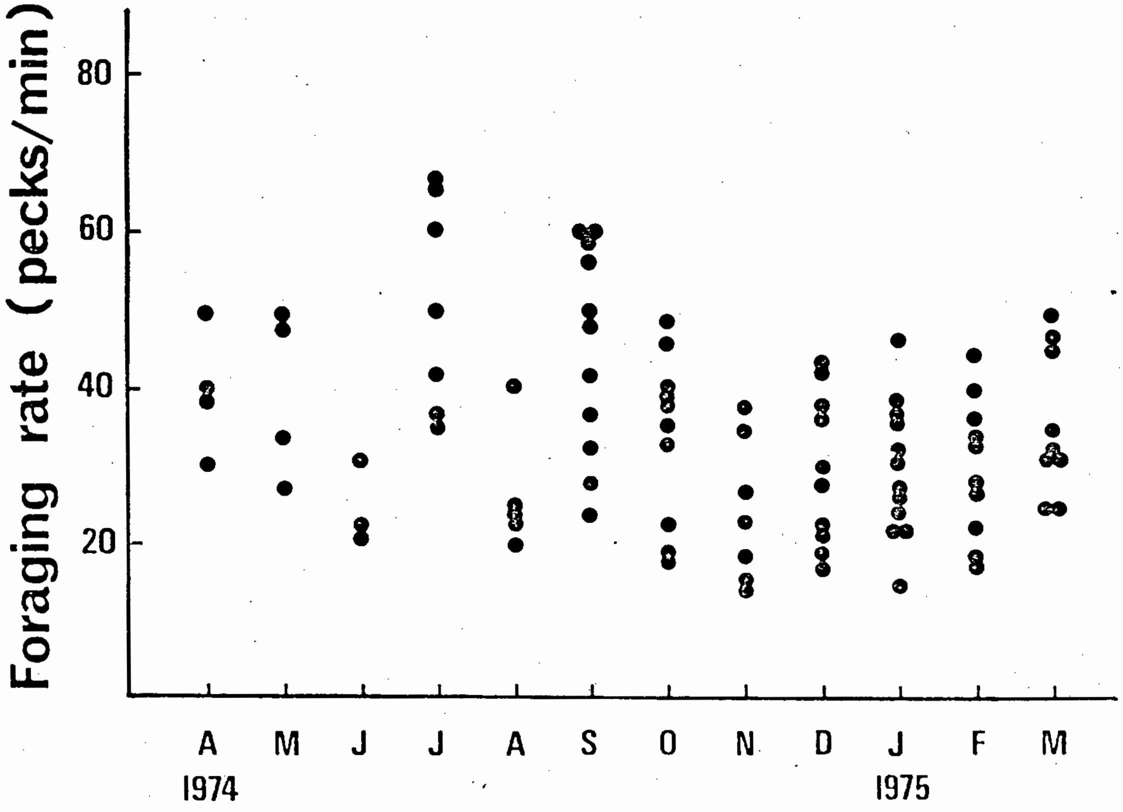

Figure 5. Monthly change in foraging rate (pecks or probes per min) of curlew sandpipers foraging on the sandflats. Each point is the mean of at least 50 observations. Points from May to August represent foraging rates of immatures only.

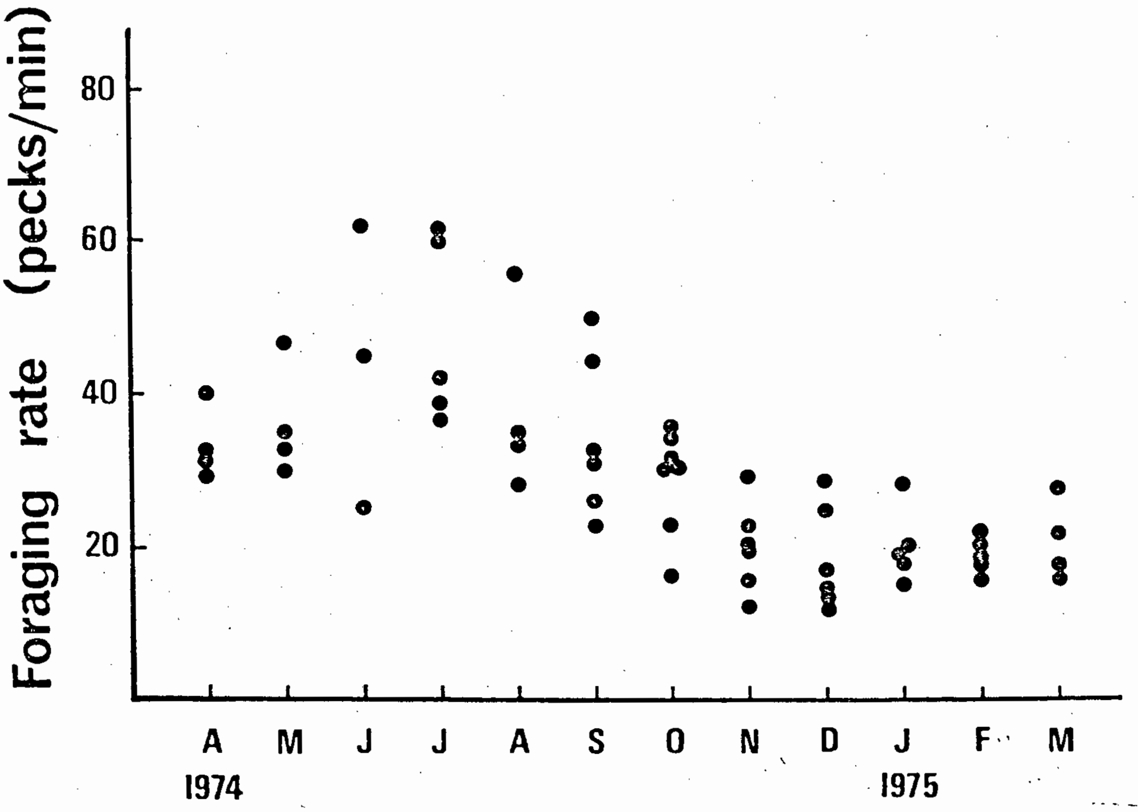

Figure 6. Monthly change in foraging rate (pecks or probes per min) of curlew sandpipers foraging in the marshes. Each point is the mean of at least 50 observations. Points from May to August represent foraging rates of immatures only.

The birds' foraging efficiency increased gradually from September through to March (Figures 7 and 8), although only the marsh increase was significant (Kruskal-Wallis one-way analysis of variance, $H = 14{,}98$, $df = 6$, $p < 0{,}05$).

Comparison of adult and immature birds

Adult curlew sandpipers foraged significantly faster than immature birds (Table 2) and also achieved a higher success rate (Table 3). A chi-squared contingency table showed that immature birds spent longer foraging on the sandflats than adults did in April 1974 ($\chi^2 = 44{,}3$, $df = 7$, $p < 0{,}001$). There was no evidence that immature birds used foraging areas or microhabitats different from those of adults.

Foraging techniques

Curlew sandpipers employed WHMPr most frequently throughout the year both on sandflats and marshes (Figures 9 and 10). The other foraging techniques (WHPr, WHP, etc.) were used more frequently in winter and spring than autumn and summer. Hence foraging diversity was greater in winter and spring (Table 4). Although highest foraging diversity does not coincide with highest dietary diversity (Table 5), the differences in rank order were not significant (Kolmogorov-Smirnov two-sample test, $K_D = 2$, $N = 4$, $p > 0{,}1$). Foraging

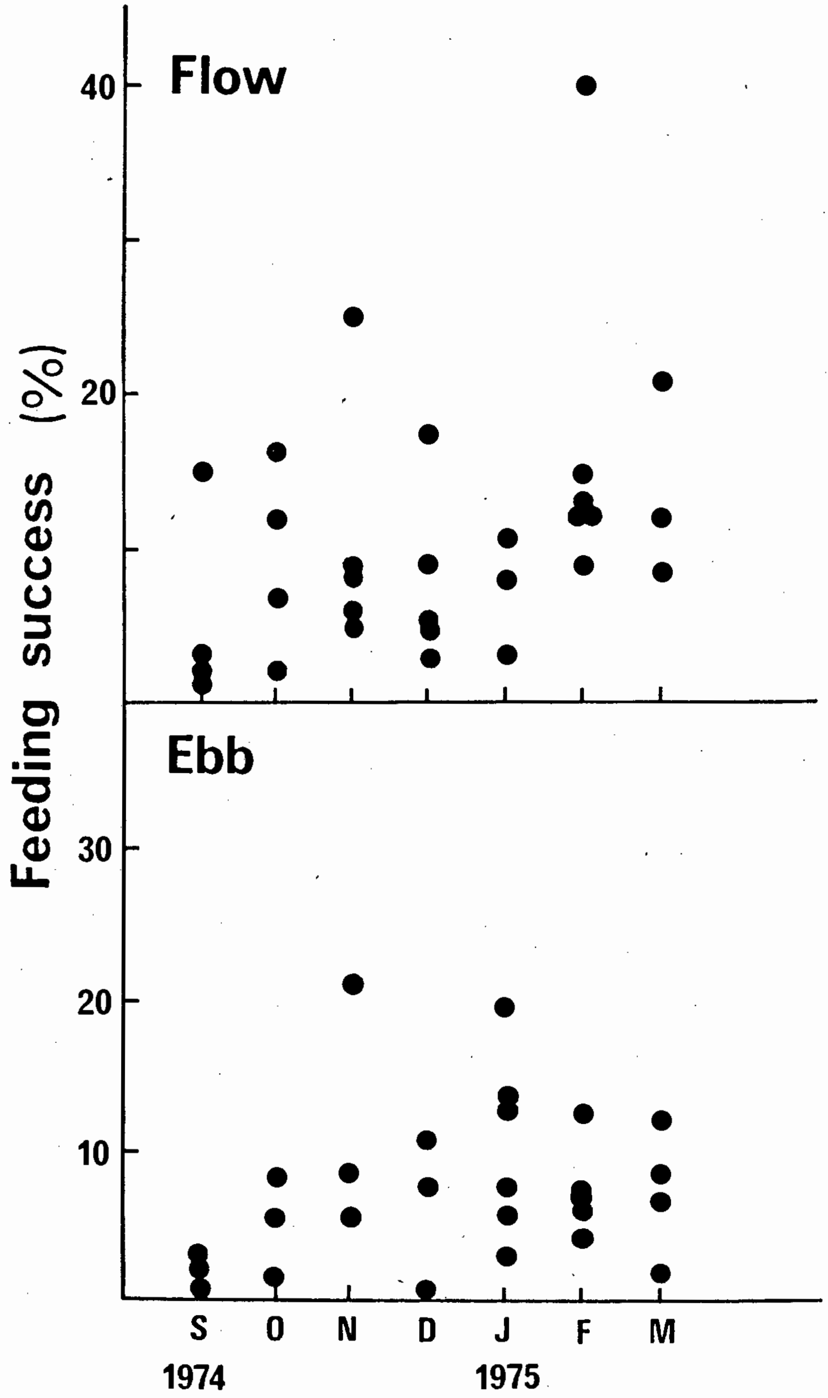

Figure 7. Differences in success rate (percentage of total foraging attempts which were successful) of curlew sandpipers foraging on sandflats during flow tides (above) and ebb tides (below) from September 1974 to March 1975.

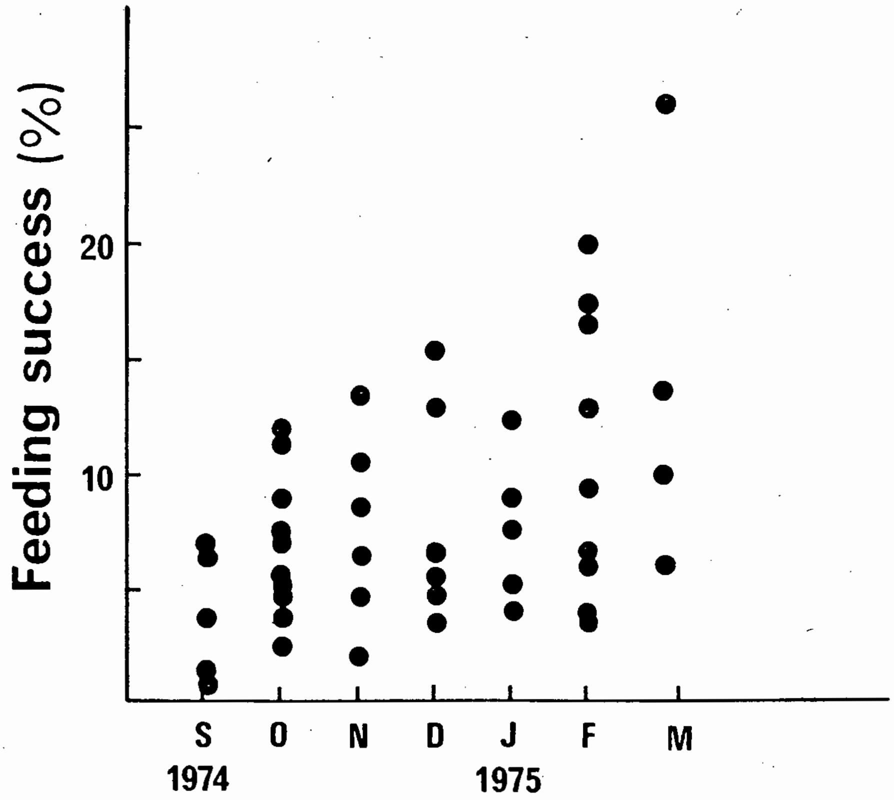

Figure 8. Differences in success rate (percentage of total foraging attempts which were successful) of curlew sandpipers foraging on the marshes during September 1974 to March 1975.

TABLE 2 Mean foraging rates (pecks or probes per min) of adult and immature curlew sandpipers in April 1974 and March 1975. Each value is the mean foraging rate of 15 separate 2-h periods of observation

ADULT			IMMATURE		
Mean	S D	n	Mean	S D	n
43,13	18,67	15	28,44	8,31	15

$U = 58, \quad p \leq 0,001$

TABLE 3 Success rates (number prey objects per min) of adult and immature curlew sandpipers during March and April 1978. Each value is the mean success rate of 24 separate 2-h periods of observation

ADULT			IMMATURE		
Mean	S D	n	Mean	S D	n
10,08	3,20	24	4,33	1,44	24

$^{*}z = 5{,}71, \quad p \leq 0{,}00003$

$^{*}z$ = standard normal variate calculated from the Mann-Whitney U-test (Siegel 1956).

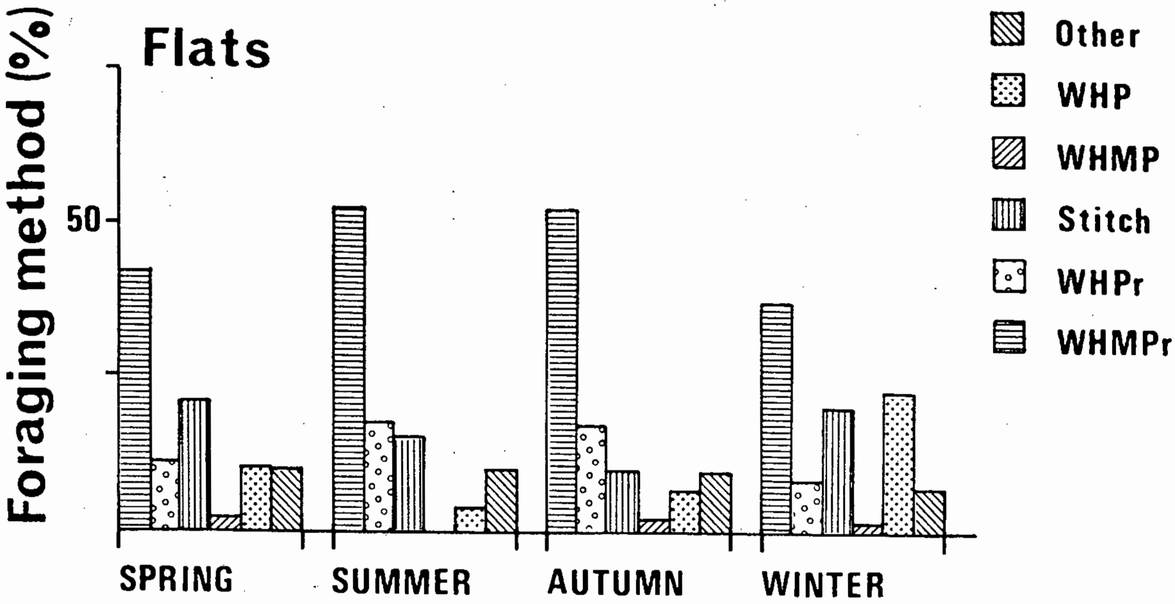

Figure 9. Seasonal change in the percentage of foraging techniques used on the sandflats by curlew sandpipers (W = walk, H = halt, M = multiple, P = peck and Pr = probe). Histograms for winter represent foraging of immatures only.

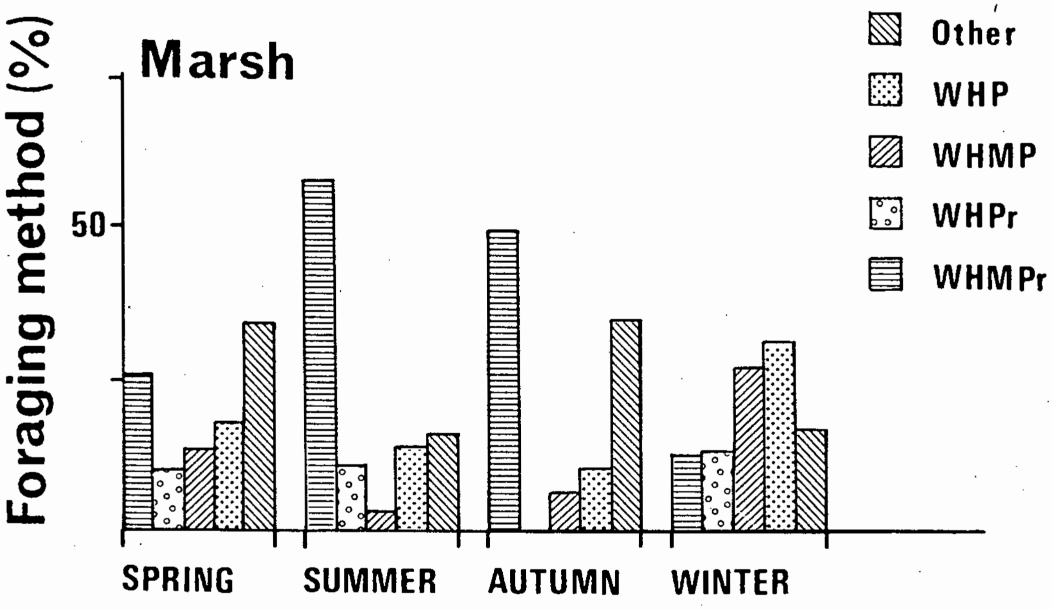

Figure 10. Seasonal change in the percentage of foraging techniques used on the marshes by curlew sandpipers (W = walk, H = halt, M = multiple, P = peck and Pr = probe). Histograms for winter represent foraging of immatures only.

TABLE 4 Seasonal changes in the foraging diversity of curlew sandpipers on sandflats and marshes

SEASON	DIVERSITY $(\bar{H})$*	
	FLATS	MARSH
Spring	1,54	1,98
Summer	1,39	1,36
Autumn	1,48	1,41
Winter	1,50	1,62

* Calculated from the formula $\bar{H} = -\sum_i P_i \log_e P_i$,

where

P_i = the proportion of observations in each category of foraging (MacArthur & MacArthur 1961).

TABLE 5 Seasonal changes in the diversity of prey taken by curlew sandpipers on sandflats and marsh (based on diet data from Part 2)

SEASON	DIVERSITY ($\bar{H}$)*	
	FLATS	MARSH
Spring	1,34	1,03
Summer	1,38	1,04
Autumn	1,25	1,29
Winter	1,26	1,14

* Calculated from the formula

$$\bar{H} = -\sum_i P_i \log_e P_i, \quad \text{where}$$

P_i = the proportion of observations in each prey category (MacArthur & MacArthur 1961).

rate decreased with increasing foraging success, although correlation was not significant ($r = 0{,}1$, $p > 0{,}1$) (Figure 11). This meant that birds took slightly longer to forage when their success rate was higher, presumably due to increased prey handling time, although prey handling times themselves were relatively short (Table 6).

Foraging microhabitats

Comparisons of foraging rate related to microhabitat were made as often as samples were large enough to allow this. Foraging rate differed significantly with microhabitat in five out of nine comparisons made (Table 7). Preliminary analysis showed no significant differences in foraging rate at different water depths (depth was judged relative to the leg of the foraging bird).

Foraging related to tide and shore level

Curlew sandpipers foraged significantly faster on incoming than on outgoing tides in five of the seven months when comparisons were made (Table 8). However, foraging success was higher on the ebb than on the flow ($U = 6$, $n_1 = 7$, $n_2 = 7$, $p \leq 0{,}01$). There was no difference in success rate between birds foraging on the marshes and sandflats.

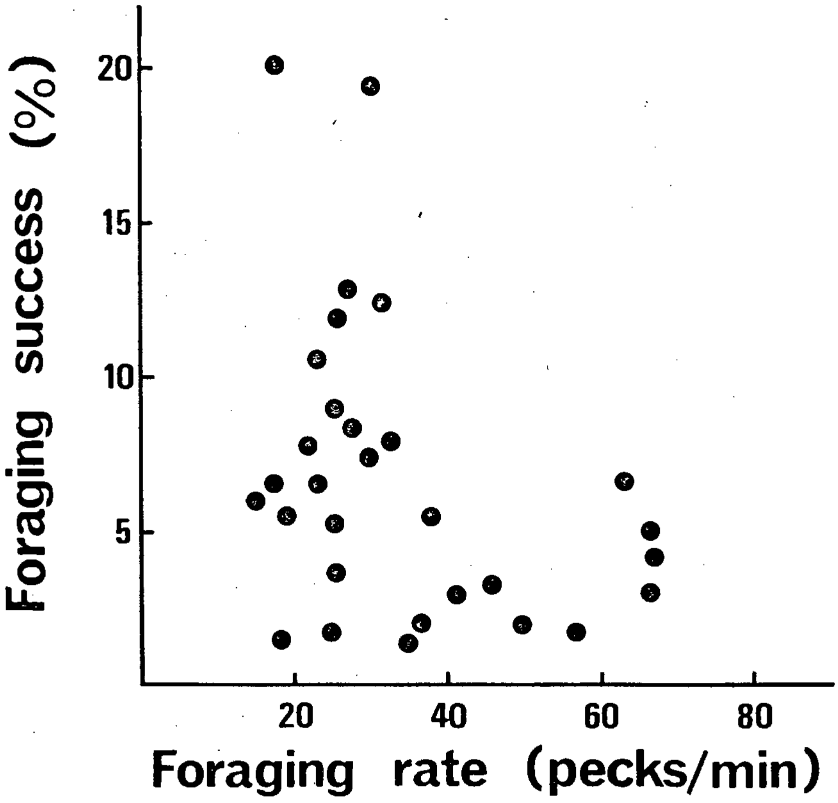

Figure 11. The relationship between foraging success (percentage of total foraging attempts which were successful) and foraging rate (pecks or probes per min).

$y = 2{,}98 + 0{,}36x$; $r = 0{,}3$; $p < 0{,}1$

TABLE 6 Mean handling times (seconds) for main prey organisms taken by curlew sandpipers

PREY ORGANISM	HANDLING TIME		
	Mean	S D	n
Worms	2,54	0,88	137
Snails	0,87	0,63	120
Crabs	2,28	0,90	47

TABLE 7 Differences associated with microhabitat in the foraging rate (pecks or probes per min) of curlew sandpipers. Microhabitats are shallow water (< 40mm) at tide edge, deeper water (> 40mm) at tide edge, exposed sand, and surface water in pools on sand

FORAGING METHOD	MICROHABITATS COMPARED	MEAN RATE	S D	n	t	p
WHMPr *	Tide edge	26,49	7,34	159	4,03	<0,001
	Exposed sand	31,14	9,45	90		
	Tide edge	27,27	6,15	96	5,64	<0,001
	Deeper water	22,27	3,49	31		
	Tide edge	29,18	9,14	81	2,78	<0,01
	Water on sand	34,01	6,90	24		
	Water on sand	34,01	6,90	24	0,25	NS
	Exposed sand	33,52	10,67	65		
Stitch	Tide edge	19,88	3,15	123	0,94	NS
	Exposed sand	19,21	5,26	65		
	Tide edge	22,35	6,91	21	2,55	<0,02
	Water on sand	18,20	5,01	68		
	Water on sand	18,20	5,01	68	0,19	NS
	Exposed sand	18,50	7,62	29		
WHPr	Tide edge	48,70	15,34	40	5,90	<0,001
	Deeper water	32,36	6,95	27		
Stand MPr	Tide edge	26,83	13,58	27	0,09	NS
	Water on sand	26,43	12,23	12		

* Symbols explained in Methods

TABLE 8 Comparison of foraging rate (pecks or probes per min) between curlew sandpipers on flow and ebb tides, September 1974 - March 1975.

Month	FLOW			EBB				
	Rate	S D	n	Rate	S D	n	t	p
September 1974	48,39	4,80	193	42,98	3,57	270	14,86	<0,001
October	29,76	2,80	321	39,42	4,40	190	27,18	<0,001
November	28,04	8,60	232	27,86	3,34	224	0,30	NS
December	33,26	2,98	317	27,05	2,76	215	24,65	<0,001
January 1975	31,61	2,07	267	28,41	2,74	304	15,85	<0,001
February	30,71	3,52	206	28,44	3,05	226	7,13	<0,001
March	37,55	4,75	117	34,88	4,87	107	4,15	<0,001

The foraging rate of curlew sandpipers decreased from the upper to the lower shore on both outgoing and incoming tides (Figure 12), i.e. they fed fastest at or near the high water mark. The number of prey taken per min decreased from upper to lower shore and was lowest about 100 m from the low water mark on the incoming tide (Figure 13).

DISCUSSION

Daily and seasonal activity budgets

Spatial and temporal variations in the seasonal availability of food to curlew sandpipers, together with seasonal variations in the birds' energy requirements, necessitate appropriate changes in the birds' activities in response to these. So, for example, during summer curlew sandpipers foraged on the intertidal sandflats when these were exposed by the tide, and roosted either at the high water mark during high water neaps or on the adjacent marsh areas during high water springs. However, the birds foraged for up to 80% of the daytime during winter, because of the shorter time available for foraging in daylight and increased energy demands brought about by relatively low ambient temperatures.

The birds do not appear to forage at night (Elliott *et al*. 1976, pers. obs.), unlike redshank *Tringa totanus* in Britain in winter (Goss-Custard 1969) and certain waders in southern

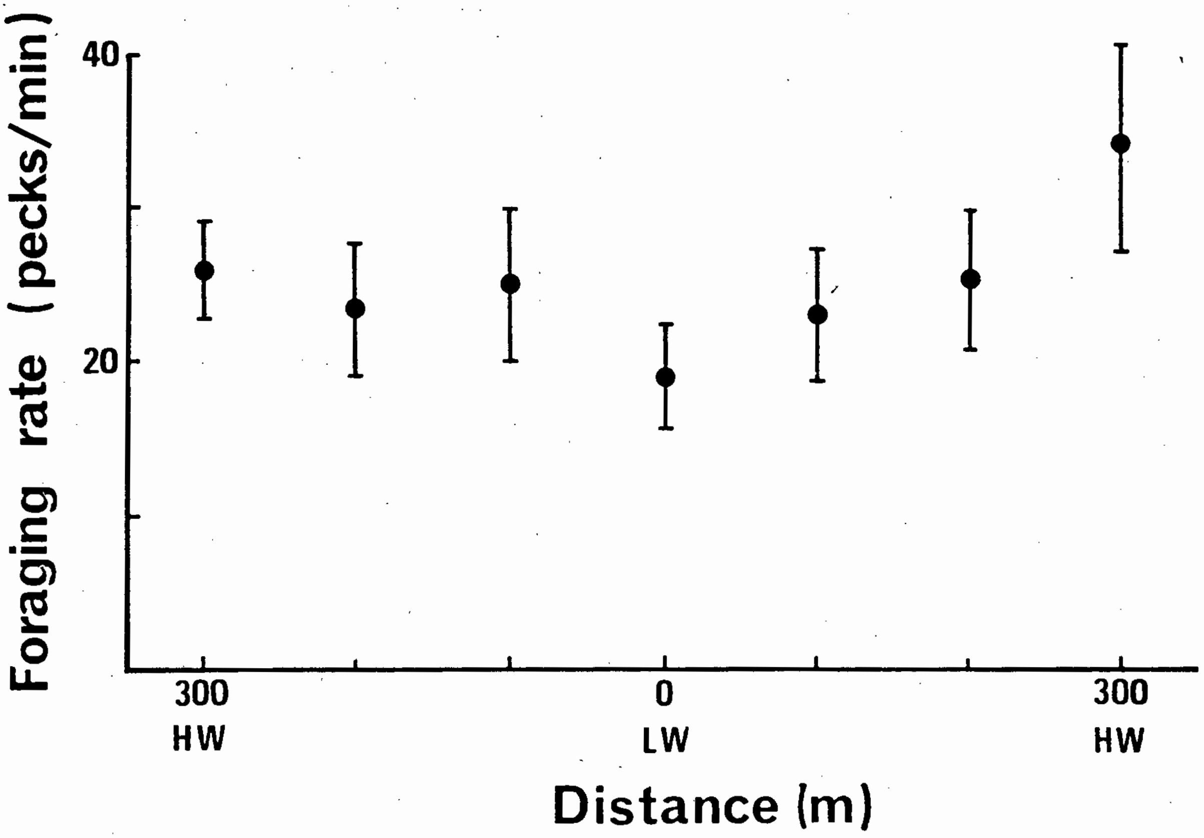

Figure 12. The relationship between foraging rate (pecks or probes per min) of curlew sandpipers and shore and tide level. Values are means ± S.D.

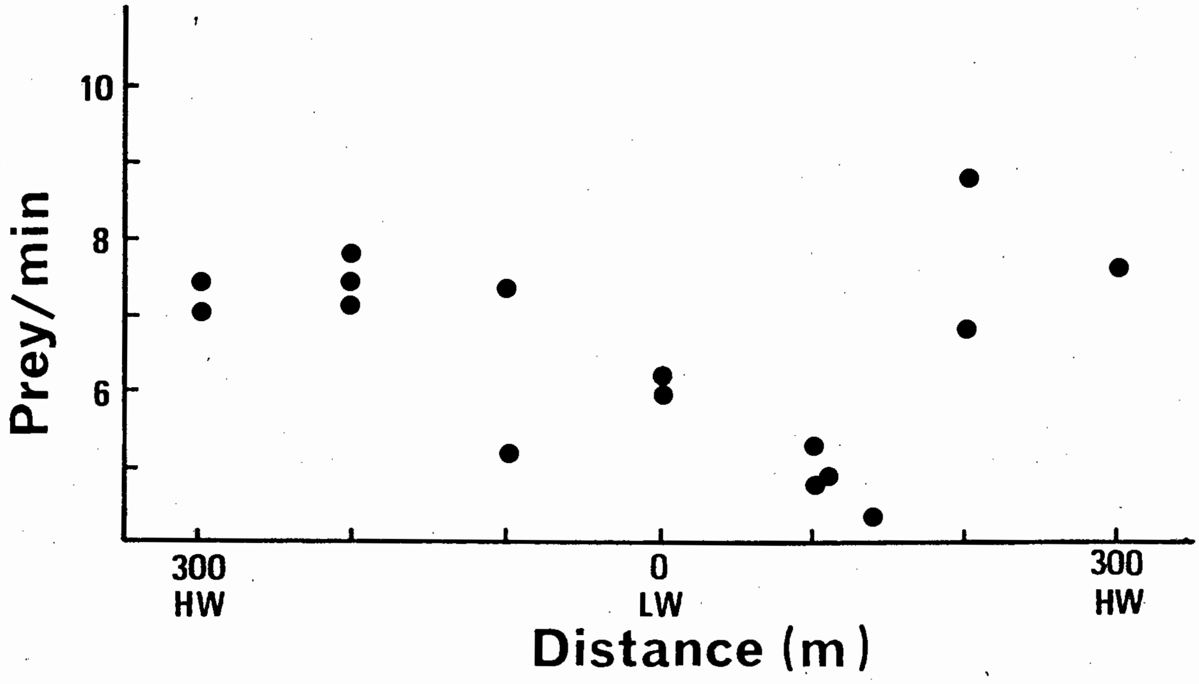

Figure 13. The relationship between success rate (number of prey taken per min) of curlew sandpipers and shore and tide level. Each point is the mean of at least 25 observations.

Florida (Baker & Baker 1973). At Langebaan, marsh areas are almost always available to curlew sandpipers when the sandflats are covered, except during four days at springs when high water covers the marshes for about 90 min each day. Foraging on the marshes is presumably not suboptimal, since

(1) the success rates of birds foraging on the marshes were not lower than those on the flats,

(2) the biomass of marsh invertebrates was high during winter (Part 1), and

(3) a quarter of the total curlew sandpiper population always foraged on the marshes at low water when they could have been foraging on the adjacent sandflats.

The birds did not spend all of the diurnal period foraging in winter, as redshank, purple sandpiper _C. maritima_ and other waders do in the northern hemisphere (Goss-Custard 1969, Feare 1966, Goss-Custard _et al._ 1977). Hence, I conclude that food availability is not a limiting factor for the immature curlew sandpipers which overwinter at Langebaan Lagoon. This seems true also for the summer populations of adult and immature birds, which spent only 55-65% of the daylight hours foraging and which I estimated achieved a fairly large positive energy balance during summer (Part 6).

An increase in the daily time spent by the birds in foraging began in late summer. Adult curlew sandpipers achieve a 40% increase in body mass by mid-April due to the accumulation of fat reserves in preparation for migration (Elliott *et al.* 1976), and longer foraging hours partly account for the increase in mass. Numbers and biomass of prey items increased during late summer and autumn (Part 1), and may also partly account for the birds' mass gain, presumably both by increasing the chances of birds encountering potential prey items and also by increasing the energy content of individual prey items taken. Two further factors contributing towards the birds' ability to achieve a pre-migratory fat store are their increased foraging and success rates. Firstly, increased foraging rate would have increased the chances of encounter with prey and this, together with the larger numbers of prey potentially available, resulted in increased success rates. Secondly, although birds took slightly longer to forage at higher success rates (Figure 11), presumably because more successes involved relatively increased prey handling times, they (the birds) presumably offset the effect of prey handling by foraging faster. Although Baker (1974) believes that handling time may be a more important variable than has previously been recognized, curlew sandpipers had relatively short prey handling times (Table 6).

The foraging rate of overwintering birds was higher in winter, presumably as a response to shorter daylength and increased energy demands due to lower ambient temperatures in winter. I was not able to observe success rates in winter but these probably did not increase, since Goss-Custard (1969) found no increase in the ingestion rate of redshank in winter to compensate for shorter daylength then. The fact that the overwintering population of curlew sandpipers at Langebaan is made up of immature birds (Elliott *et al.* 1976) suggests that they are unable to deposit the necessary fat reserves for migrating. Groves (1978) found that adult ruddy turnstones *Arenaria interpres* had significantly higher foraging and success rates than juveniles, and suggested that this was due to the greater experience of the adults. Adult little blue herons *Florida caerulea*, brown pelicans *Pelecanus occidentalis* and royal terns *Sterna maxima* all fed more efficiently than immature birds of the same species (Recher & Recher 1969, Orians 1969, Buckley & Buckley 1974). Buckley & Buckley (ibid.) also suggest that inexperience handicaps the foraging efficiency of immatures. Immature curlew sandpipers foraged more slowly and with less success than adults did (Tables 2 and 3), and it seems likely that inexperienced foraging prevented the immature birds from accumulating sufficient fat reserves for migration. In particular, immatures showed no sign of pre-migratory fattening (Elliott *et al.* 1976), even though they spent longer foraging each day in autumn than adults did.

Foraging

Optimal predator strategy should lead to more selective feeding and a more restricted diet if food density increases (Emlen 1966, MacArthur & Pianka 1966, Schoener 1971). Selectivity may be indicated by the degree of foraging and dietary diversity displayed. Contrary to expectation, curlew sandpipers displayed greatest foraging diversity on the sandflats in spring (Table 4), when prey numbers were greatest (Part 1), and lowest foraging diversity in summer when prey numbers were lower. However, as would be expected, dietary diversity was highest in summer. On the marshes at Geelbek, highest foraging diversity does coincide with lower prey density, consistent with the predictions of the optimal predator strategy model (see above). Baker & Baker (1973) pointed out that birds foraging by tactile methods (as curlew sandpipers do when probing on the sandflats) cannot 'evaluate' items until they have been touched or even grasped by the bill. Presumably, this means that probers cannot 'afford' to be as selective as peckers can. Ninety per cent of the marsh invertebrates were epifaunal (Part 1), so it is significant that foraging diversity on the marshes was consistent with the predictions of the model.

Tidal fluctuations affect the foraging patterns of avian predators by regulating the potential availability of intertidal invertebrates. The birds' foraging in different microhabitats in any particular tidal zone on the sandflats suggests that they were exploiting temporal differences in the potential availability of prey. The microhabitats recognized in this study (Table 6) were not so different as to suggest a diverse fauna associated with each, since they differed only in moisture content or water level and these were controlled by tidal fluctuations. Although different foraging rates were sometimes associated with specific microhabitats (Table 6), these differences were a function of the foraging technique used. This means that each foraging technique in association with a particular microhabitat probably represented a temporally different food resource. The behaviour of benthic invertebrates at Langebaan needs investigation, especially in relation to tidal fluctuations, since prey behaviour is known to influence its potential availability to predators (Goss-Custard 1969, Vader 1964).

Curlew sandpipers fed faster on incoming tides (Table 7), probably because prey species become active after quiescence during the preceding exposure period (Vader 1964). However, it is difficult to explain why success rates were lower on the incoming tide, since Goss-Custard (1977a) found no differences in feeding or success rates of redshank between three hours before and after low water. Increased activity on the part of prey, while eliciting a faster foraging rate from curlew sandpipers, may possibly have made actual capture more difficult.

Higher foraging and success rates occurring at the upper shore levels (Figures 12 and 13) were related to the density and availability of potential prey items. The small gastropod Assiminea globulus occurred there in high numbers (Part 1), and was readily available to the birds feeding there. Goss-Custard (1970, 1977b) reported that redshank fed faster in zones with small prey and that their ingestion rate increased with increasing prey density.

ACKNOWLEDGEMENTS

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APPENDIX 1 Total numbers of curlew sandpipers observed on the sandflats from which figures for daily activity were obtained

HOUR	MONTH											
	1974										1975	
	M	A	M	J	J	A	S	O	N	D	J	F
06h00	17	0	0	0	19	39	88	120	121	202	71	90
07h00	63	54	14	17	21	37	67	139	135	204	114	88
08h00	75	19	20	24	21	38	72	99	138	207	115	93
09h00	60	20	21	29	40	47	56	122	158	239	118	55
10h00	62	45	19	35	37	48	16	143	170	259	79	143
11h00	71	58	16	20	21	44	0	90	173	250	80	130
12h00	0	35	17	19	23	59	0	55	160	188	108	94
13h00	0	7	0	27	23	51	0	0	0	169	93	78
14h00	0	0	0	35	23	41	90	0	0	153	120	81
15h00	0	0	0	31	36	42	65	0	180	153	120	101
16h00	101	0	0	21	30	30	66	158	144	127	116	160
17h00	78	0	0	0	10	0	63	170	91	108	127	168
18h00	48	0	0	0	0	0	60	170	91	42	124	212

APPENDIX 2 Total numbers of curlew sandpipers observed on the marshes from which figures for daily activity were obtained

HOUR	MONTH											
	1974										1975	
	M	A	M	J	J	A	S	O	N	D	J	F
06h00	30	40	0	0	0	0	26	28	21	29	93	62
07h00	35	41	28	21	29	31	28	28	50	48	73	50
08h00	29	38	20	20	37	30	31	16	53	49	68	140
09h00	25	36	27	21	56	44	48	8	49	17	142	190
10h00	16	23	31	22	45	39	94	17	59	0	130	122
11h00	95	14	37	30	64	47	92	45	86	0	42	78
12h00	45	21	29	30	54	44	80	55	86	0	72	66
13h00	98	31	17	35	44	41	68	65	52	86	50	76
14h00	267	32	34	19	25	52	46	220	54	94	82	82
15h00	346	15	27	24	28	33	44	224	45	99	0	130
16h00	307	24	35	24	25	36	46	60	40	104	0	190
17h00	204	28	39	22	29	36	50	70	80	108	0	140
18h00	211	15	0	23	29	36	43	15	78	94	0	135

Part 4

The foraging of curlew sandpipers in relation to prey density

SUMMARY

The foraging of wintering curlew sandpipers *Calidris ferruginea* was observed in relation to the density of the birds and to the density of their prey. Foraging and success rates, and the biomass of prey taken per unit time, all accorded with Royama's (1971) profitability model. A feature not represented in the model was that small prey may have reduced the foraging and success rates of curlew sandpipers by decreasing profitability at high prey densities. Bird density increased with prey density up to an asymptotic level, meaning that the birds were concentrating their foraging effort where profitability was greatest. The success rate of birds foraging in groups was higher than that of birds foraging alone. An increase in aggressive interactions among birds when they were close together counteracted an increase in bird density.

INTRODUCTION

Theories of optimal foraging formulated during the last decade or so have predicted that predators should attempt to maximize their intake while foraging (MacArthur & Pianka 1966, Schoener 1971). The foraging 'decisions' which confront an avian predator in this are : which areas to forage in, what search strategy to use, what prey items to choose, and whether flock foraging enhances success or not (Krebs & Cowie 1976). Royama (1970, 1971) proposed that the first of these was determined by the profitability of different areas, and that birds which sampled many feeding areas quickly but concentrated their search effort in a few highly productive areas would capture the most prey with the least expense of time and energy. However, profitability need not imply most prey per unit time but may be related to biomass or energy intake per unit time.

This paper examines the foraging of wintering curlew sandpipers *Calidris ferruginea* (Aves : Charadrii) in relation to their density and the density of their prey at Langebaan Lagoon (33°S, 18°E), South Africa, in the light of Royama's (1971) theory of profitability.

STUDY AREA AND METHODS

The study area at Oesterval on the eastern shore of Langebaan Lagoon (Fig. 1) was chosen because this area supports a higher density of waders than any other in the lagoon (Summers 1977). Three main foraging zones or habitats were recognized : *Assiminea* and *Zostera* zones, on the upper shore, and a sandflat zone. The *Assiminea* zone was a fairly narrow strip (*ca.* 25 m) of shore extending from high water springs to just below high water neaps. The small hydrobiid gastropod *Assiminea globulus* occurred there in densities of up to 71 000 individuals per m^2 (in January 1978). *Zostera capensis* was patchily distributed at high water neaps, with a patch of 2 500 m^2 occurring in the study area. The most abundant organisms in *Zostera* were *Assiminea globulus*, two small crabs *Cleistostoma edwardsii* and *Hymenosoma orbiculare*, and the polychaete worm *Perinereis nuntia* v. *vallata*. The sandflat zone extended from below the *Zostera* zone to low water springs. A diverse fauna was found there similar to that found farther south in the lagoon, at Bottelary (Part 1).

Observations of the birds' foraging were made once a month during January - March 1978 and twice during April 1978, using a 20 - 45X zoom telescope. Foraging rate (number foraging attempts per unit time), success rate

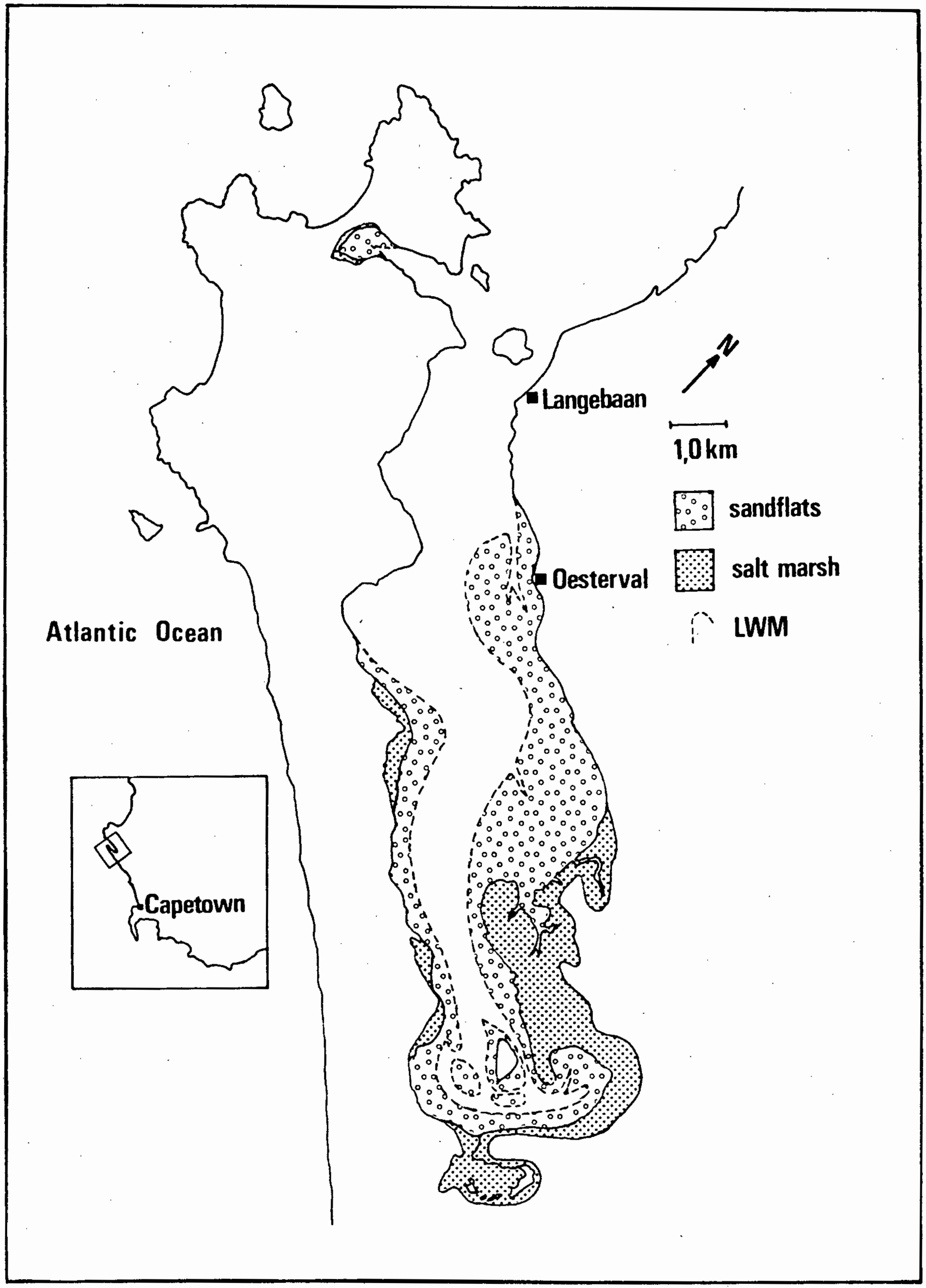

Figure 1. Map of Langebaan Lagoon showing Oesterval study area.

(number prey captured per unit time), distance to nearest neighbour, and foraging habitat were recorded. Observations were made for two-hour periods starting two hours after high tide, when the flats became exposed, and two hours after low tide when the tide had advanced sufficiently to allow observation of what the birds were taking. Prey were sampled in each habitat each month, after foraging observations were completed. Ten core samples of 50 mm diameter and 60 mm depth were taken of the substrate in each habitat and sieved through 0,5 mm mesh to retain the animals. These were sorted in the laboratory, identified and counted, dried at 60°C to constant mass and then weighed.

RESULTS

Foraging and prey density

The foraging rate of curlew sandpipers increased with increasing prey density until a density between 30 000 and 40 000 prey per m^2 was reached (Fig. 2). Foraging rate declined at higher prey densities. A similar relationship was found between the success rate of foraging birds and prey density (Fig. 3). The biomass taken by the birds apparently increased with increasing availability of prey biomass (Fig. 4), but the correlation was not statistically significant ($r = 0,22$, $p > 0,1$). Figure 4 should be

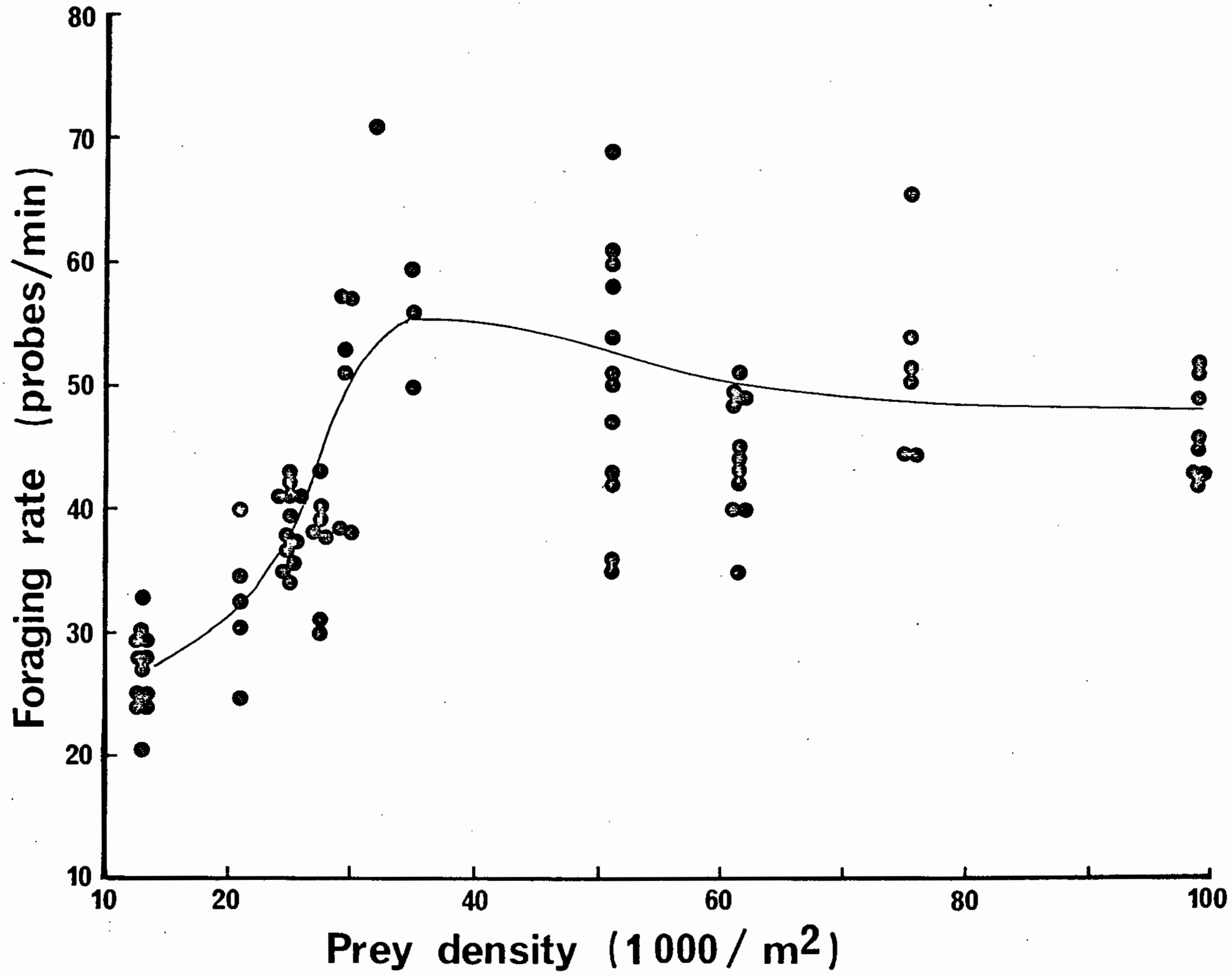

Figure 2. Relationship between foraging rate (Number of probes per min) of curlew sandpipers and prey density in three different foraging habitats combined, from January - April 1978. Each point is the mean of 30 observations.

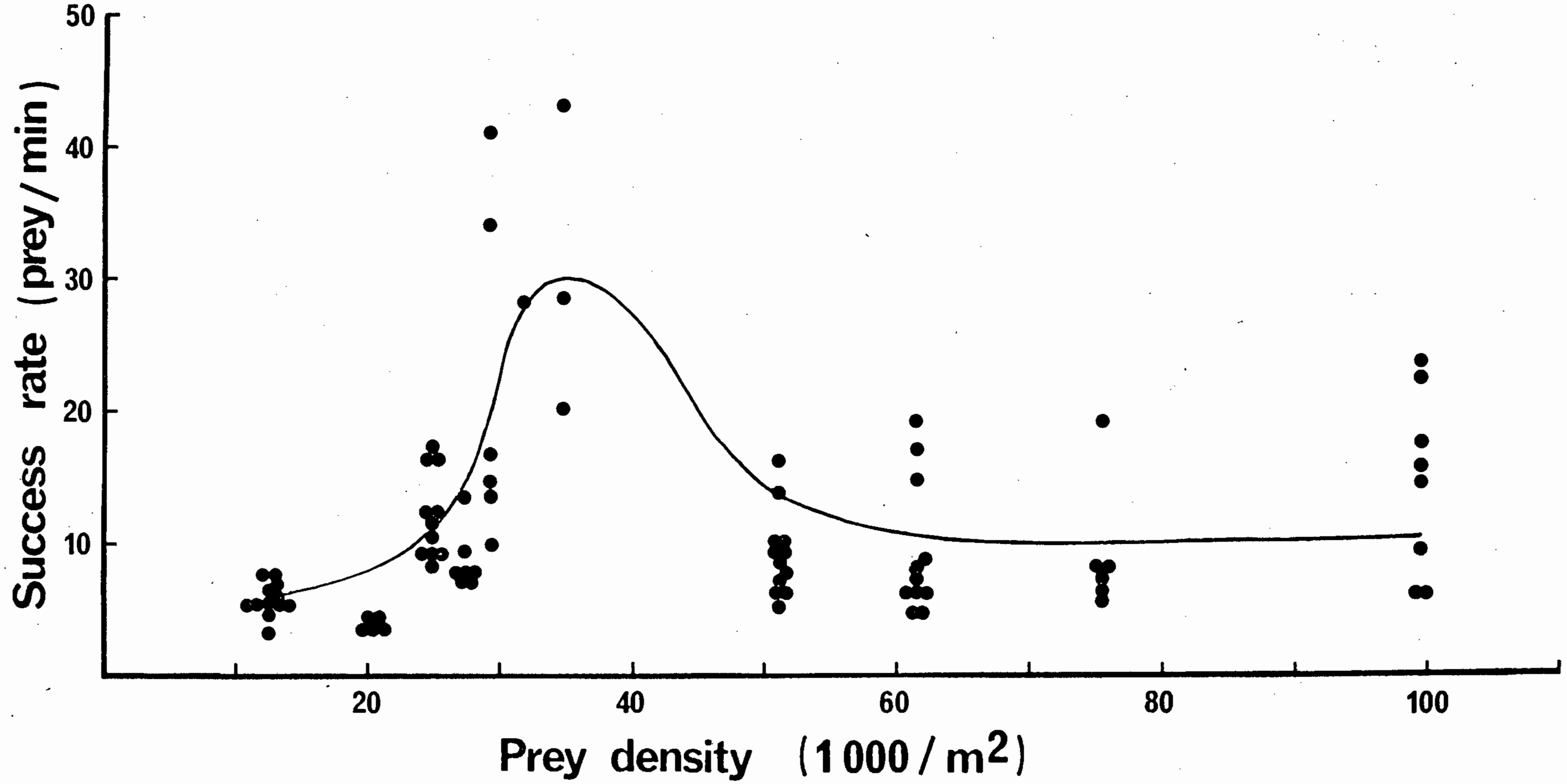

Figure 3. Relationship between success rate (number of prey taken per min) of curlew sandpipers and prey density in three different foraging habitats combined, from January - April 1978. Each point is the mean of 30 observations.

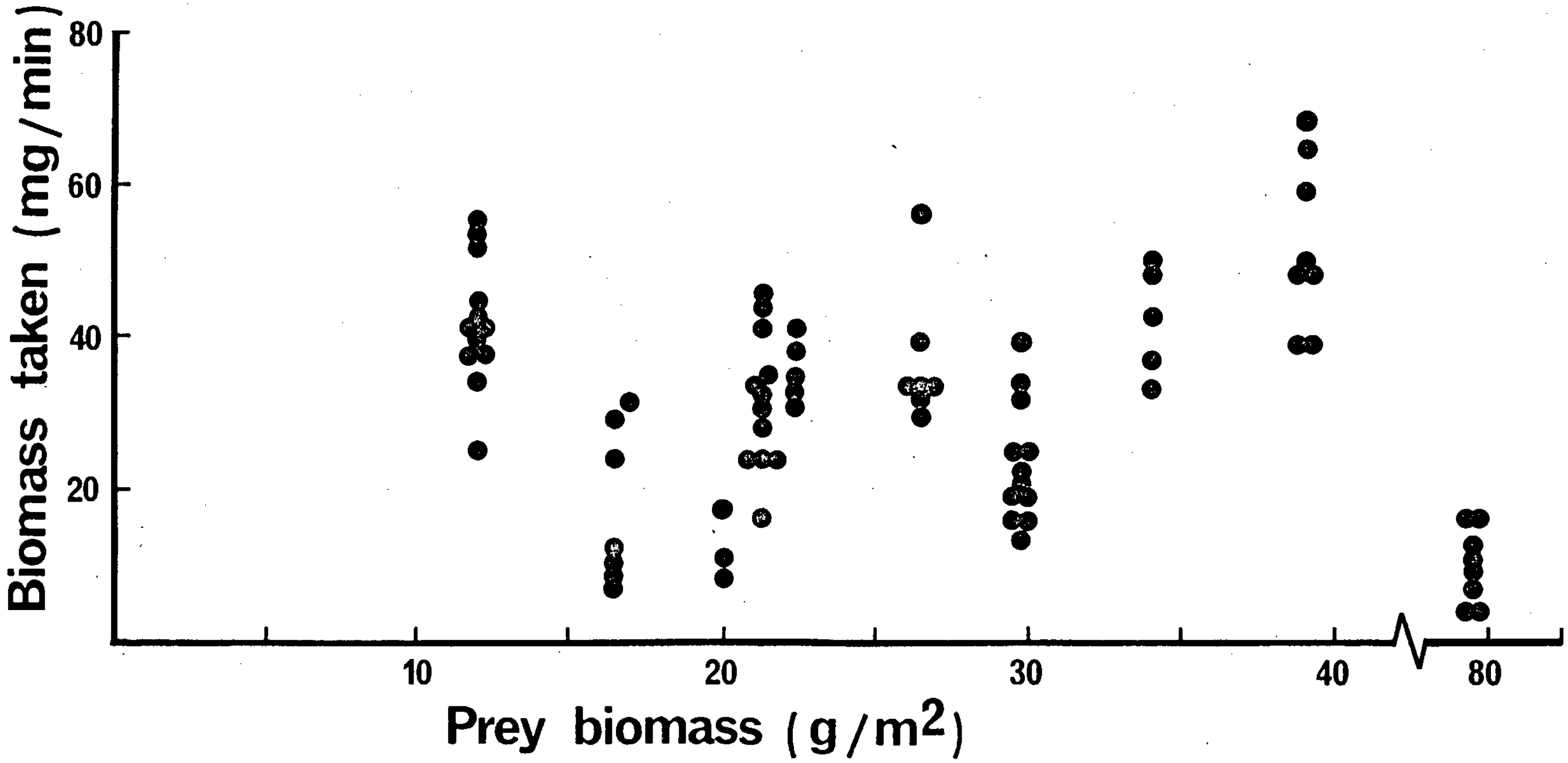

Figure 4. Relationship between prey biomass taken by curlew sandpipers and prey biomass available in three different foraging habitats combined, from January - April 1978. Each point is the mean of 30 observations.

interpreted with caution, because the biomass figures were extrapolated from mean values of prey in the stomachs of curlew sandpipers (Part 2).

In the field, nereid worms, crabs and Assiminea were the only prey items which could be identified definitively when taken by the birds. The remaining prey items, mostly amphipods and bivalves, were grouped and classified as 'small prey'. The relative proportion of nereids to total prey taken ($\frac{n_w}{N_t}$) increased with an increase in the relative proportion available (Fig. 5), but only at a low availability (up to 0,15) of worms. The ratio of worms taken dropped at a higher availability ($>$ 0,4) (Fig. 5). These worms were relatively small (Table 1). At intermediate relative prey densities (0,15 - 0,4), the birds switched to taking 'small prey' ($\frac{n_s}{N_t}$) (Fig. 6). The inclusion of worms in the diet again when their relative available density was higher explains why the proportion of 'small prey' taken dropped slightly (Fig. 6). The relative proportion of crabs taken ($\frac{n_c}{N_t}$) was presumably determined by factors similar to those influencing nereid worms, although the relative density of crabs available was very much lower (Fig. 7). The relative proportion of Assiminea taken ($\frac{n_a}{N_t}$) (Fig. 8) is a reflection of this animals' distribution on the substrate. When the birds fed on Assiminea they did so almost exclusively, since there were relatively few other prey items available.

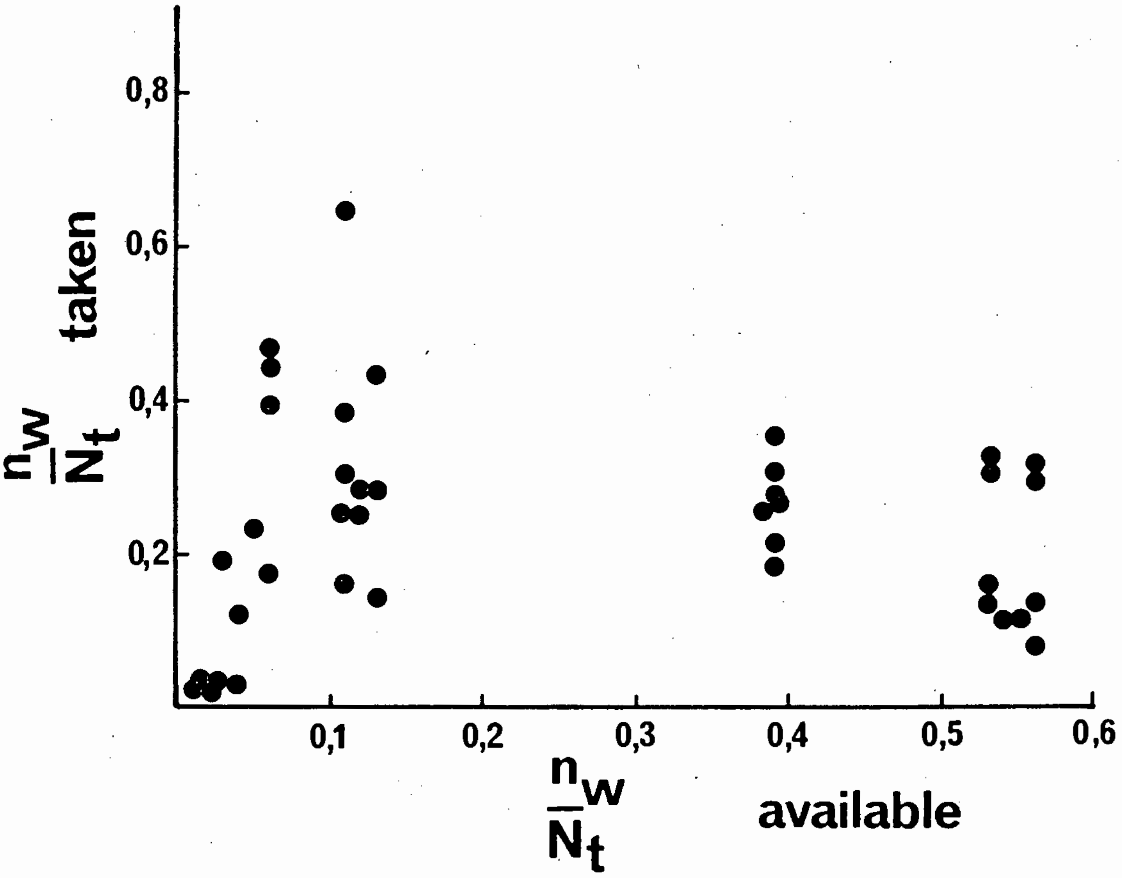

Figure 5. Relationship between $\frac{\text{Number of nereid worms}}{\text{Total number of prey items}}$ taken and $\frac{\text{Number of nereid worms}}{\text{Total number of prey items}}$ available. Each point represents the ratio of prey taken during a 2-hour period of observation.

TABLE 1 Mean mass (g dry weight) of polychaete worms at relative worm densities of 0,01 - 0,15 and 0,4 - 0,5 (see Fig. 5). n = number of core-samples taken.

0,01 - 0,15 density			0,4 - 0,5 density		
$\bar{x}$	S D	n	$\bar{x}$	S D	n
1,62	1,23	15	0,85	0,36	22

z* = 2,74, p = 0,0031

*z = standard normal variate calculated from the Mann-Whitney U-test (Siegel 1956)

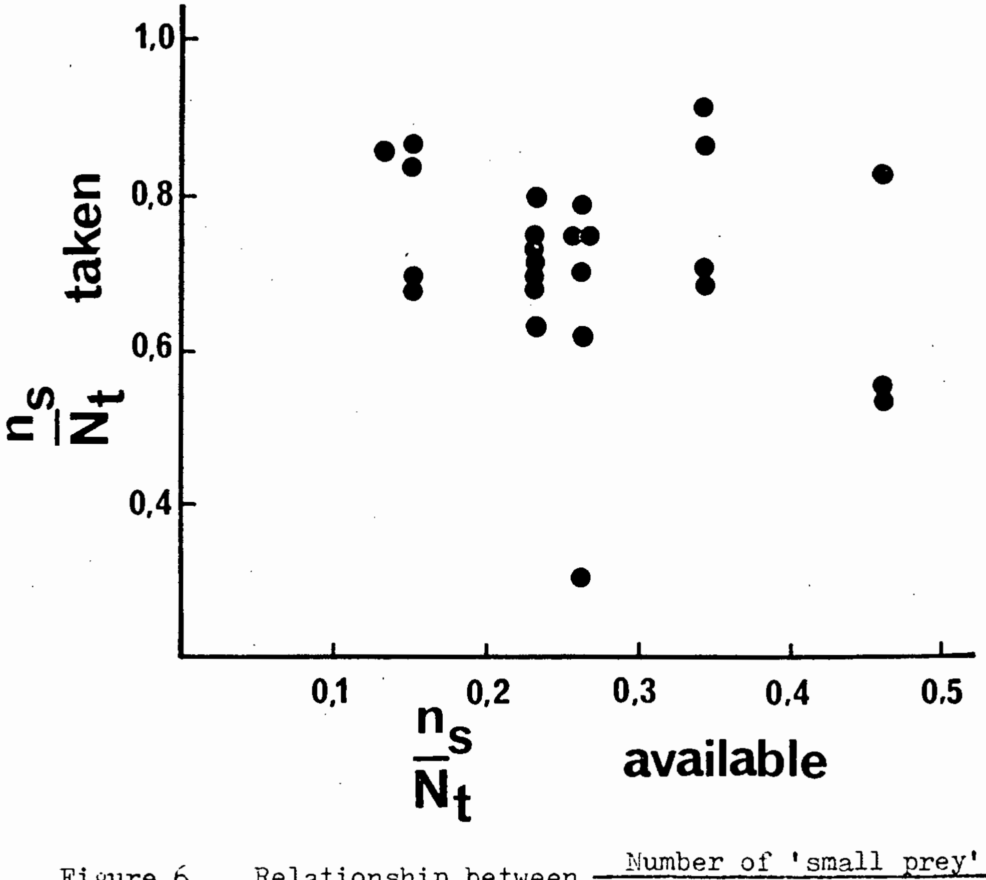

Figure 6. Relationship between $\frac{\text{Number of 'small prey'}}{\text{Total number of prey items}}$ taken and $\frac{\text{Number of 'small prey'}}{\text{total number of prey items}}$ available. Each point represents the ratio of prey taken during a 2-hour period of observation.

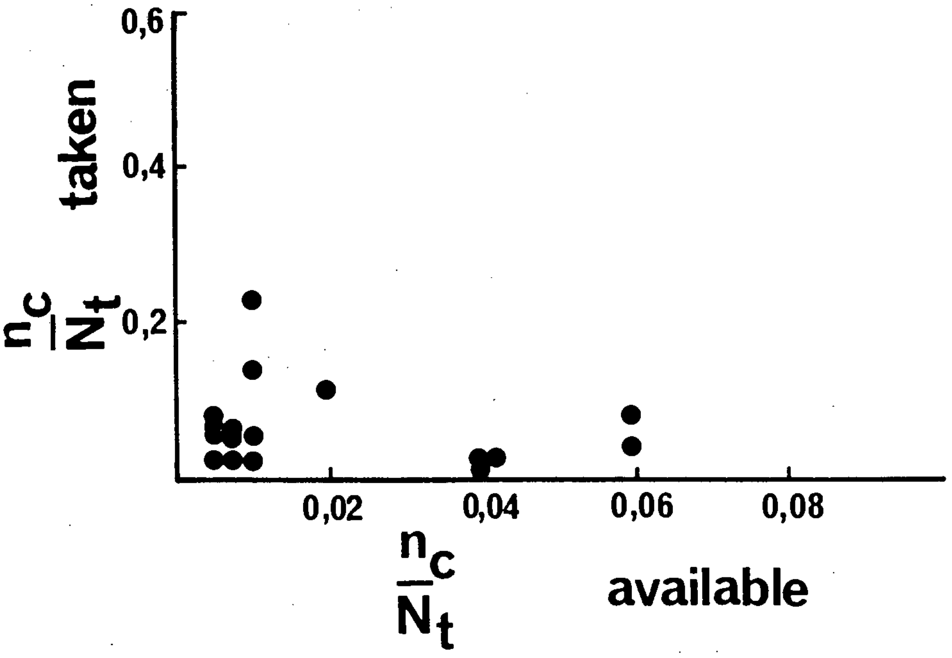

Figure 7. Relationship between $\frac{\text{Number of crabs}}{\text{Total number of prey items}}$ taken and $\frac{\text{Number of crabs}}{\text{Total number of prey items}}$ available. Each point represents the ratio of prey taken during a 2-hour period of observation.

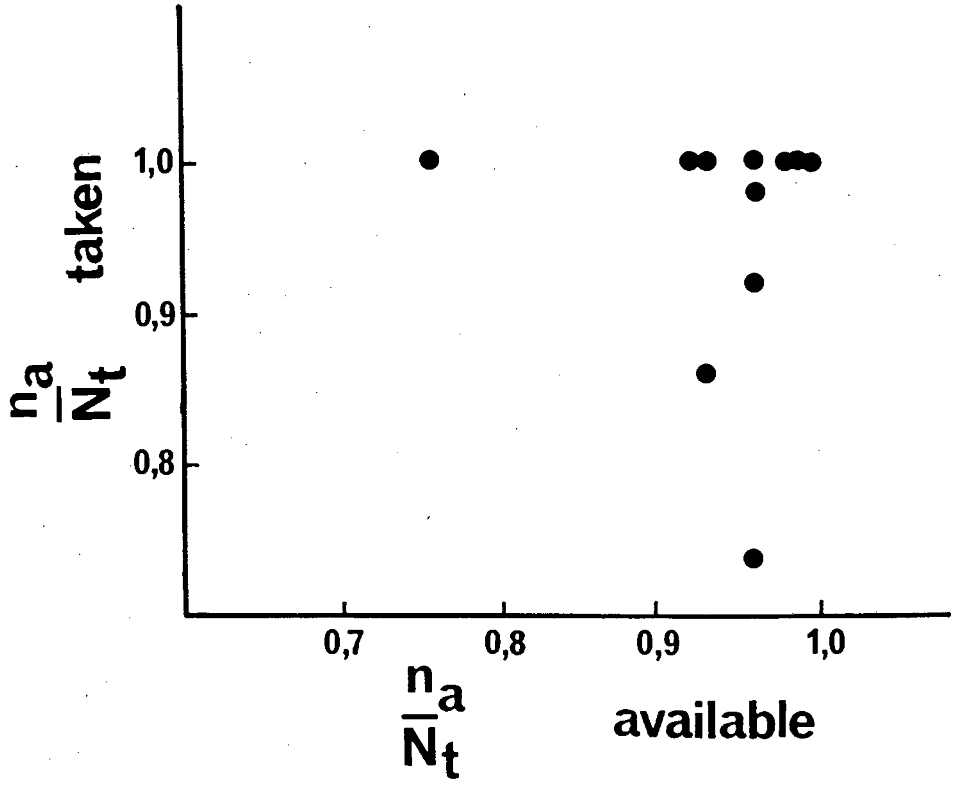

Figure 8. Relationship between $\frac{\text{Number of Assiminea}}{\text{Total number of prey items}}$ taken and $\frac{\text{Number of Assiminea}}{\text{Total number of prey items}}$ available. Each point represents the ratio of prey taken during a 2-hour period of observation.

The size of individual *Assiminea* and of individual *Ceratonereis* occurring in the substrate was negatively correlated with their own densities ($r = 0,67$, $p < 0,001$ for *Assiminea* (Fig. 9); $r = 0,45$, $p < 0,01$ for *Ceratonereis* (Fig. 10)). The size of individual *Urothoe*, however, was positively correlated with its own density (Fig. 11), although the correlation was not statistically significant ($r = 0,34$, $p > 0,1$).

Foraging and bird density

The density of foraging curlew sandpipers increased with increasing prey density until a density of between 25 000 and 35 000 prey per m^2 was reached (Fig. 12). Bird density declined at higher prey densities. Foraging success rate was correlated with bird density ($r = 0,68$, $p < 0,001$), increasing initially but levelling off at higher densities (Fig. 13). Related to this, the frequency of aggressive interactions among foraging birds decreased with increasing distance separating individuals ($r_s = 0,76$, $p < 0,05$) (Fig. 14).

Curlew sandpipers always arrived at the feeding areas in compact flocks including as many as 200 individuals. Soon, however, they dispersed to forage in small, loosely-knit groups which split up and coalesced apparently at random. Most birds in groups foraged between four and

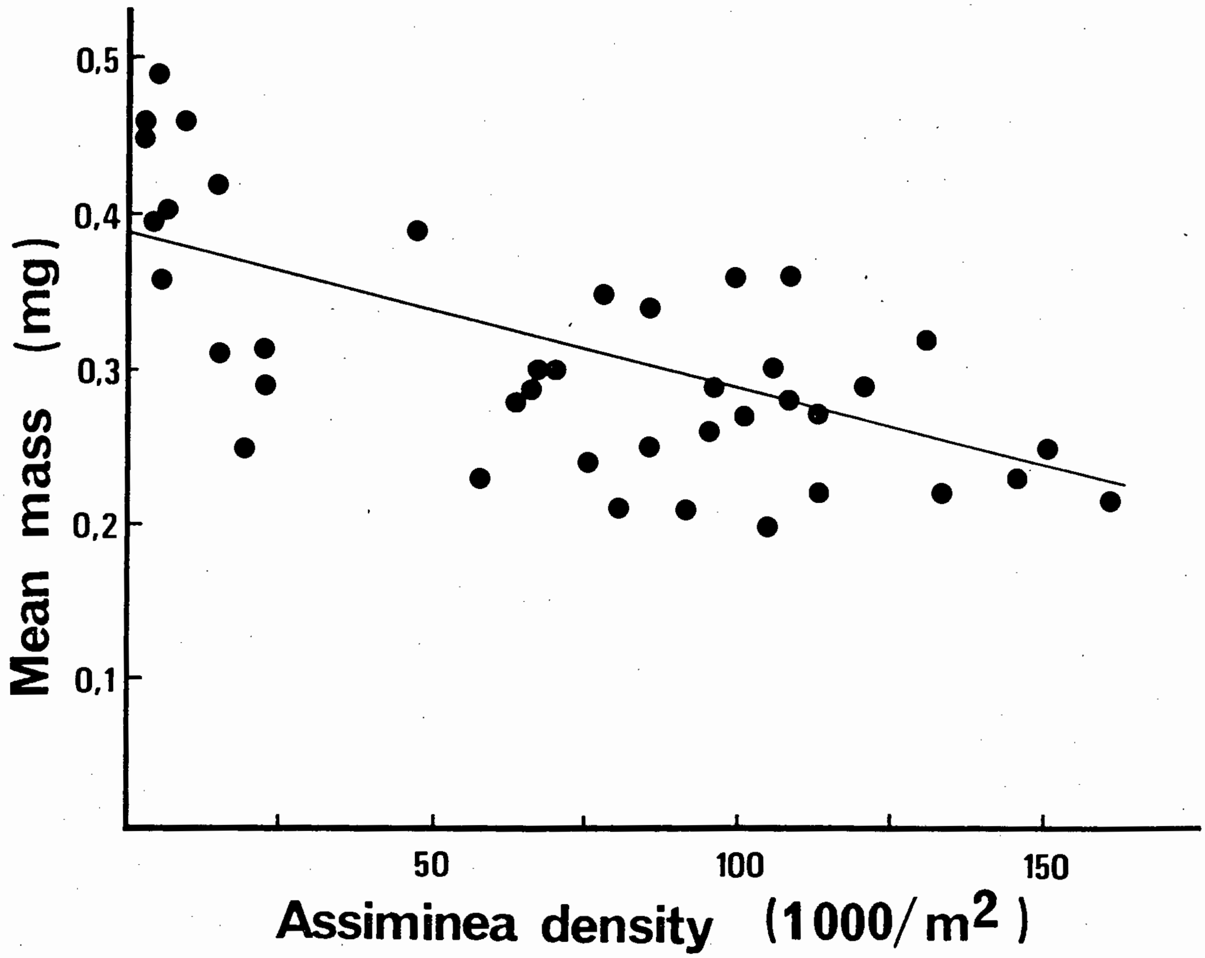

Figure 9. Relationship between mean mass of individual Assiminea globulus and its density on the substrate.

$y = -0{,}01x + 3{,}88$; $r = 0{,}67$; $p < 0{,}001$

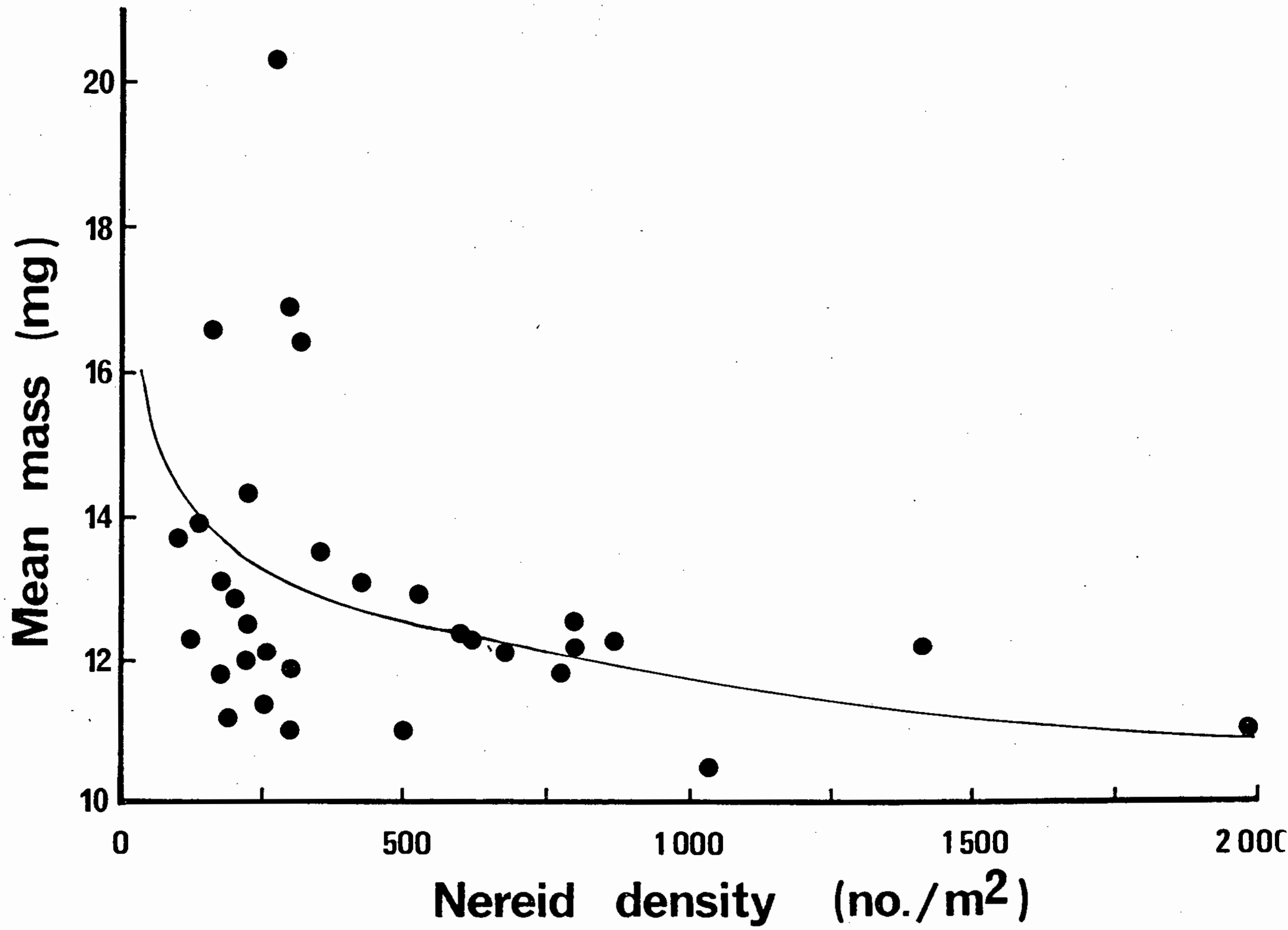

Figure 10. Relationship between mean mass of individual Ceratonereis erythraensis and its density in the substrate.

$y = 21{,}88x^{-0{,}09}$; $r = 0{,}45$; $p < 0{,}01$

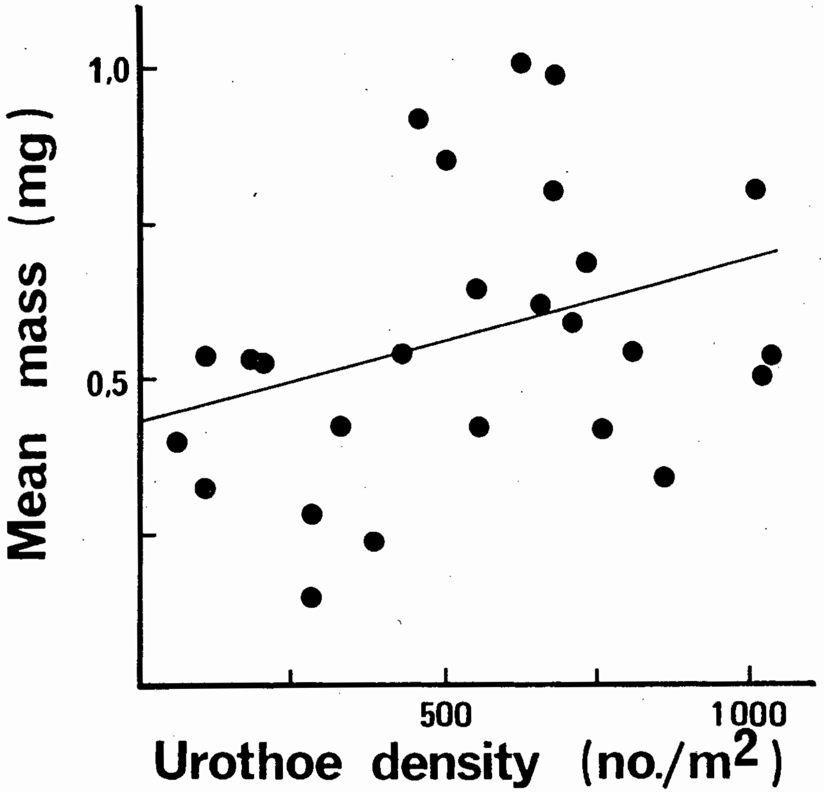

Figure 11. Relationship between mean mass of individual *Urothoe grimaldi* and its density in the substrate.

$y = 0{,}0027x + 0{,}42$; $r = 0{,}34$; $p < 0{,}1$

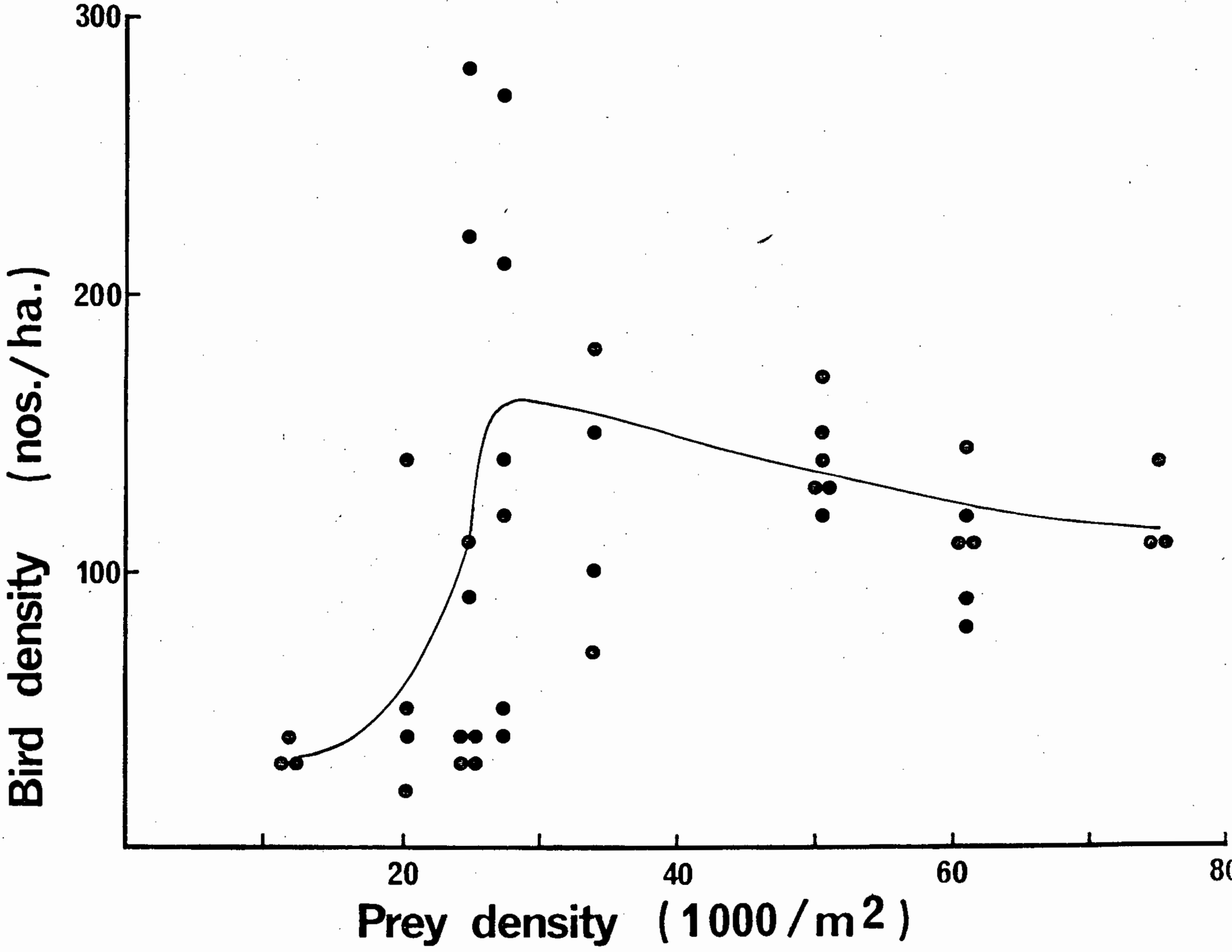

Figure 12. Relationship between density of foraging birds and prey density in three different foraging habitats combined, from January - April 1978.

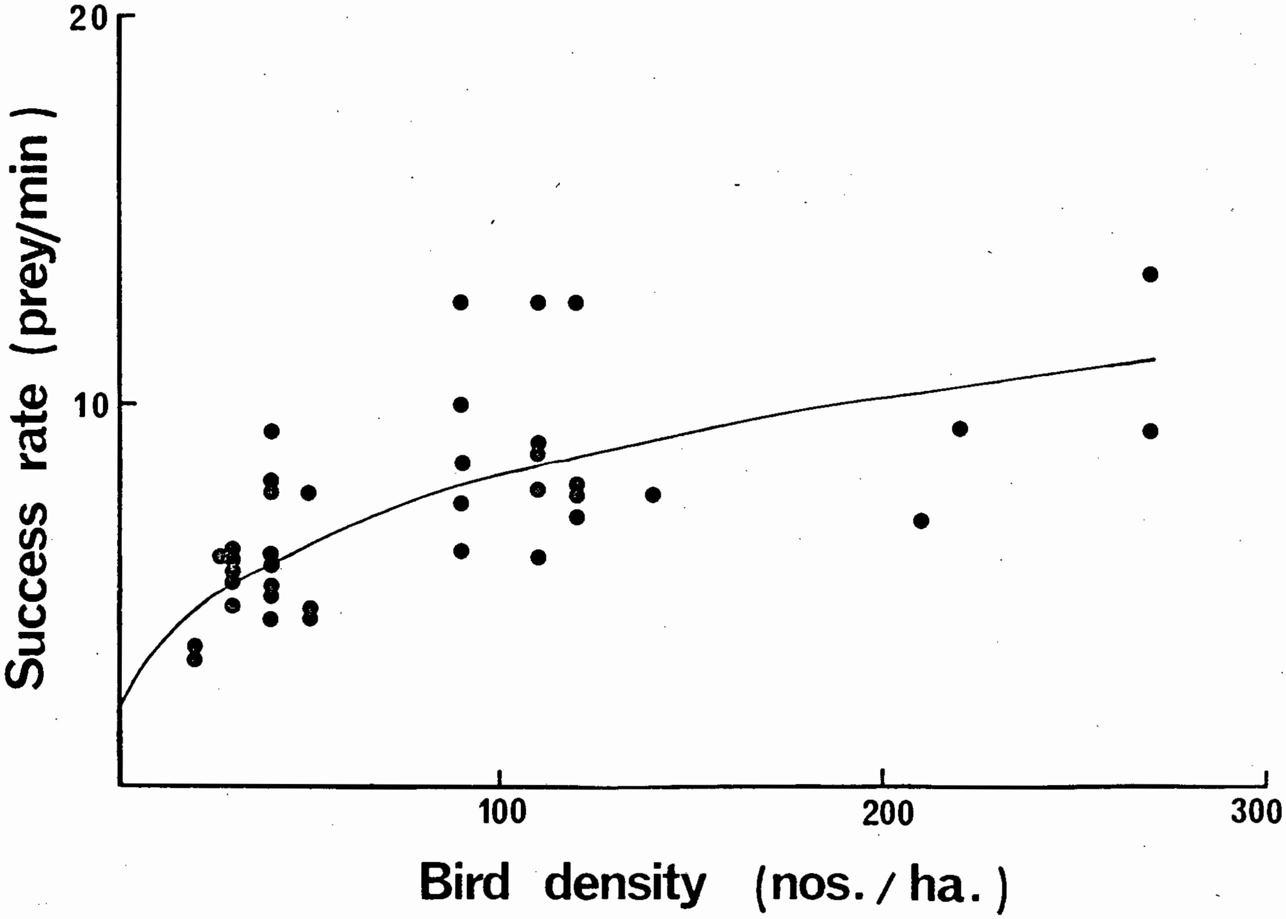

Figure 13. Relationship between success rate of curlew sandpipers and their density while foraging.

$y = 1{,}86x^{0{,}32}$; $r = 0{,}68$; $p < 0{,}001$

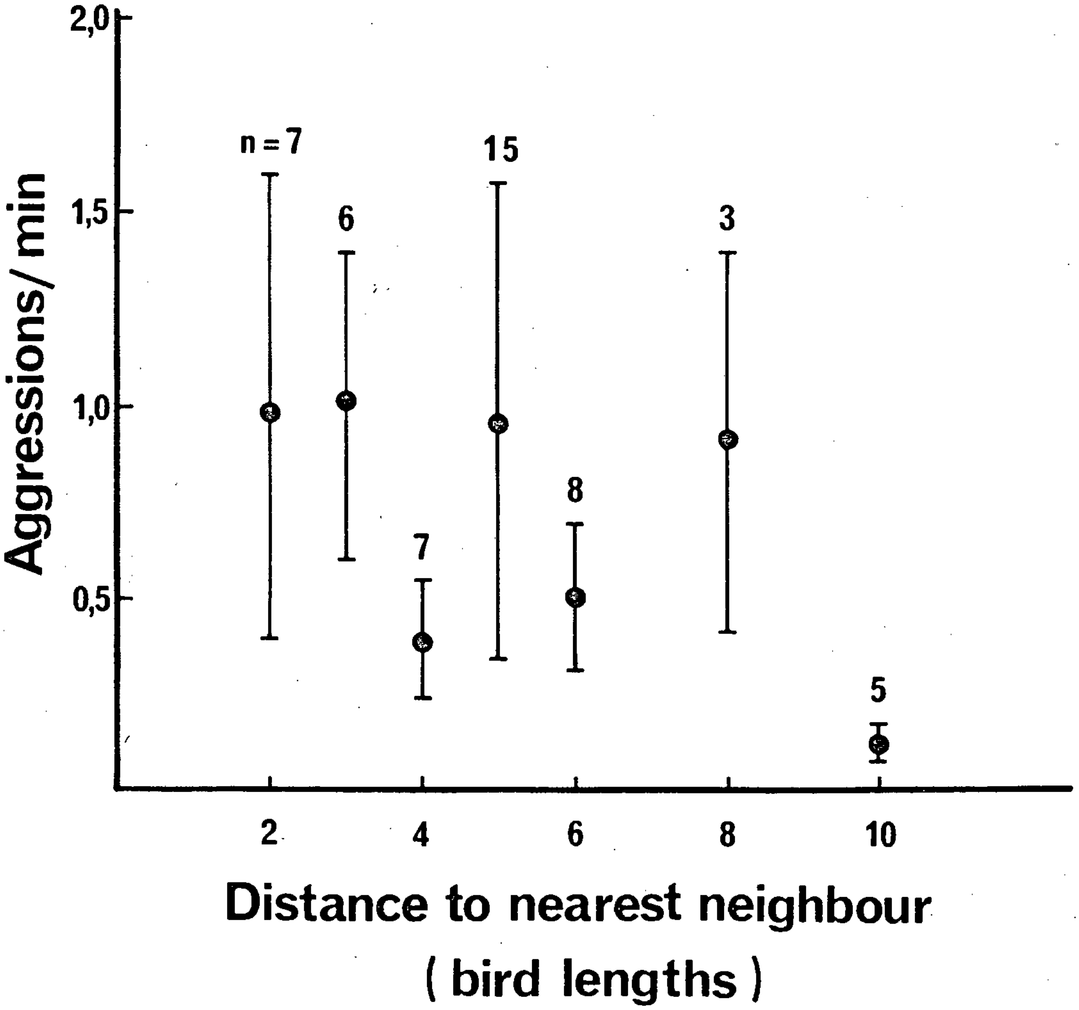

Figure 14. The frequency of aggressive interactions between curlew sandpipers (mean ± S.D.) related to distance separating individuals.

twelve bird-lengths apart (Fig. 15). There was no definitive relationship between either foraging rate or success rate and distance separating birds on the upper shore (Fig. 16). On the lower shore, however, the variance in foraging rate of individuals stationed between 7 and 12 bird-lengths apart was lower than that of individuals less than 7 ($F = 6,27$, $p < 0,01$) and more than 12 ($F = 5,27$, $p < 0,05$) bird-lengths apart (Fig. 17). Success rates were highest when birds foraged 4-6 bird-lengths apart, and decreased significantly with increasing distance apart ($r_s = 0,62$, $p < 0,001$).

DISCUSSION

The foraging and success rates of curlew sandpipers clearly resemble Holling's (1959) type-3 predator response to prey density. The curves are S-shaped in rising to a plateau, and then fall off at higher prey densities (Figs. 2 & 3). This indicates that curlew sandpipers responded to the density of their prey in a way consistent with Royama's (1971) profitability model. To the best of my knowledge, evidence in support of the profitability model (Royama 1971, Alcock 1973, Smith 1974, Goss-Custard 1977a, 1977b, O'Connor & Brown 1977) shows predators responding to variations either in the density of one prey type or to a preferred prey occurring among a few other non-preferred prey types. However, I observed the responses of curlew

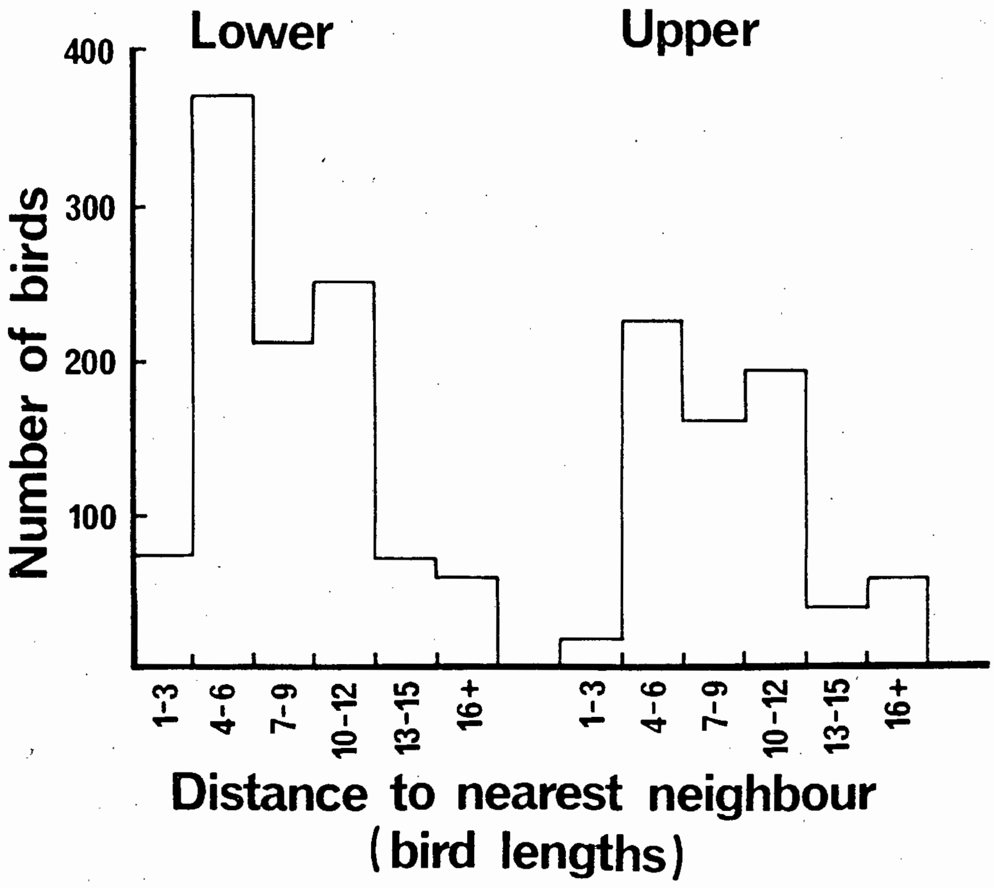

Figure 15. The total number of curlew sandpipers observed foraging in each distance-to-nearest-neighbour category in the upper (Assiminea and Zostera) and lower zones.

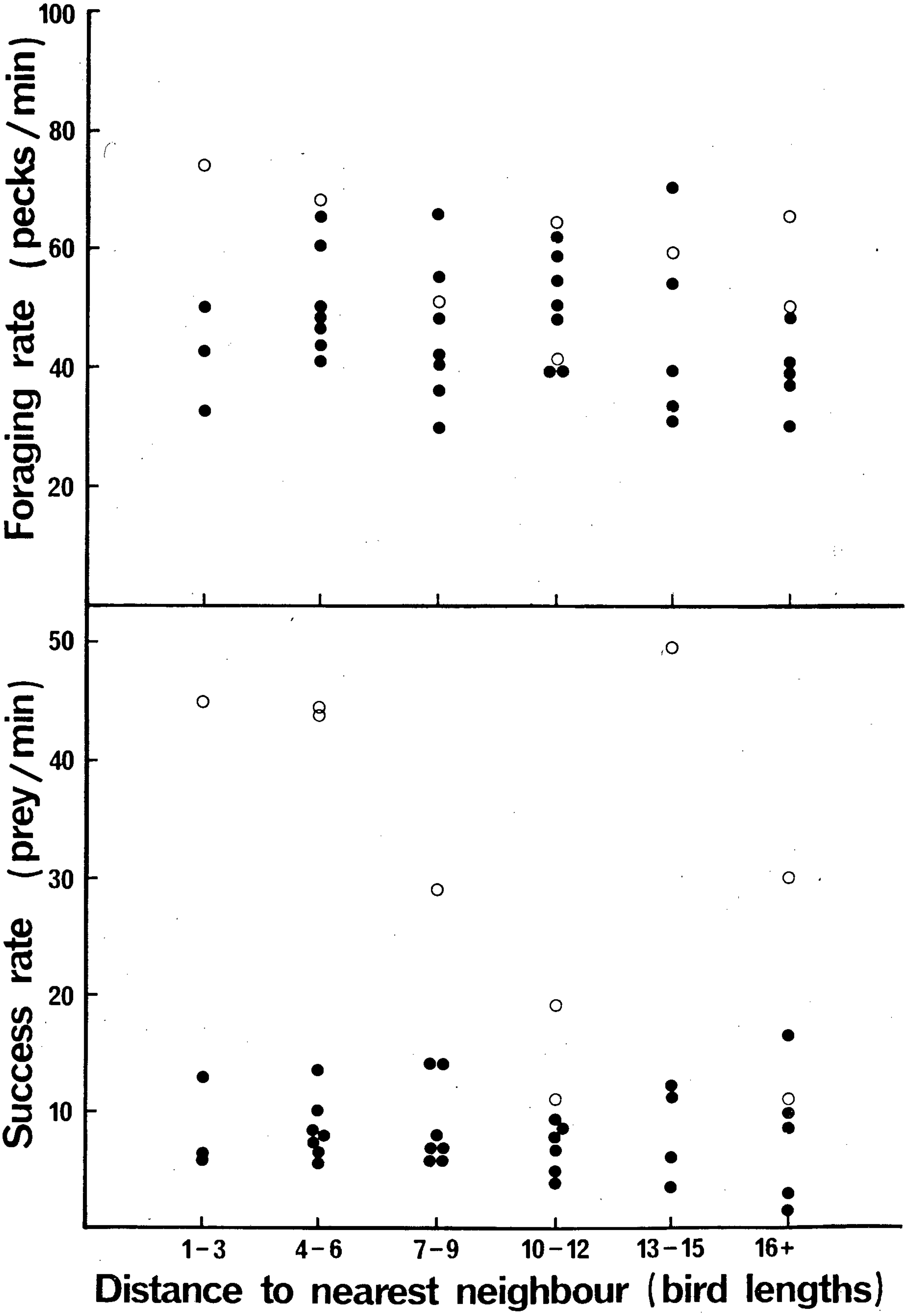

Figure 16. The foraging rate (above) and success rate (below) of curlew sandpipers in the upper (*Assiminea* and *Zostera*) zones in relation to distance separating the birds. Open circles are values for *Assiminea* and dots for *Zostera* zones.

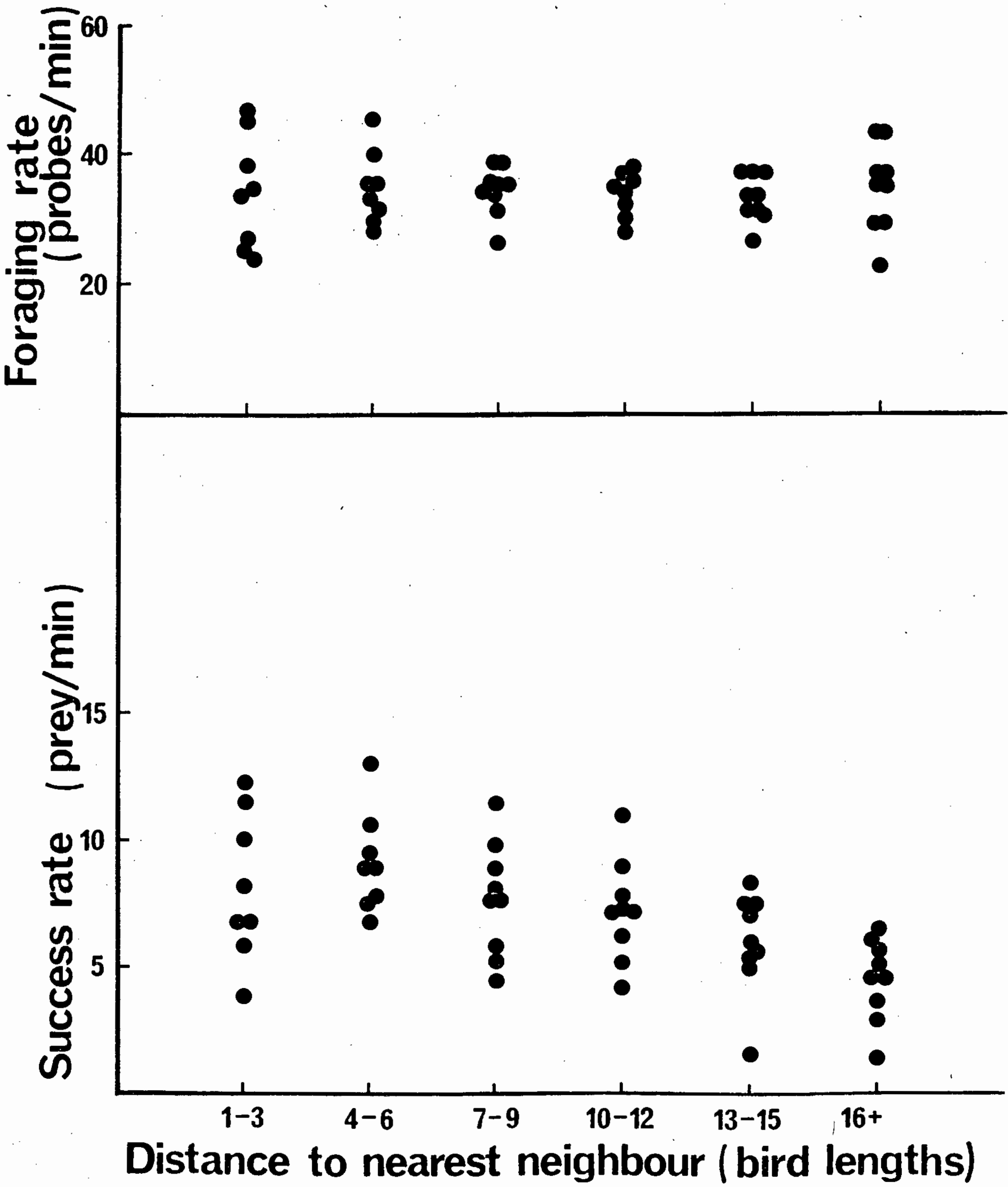

Figure 17. The foraging rate (above) and success rate (below) of curlew sandpipers in the lower zone in relation to distance separating the birds.

sandpipers to variations in prey density within three different prey spectra, and, combined, these show a foraging-prey density relationship consistent with Royama's hypothesis. That is, not only do curlew sandpipers respond to the profitability of different areas within one prey habitat but also to a spectrum of prey habitats. Such a response is implicit in Royama's model : a predator choosing a particular foraging habitat with a particular prey spectrum optimizes intake as much as it does by choosing the optimum prey density areas within that habitat to forage in. Prey biomass taken by curlew sandpipers increased in relation to increasing prey biomass available. This result is also broadly in accord with Royama's profitability hypothesis, although it should be recalled that the figures for biomass taken were extrapolated values (Fig. 4).

Evans (1976) and Goss-Custard (1977a) noted that factors other than prey density influence the allocation of hunting effort by waders in different areas. Prey availability and prey size are two factors which influenced 'selection' of foraging habitat by curlew sandpipers. I shall consider prey availability first. The small gastropod Assiminea globulus is one of the main prey items of curlew sandpipers, based on numerical abundance in gut samples (Part 2). It is abundant on the upper shore at Langebaan Lagoon and is exposed by the tide for longer than any other prey species on the sandflats (Part 1). Yet the birds do not concentrate their foraging activity in this zone but forage lower on the shore, as soon as the tide permits, taking mainly polychaete worms there (Part 2). The snails bury themselves once they have been exposed for some time and the birds then have to probe in order to capture them, an activity which probably requires the expenditure of more energy than pecking at the surface does. Therefore, the birds achieved a high success rate when they fed on surface Assiminea, but temporal changes in the relative availability of the snails presumably made them unprofitable at certain times of the tidal cycle. Other factors which possibly made Assiminea unprofitable, at least at those times when alternative prey were available, were their small size and shells. A curlew sandpiper would need about 890 snails to fill its stomach, and could obtain a maximum of 8 kJ from this (Table 2). Although this is 27% more than the comparable amount of energy obtainable from polychaete worms, the latter of course have no indigestible shell and are presumably digested more quickly and have a faster through-put time. Also, only 27 worms are needed to fill the stomach once, as opposed to 890 snails. Therefore, it appears that curlew sandpipers may be ranking prey types according to profitability (reward per unit handling time) as do captive great tits Parus major (Krebs et al. 1977) and captive ovenbirds Seiurus aurocapillus (Zach & Falls 1978).

TABLE 2 The stomach capacity (4,2 cm^3) of a curlew sandpiper for accommodating different prey items, based on mean size of prey found in stomachs (Part 2) and calorific values obtained by means of microbomb calorimetry (Part 6).

Prey item	Number of prey		Mass (g)		Energy content (kJ)	
	$\bar{x}$	S D	$\bar{x}$	S D	$\bar{x}$	S D
<u>Assiminea</u>	887	24	0,6	0,3	8,0	4,5
Nereid worm	27	1	0,3	0,1	5,8	2,3
Crab	23	4	0,8	0,2	9,1	2,6
Amphipod	582	89	0,5	0,1	9,4	2,1

Royama (1971) attributed the drop-off in percentage predation at high prey densities to social interaction among predators. Goss-Custard (1970) suggested that high densities of redshank foraging on high densities of Corophium altered the availability of the prey, either by driving them deeper into their burrows or by causing local depletions. Redshank foraging by sight also showed decreased foraging rates at high bird densities due to intraspecific interference (Goss-Custard 1976). However, greatest curlew sandpiper densities occurred at prey densities of 25 000 - 35 000 individuals per m^2, while greatest success occurred at higher prey densities (30 000 - 40 000 individuals per m^2). Hence, some factor reduced bird density before optimal success rates were reached, not after, which would be expected if it were social interaction causing the decrease in success rate at high prey density. Intraspecific interference and local prey depletion cannot be discounted as factors involved in decreasing success rates at high prey densities. However, evidence for individual prey size, especially of Assiminea, being smaller at high prey densities (Table 1, Figs. 9 & 10), the fact that size classes of Assiminea were spatially segregated (Part 1), and the fact that the birds tend to select larger Assiminea (Part 2), may mean that profitability was decreased at these densities, and this would account for a lower success rate. Conceivably, birds must sample a wider area when they begin to encounter smaller prey at higher densities, and this would reduce their success rate.

O'Connor & Brown (1977) found that size classes of cockles *Cerastoderma edule* were spatially segregated in Strangford Lough, Northern Ireland. Oystercatchers *Haematopus ostralegus* annually concentrated their foraging effort where second-winter cockles were located, and only exploited areas where smaller cockles were located later in the season. However, Goss-Custard (1970) found that high densities of large *Corophium* and low densities of small *Corophium* occurred at the Ythan estuary, Scotland, and Fig. 11 suggests that this may have been so for *Urothoe* at Langebaan also. But *Urothoe*, unlike *Corophium* which is the main prey item of redshank, was a relatively less important component of the curlew sandpipers' diet. Royama's (1971) profitability model, for curlew sandpipers at least, does not take into account that at high prey density the prey may be smaller, and that this may result in a drop-off of predation success. Figure 18 summarizes the proposed relationships between prey and bird densities and optimal foraging success in the curlew sandpiper.

As discussed above, prey size, apart from affecting the profitability of different foraging areas and hence the birds' choice of foraging habitat, must also affect the predators' choice of actual prey item. The response of curlew sandpipers to the relative density of specific prey items is explicable in terms of the size of these items and of their distribution. The birds took increasing

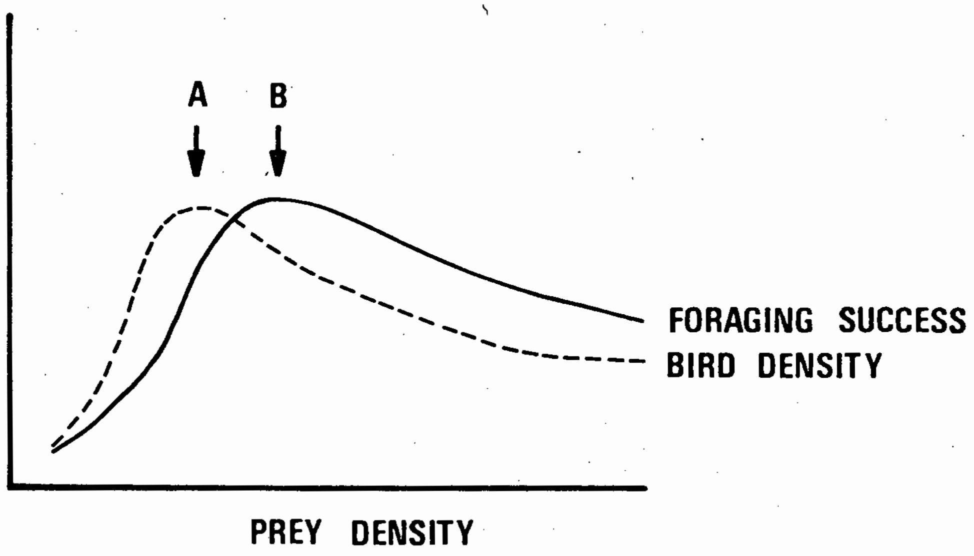

Figure 18. Bird density and optimal foraging success in relation to the density of prey. At A social factors operate to reduce bird density. At B birds begin to encounter smaller prey and profitability is thereby reduced.

numbers of polychaete worms with increasing numbers available, but only at low relative densities. At slightly higher relative densities, the birds switched to 'small prey' items; at still higher relative densities worms were again included in the diet. The worms accounting for the two relative densities (0,01 - 0,15 and 0,4 - 0,5) were significantly different in size (Table 1), and it is possible that they represented two age classes.

Because foraging success rate and bird density had the same relationship to prey density (Figs. 3 & 12), it follows that success rate should increase with bird density until a plateau is reached (Fig. 13). In effect, the birds were concentrating their foraging efforts where profitability was highest. Thus, feeding in flocks or loose groups was positively correlated with enhanced success rates. The greatest number of birds foraged 4 - 12 bird-lengths apart, and the highest success rate coincided with this density, at least in the lower zone. Also, the foraging rate was least variable in those individuals which foraged between 4 and 12 bird-lengths apart. An increase in aggressive interactions among foraging curlew sandpipers when they were closer together counteracted an increase in bird density.

Bar-tailed godwit <u>Limosa lapponica</u>, knot <u>C. canutus</u> and great blue heron <u>Ardea herodias</u> were all more successful feeding in flocks than alone (Smith & Evans 1973, Prater 1973, Krebs 1974). Page & Whitacre (1975) suggested that predation was a strong selective force causing flocking in waders at Bolinas Lagoon, California. Silliman _et al._ (1977) suggested that a relatively high foraging rate of sanderlings _C. alba_ in flocks was due to the birds spending less time watching for predators. However, no diurnal predation on foraging curlew sandpipers has been observed at Langebaan, where ornithologists have spent hundreds of days observing waders. While predation cannot be discounted as a factor promoting flocking, it appears likely that foraging curlew sandpipers gathered together in response to optimal prey densities.

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Part 5

Sex-related differences in foraging behaviour of curlew sandpipers

SUMMARY

1. Differences in foraging behaviour and spatial distribution of male and female curlew sandpipers are described.

2. Males and females occurred more often in segregated than in mixed groups, and agonistic behaviour was more frequent in single-sex than in mixed groups.

3. Females foraged faster than males and achieved a higher success rate.

4. It is suggested that competition on the breeding grounds rather than on the wintering grounds, and the fact that females alone incubate the eggs, both favour sexual dimorphism in the species, since food does not appear to be limiting in southern Africa.

INTRODUCTION

The curlew sandpiper *Calidris ferruginea* exhibits sexual dimorphism, as do other *Calidris* species, with females being larger than males (Thomas & Dartnall 1970, Elliott *et al*. 1976). Females exploit a slightly different food spectrum, taking a wider size range of prey items but fewer prey species than males (Part 2). This seems to imply that spatial segregation occurs between the sexes and that competition for food is reduced. Elliott *et al*. (1976) found a sex ratio of 1:1,23 favouring females and concluded that an excess of females exists in the species. They suggested that being larger may allow females to compete more successfully than males in times of food shortage.

This paper describes patterns of resource utilization by male and female curlew sandpipers at Kommetjie beach, South Africa, and discusses possible factors favouring the evolution of sexual dimorphism in the species.

STUDY AREA AND METHODS

The shoreline at Kommetjie (34 08°S, 18 19°E) is composed of rocky platforms interspersed with sheltered sandy beaches, which usually have a heavy deposit of kelp *Ecklonia maxima* and of other seaweeds at or near high water mark. During summer the weed harbours large numbers of fly larvae and pupae (Family Muscidae). Curlew sandpipers, and other waders, roost on the rocks at high tide and forage among the weed when retreat of the tide allows.

Ninety-seven curlew sandpipers were mist-netted after dark near their roosting area during 4 November - 6 December 1977. On 15 December 1977 108 birds were cannon-netted in the early morning at their feeding area. The birds were colour-ringed to accord with four culmen 'classes' : culmens<36mm in length, 37-38mm, 39-40mm and>41mm. Since females have significantly longer culmens than males (Elliott et al. 1976), I treated the first two classes as males and the second two as females. A total of 800 observations of the birds' foraging was made from a vehicle parked near the study beach, or occasionally from a vantage point on the beach itself, using a 20 - 45X zoom telescope. The following parameters were recorded : foraging rate (probes per min), success rate, 'colour' of the bird observed and the distance to it's nearest neighbour, identity of prey taken, and occurrence of agonistic behaviour. In addition, the occurrence of colour-ringed birds foraging in groups was noted, as well as the frequency of agonistic behaviour in these groups. Prey density was sampled in January and March 1978 by collecting all the weed within two 0,25 m^2 quadrats to a depth of 6 cm (assumed to include all the food potentially available to the birds since they have a maximum culmen length of 45mm), and later sorted by hand in the laboratory. Prey items were identified to ordinal level and counted, dried to constant mass at 60°C and weighed. Their energy content was determined using a Phillipson microbomb calorimeter.

The non-parametric statistical tests used in the analysis of data are described in Siegel (1956).

RESULTS

Thomas & Dartnall (1970) and Elliott *et al.* (1976) showed that female curlew sandpipers were significantly larger than males in wing, culmen and tarsus length. The mean mass of females is also significantly higher than that of males (Table 1). Evidence for a sex ratio in favour of females is equivocal. I found that females slightly outnumbered males at Langebaan Lagoon and that males outnumbered females at Kommetjie (Table 2).

Both the biomass and numbers of prey potentially available to curlew sandpipers were relatively high in the stranded weed at Kommetjie (Table 3). The fly larvae and pupae occurred 0,5 - 4 cm below the surface of the weed layer. Foraging close together in compact groups, the birds fed almost exclusively on these, using multiple probes into the weed to extract their prey. Three birds were

TABLE 1 Mean mass (g fresh weight) of curlew sandpipers at Langebaan Lagoon during 1974-5 (see Part 2 for further particulars)

Sex	No. birds	Mean	S.D.	t	p
Female	103	62,71	5,45	3,09	<0,01
Male	106	60,51	4,79		

TABLE 2 Sex ratios of curlew sandpipers in the south-western Cape.

Number birds		Ratio	z	p	Location	Source
Female	Male					
129	127	1,02 : 1	0,06	0,88	Langebaan	Puttick, unpubl. data
123	103	1,19 : 1	2,47	0,01	Langebaan	Elliott *et al.* 1976
2 076	1 635	1,27 : 1	14,64	<0,0006	Langebaan	Elliott *et al.* 1976
37	49	0,76 : 1	2,51	0,01	Kommetjie	Present study (mist-netted)
50	58	0,86 : 1	1,51	0,13	Kommetjie	Present study (cannon-netted)

TABLE 3 Biomass (g dry weight ± S.D.) and numbers of prey potentially available to curlew sandpipers in stranded weed at Kommetjie.

Month	Prey item	Biomass (g/m^2)	Numbers (per m^2)
January 1978	Oligochaetae	2,13	26 560
	Muscidae (larvae)*	12,37	4 416
	Muscidae (pupae)	33,44	11 814
	TOTAL	46,94 ±6,20	42 560 ± 1 452
March 1978	Oligochaetae	0	0
	Muscidae (larvae)*	33,28	6 400
	Muscidae (pupae)	44,55	4 736
	TOTAL	77,83 ± 10,30	11 136 ± 380

* Energy content 25,8 kJ/g

accidentally killed by the cannon-net. Examination of their stomach contents confirmed that they were taking fly larvae and pupae. Aggressive interactions among the birds was related to the distance between them ($r_s = 0{,}93$, $p < 0{,}01$) (Figure 1). Males and females occurred significantly more often in segregated than in mixed groups (Kolmogorov-Smirnov one-sample test $K_D = 0{,}81$, $n = 3$, $p < 0{,}01$) (Table 4). The frequency of aggressive interactions was significantly higher among birds in single-sex than in mixed groups ($\chi^2 = 10{,}84$, $df = 2$, $p < 0{,}01$) (Table 5), and more frequent between males than females ($\chi^2 = 5{,}12$, $df = 1$, $p < 0{,}05$).

Females foraged significantly faster than males in four out of eight comparisons made (Table 6), although they foraged faster than males in ten out of eleven cases altogether. Females also achieved significantly greater foraging success ($K_D = 6$, $n = 11$, $p < 0{,}05$) than males (Table 7).

DISCUSSION

Elliott _et al_. (1976) have suggested that being larger allowed female curlew sandpipers to out-compete males in times of food shortage, and that this explained why they found an excess of females at Langebaan Lagoon. However, food is apparently not in short supply at Langebaan Lagoon (Part 6) nor at Kommetjie, so this seems an

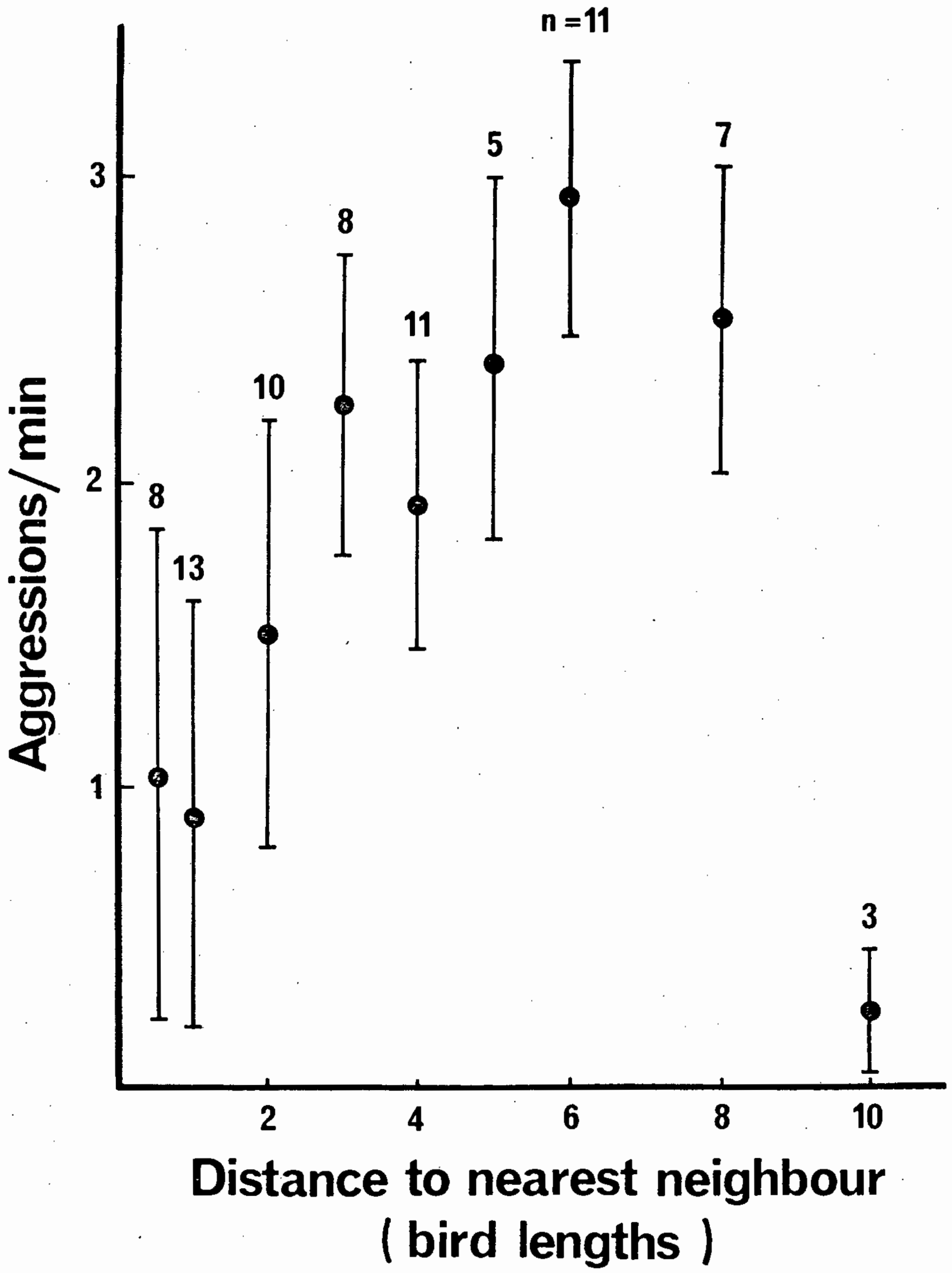

Figure 1. Frequency of agonistic behaviour between curlew sandpipers foraging in flocks in relation to the distance separating individuals. Bars indicate ± 1 S.D.

TABLE 4 Frequency of sexual segregation in foraging curlew sandpipers, based on observation of 53 colour-ringed groups.

	No. groups observed	
Female	Male	Mixed
24	19	10

TABLE 5 Frequency of agonistic behaviour among colour-ringed curlew sandpipers while foraging. A total of 34 aggressive interactions was observed.

Female[1]	Male[1]	Mixed[2]
10	23	6

[1] Observed 4-6 March 1978

[2] Observed 14-16 February 1978

TABLE 6 Comparison of foraging rates (probes per min) between male and female curlew sandpipers while foraging both in single-sex and mixed flocks. In three cases no t-test was possible, because variances were large (see F values in footnote)

Date	Females			Males				
	n	Mean	S D	n	Mean	S D	t	p
6.12.77	22	29,23	12,69	37	32,14	9,39	No test[1]	
19.12.77	18	33,99	10,59	15	33,52	6,60	No test[2]	
18. 1.78	74	36,86	7,83	54	33,20	8,27	2,57	<0,02
19. 1.78	49	36,36	8,99	63	33,18	8,93	1,87	<0,1
14. 2.78	28	36,72	9,32	36	34,57	9,76	0,89	NS
15. 2.78	39	40,83	9,89	38	37,28	7,49	1,78	<0,1
16. 2.78	37	35,37	10,60	45	30,21	7,65	2,48	<0,02
2. 3.78	46	38,00	8,94	27	34,28	6,24	2,08	<0,05
3. 3.78	40	38,94	10,99	25	34,02	8,11	2,07	<0,05
4. 3.78	33	39,44	10,23	24	33,83	11,82	1,87	<0,1
7. 3.78	15	38,24	7,09	14	37,42	11,30	No test[3]	

[1] F = 1,82, p <0,05

[2] F = 2,57, p <0,05

[3] F = 2,95, p <0,05

TABLE 7 Comparison of foraging success (prey taken per min) between male and female curlew sandpipers while foraging both in single-sex and mixed flocks.

Date	Females	Males
6.12.77	7,89	4,69
19.12.77	15,89	10,46
18. 1.78	15,41	10,16
19. 1.78	15,78	10,68
14. 2.78	11,75	8,61
15. 2.78	16,98	8,65
16. 2.78	12,87	9,43
2. 3.78	13,00	7,82
3. 3.78	11,60	7,62
4. 3.78	12,46	9,00
7. 3.78	11,24	12,80

unlikely explanation. It seems more likely that the ratio in favour of females may have been an artefact of collection method since ratios in favour of males were also obtained (Table 2). There is evidence that sexual segregation occurs among curlew sandpipers (Table 6) and this may have affected capture ratios, since sampling may have been biased. The total number of birds from which ratios have been obtained (4 387 birds) represents slightly less than 8% of the total summer population that occurred in the south-western Cape in 1974 (Pringle & Cooper 1975). It is possible that this sample was not large enough to provide an accurate estimate of a population parameter such as sex ratio. Sampling should also span several seasons in order to account for possible differences in sex distribution between years.

Sexual dimorphism may reduce intraspecific competition for food (Pianka 1974), and the composition of the diets of male and female curlew sandpipers reflected this (Part 2). Baker & Baker (1973) concluded that resource partitioning among waders in North America was greatest in wintering areas and density-dependent mortality acted then to limit population size. They based this conclusion on the observation that foraging diversity was lowest on wintering grounds, assuming that foraging diversity is a measure of resource diversity. However, high resource diversity does not necessarily imply high availability. Foraging diversity of curlew sandpipers on the sandflats at Langebaan Lagoon during the austral spring and summer did not comply with their assumption (Part 3). Also, food supplies were high during the austral summer at Langebaan Lagoon (Part 1) and it appears that food is not limiting (Part 6). However, Siegfried (in prep.) notes that food may not be limiting to migrant waders in southern African estuaries since southern Africa is right at the end of the curlew sandpiper's wintering range and consequently they may be exploiting only a part of the available resources. He concludes that if food is not limiting, then conditions outside southern Africa could be responsible for competition between the sexes and for the apparent disparity in sex ratio.

Apart from reducing intraspecific competition for food, larger female body size may also be related to the fact that only the females incubate the eggs (Holmes & Pitelka 1964). Presumably, they require extra energy reserves for this. Holmes & Pitelka noted that the female may also undertake nest construction alone. Egg production is another energy drain for which extra energy reserves are necessary. Elliott et al. (1976) found that fat content and fresh mass of birds was linearly related, which means that females would accumulate a larger fat store than males on account of their larger body size. It would be interesting to monitor the relative rate at which males and females accumulate fat reserves prior to migration. Larger body size also means that females are more efficient fliers (Burger & Hart 1974), meaning in turn that they should consume relatively less energy for migration. Conceivably, they would have a larger energy reserve on arrival at the breeding grounds.

The fauna associated with the stranded weed at Kommetjie constituted a rich and readily available food source for curlew sandpipers, equalling or exceeding that which occurred in the rich lagoonal system at Langebaan (Part 1); and the fly larvae had a high energy content (Table 3). Thus, the birds appeared able to meet their daily energy requirements in 1½ - 2 h (females) and 1 - 3 h (males) at Kommetjie (based on energy requirement calculated in Part 6 and foraging success in Table 7). These periods were considerably shorter than those found at Langebaan (Part 3). Although the foraging birds were frequently disturbed by human activities (since the beach lies adjacent to an urban area and is heavily used for recreational purposes), presumably food resources were high enough to offset this disadvantage.

Recher & Recher (1969) suggested that aggression among dense aggregations of wading birds would be suppressed if high concentrations of food were present, and this seemed to occur at Kommetjie (Figure 1). Here curlew sandpipers normally foraged 0,5 - 3 bird lengths from each other (pers. obs.) and aggressive interactions were relatively infrequent. The prey were also relatively immobile and therefore not disturbed by the birds' foraging close together. In such a situation, it was advantageous to suppress aggression and so enhance foraging efficiency.

Curlew sandpipers showed indications of spatial segregation between the sexes while foraging at Kommetjie (Table 4). Spatial segregation is another means whereby competition for food is reduced. Hence, although prey density was high at Kommetjie, birds densities were also high (up to 15 birds per m^2) and this may have accounted for the incidence of spatial segregation. Smith & Evans (1973) found spatial segregation among foraging male and female bar-tailed godwit *Limosa lapponica* at Lindisfarne, Northumberland, and also suggested that this was important in areas where bird density was high in relation to available foraging area. The frequency of aggressive interactions among birds (Table 5) reflected their spatial segregation, with intrasexual aggression having been more common than intersexual aggression. Eighty percent of aggressive interactions occurred during March, close to the end of the birds' stay in the wintering areas. There is evidence that curlew sandpipers form pair bonds before leaving the wintering grounds (Holmes & Pitelka 1964), and it is possible that this accounts for the pattern of aggression observed at Kommetjie.

Females appeared to utilize food resources more efficiently than males both by foraging faster and by achieving a higher success rate. The culmen is on average 4 mm longer in females (Elliott et al. 1976) which presumably enables them to probe more deeply into the substrate than males. This means in turn that females had access to deeper prey. Female bar-tailed godwits also fed faster and more successfully than males of the same species (Smith & Evans 1973). Smith & Evans suggested that the larger females may be at an advantage in cold weather, since two important prey species occurred deeper in the substrate during cold spells, and therefore only the females were able to feed on these. Very little information is available on the behaviour of intertidal organisms on sandy shores in southern Africa. Hence, the effect of prey behaviour on prey availability to wading birds is unknown, and requires further investigation.

Although food is apparently abundant for curlew sandpipers in the south-western Cape, local and seasonal food shortages do occur in the breeding grounds (Holmes 1966). Competition between male and female curlew sandpipers may therefore be a crucial factor then. Related to this may be the fact that males seem to leave the breeding areas soon after egg-laying (Holmes & Pitelka 1964), although avoidance of competition with newly-hatched young also needs to be considered. Apart from reducing competition on the breeding grounds, sex differences may also minimise competition on migration routes to and from the breeding grounds (Recher 1966). An equally important factor favouring sexual dimorphism in curlew sandpipers may be that the females need to accumulate sufficient energy reserves firstly for egg formation and secondly for incubation of the eggs. However, this will remain speculation until the availability and diversity of food in the rest of the wintering range is examined. The breeding biology of curlew sandpipers and of calidritines in general also requires study. In particular, the questions which need to be answered are : What is the pattern of incubating behaviour in congenerics? What is the energy cost of incubation? What is the degree of sexual dimorphism in other calidritines? and What effect does this have on foraging success?

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PART 6

Energy budgets of curlew sandpipers at Langebaan Lagoon, South Africa

SUMMARY

The energy requirements and energy consumption of curlew sandpipers <u>Calidris ferruginea</u> at Langebaan Lagoon, South Africa, are described. The paper also includes estimates of the gross annual production of the benthic invertebrates potentially available to the birds, and of the birds' impact on this.

Mean estimated energy requirement of a free-living curlew sandpiper was 125 kJ per day. Mean energy intake was 180 kJ per day, with 144 kJ assimilated at an assumed assimilation efficiency of 80%. Overwintering immature birds had a negative energy balance. A substantial positive balance existed in late summer and autumn, when adult birds moult and lay in fat reserves for migration. The estimated mean gross annual production of benthic invertebrates potentially available to curlew sandpipers was 705 ± 444 kJ/m^2 per year. The birds took 12,9% of this, or 91 kJ/m^2 per year. It appears that the carrying capacity of Langebaan Lagoon for curlew sandpipers has not been reached with respect to food, but food is unlikely to be the only limiting factor.

INTRODUCTION

Curlew sandpipers Calidris ferruginea are palaearctic migrants which winter in the southern hemisphere. The population of curlew sandpipers at Langebaan Lagoon, South Africa, varies between 37 000 and 55 000 birds in the austral summer (Pringle & Cooper 1975, Summers 1977) and is as high as 12 000 in the austral winter (Pringle & Cooper 1975). The latter population is mainly composed of immature birds (Elliott et al. 1976) which appear unable to forage efficiently enough to deposit the necessary fat reserves for migration (Part 3). The energy requirements of wading birds in southern Africa have not been studied, although Summers (1977) estimated that the wader community at Langebaan consumed prey at a rate equivalent to 20,8 kcal/m^2 per year.

In this paper, the energy requirements and energy consumption of curlew sandpipers are described and the impact of the birds on the estimated gross annual production of the intertidal invertebrates at Langebaan Lagoon estimated.

METHODS

The energy requirements of curlew sandpipers were calculated using the formula adapted from Aschoff & Pohl (1970)

$$BMR = 0{,}0808\ W^{0{,}734}$$

where BMR is basal metabolic rate in kJ/h and W is body mass in grams. The BMR was multiplied by factors allocated to each activity category to provide estimates of the daily energy required for free living.

The actual energy ingested by the birds was calculated from the expression

$$T_F \cdot F \cdot \frac{S}{100} \sum \frac{n_i}{100} \cdot m_i \cdot c_i$$

where

T_F = total time spent foraging (min)
F = foraging rate (pecks or probes per min)
S = success rate (%)
n_i = percent of i^{th} prey item in diet
m_i = mass of i^{th} prey item (g)
c_i = energy content of i^{th} prey item (kJ/g)

This simplifies to

$$\frac{T_F.F.S}{100} \quad \Sigma \quad \frac{n_i.m_i.c_i}{100},$$

Mean mass of prey items and percentage composition of the diet were determined from analysis of stomach contents (Part 2). Total time spent foraging, and foraging and success rates were determined by observation of the birds (Part 3).

Gross annual production of the benthic invertebrates available to the birds (i.e. those occurring in the top 6cm of the substrate) was estimated from biomass values in Part 1 and the P : B ratios and energy contents of prey given in Appendices 1 and 2.

RESULTS

The estimated energy requirement of a free-living curlew sandpiper varied seasonally between 110 and 163 kJ per day (Table 1) with an average value of 125,0 ± 13,5 kJ per day. The $\frac{DEE}{BMR}$ ratio (where DEE = daily energy expenditure) is 3,43, which is within the range of other values obtained (King 1974).

TABLE 1 Estimated energy requirements of curlew sandpipers at Langebaan Lagoon

Month	Mean Body Weight[a] (g)	BMR[b] (kJ/h)	Foraging (5,8 X BMR)[c]	Roosting (1,35 X BMR)[c]	Flying (12 X BMR)[c]	Standing (1,5 X BMR)[c]	Night (1,24 X BMR)[c]	Total (kJ/day)
March 1974	63,4	1,6990	86,21	4,02	12,23	3,14	24,58	130,18
April	79,3	2,0034	110,41	1,55	18,42	1,26	31,69	163,33
May	53,1	1,4918	74,23	0,67	8,37	2,14	25,29	110,70
June	57,3	1,5776	72,01	0,88	20,81	1,47	27,38	122,55
July	58,9	1,6098	72,35	1,63	18,05	1,38	27,93	121,34
August	56,5	1,5533	76,83	1,13	13,36	2,05	25,67	119,04
September	58,3	1,5977	69,21	6,49	18,21	0,80	24,28	118,99
October	57,0	1,5713	69,25	8,33	23,24	3,52	22,06	126,40
November	56,8	1,5675	66,19	7,45	16,62	4,65	20,10	115,01
December	54,8	1,5629	70,84	8,25	14,95	3,48	18,30	115,82
Jan. 1975	56,7	1,5654	77,16	3,60	18,46	6,99	19,09	125,30
February	57,8	1,5872	78,25	3,73	22,86	4,52	21,02	130,38

[a] From Elliott *et al*. (1976)

[b] Based on Aschoff & Pohl (1970)

[c] Based on values in King (1974)

Estimated energy ingested varied seasonally between 115 and 266 kJ per day (Figure 1, Table 2) with a mean value of 180 ± 47 kJ per day. Mean assimilated energy would thus be 144 kJ per day, assuming an assimilation efficiency of 80%. (80% was chosen from a range of 70-90% for carnivorous birds surveyed by Ricklefs (1974)).

Curlew sandpipers had a negative energy balance during the winter months, which was possibly offset by a positive balance in autumn (Table 3). A substantial positive balance existed in late summer and autumn.

The population took an estimated 10,3, 11,1 and 17,2% of the estimated gross annual production of the benthic invertebrates potentially available to them on the marshes, the Assiminea zone, and the lower shore respectively (Table 4). Thus, they took an estimated mean of 12,9 ± 3,8% (± S D) annually, or 91,0 ± 26,7 kJ/m^2 (± S D) per year.

DISCUSSION

The choice of suitable factors for obtaining the energy requirements of free-living curlew sandpipers was problematical, in the absence of laboratory experiments. The factors employed were those of several authors, either obtained experimentally or estimated from equations. Their

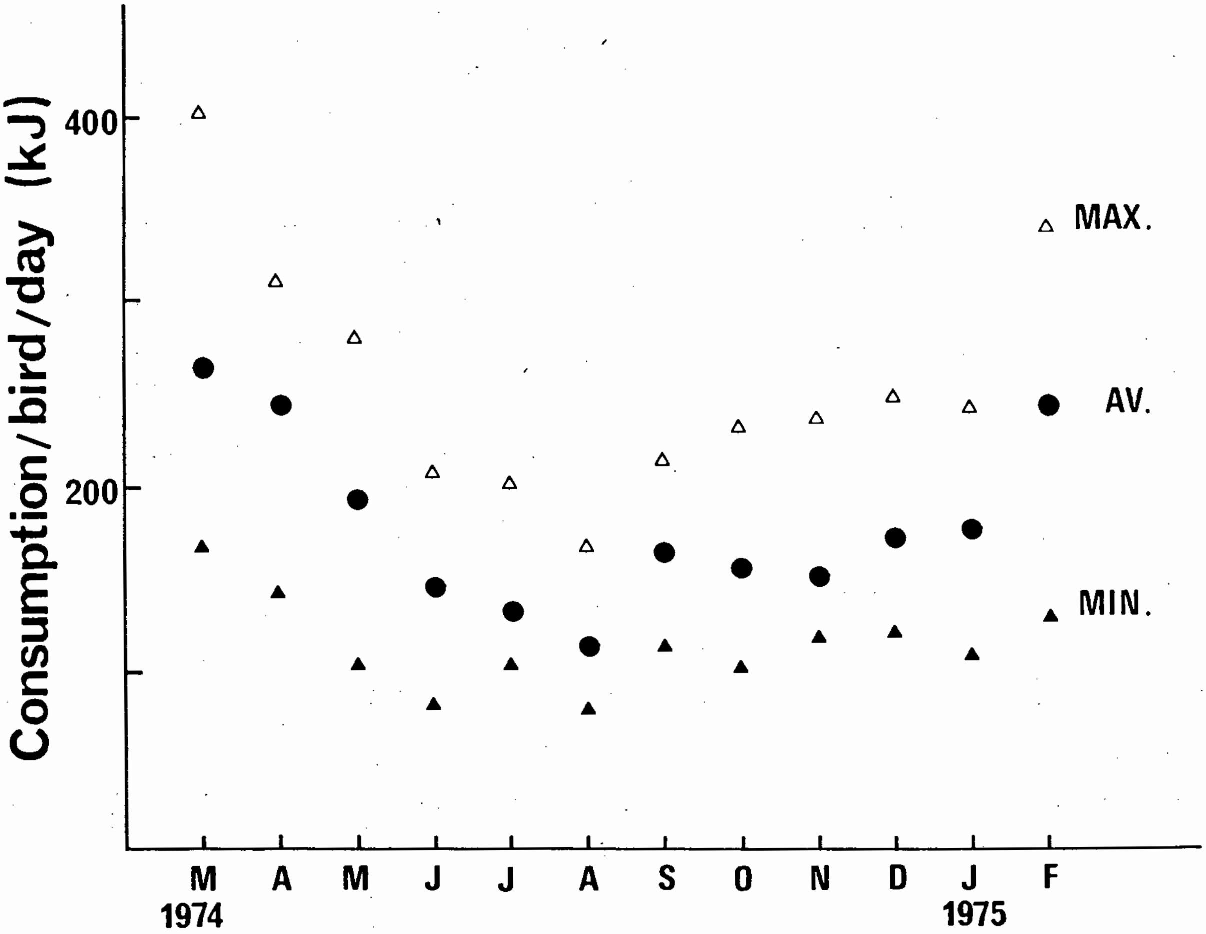

Figure 1. The maximum, average and minimum energy intake per curlew sandpiper per day during March 1974 - February 1975. Data points for May to August represent energy intake of immatures only.

TABLE 2 Estimated energy intake (kJ/bird/day) of curlew sandpipers at Langebaan Lagoon on the marshes, in the "*Assiminea* zone" (0,5 m above LWS to HWN) and on the lower shore

Month	Marsh	*Assiminea* Zone	Lower Shore	Total
March 1974	14,8	68,1	183,1	266,0
April	55,3	28,1	160,1	243,5
May	59,0	54,4	79,2	192,6
June	42,6	40,4	61,9	144,9
July	54,1	37,1	44,7	135,9
August	29,4	38,4	47,3	115,1
September	6,0	59,1	98,4	163,5
October	3,4	73,2	81,4	158,0
November	3,4	48,1	101,5	153,0
December	3,5	73,0	96,9	173,4
January 1975	15,5	76,2	86,2	177,9
February	12,1	81,9	151,0	245,0

TABLE 3 Mean daily energy budget (kJ per day) of curlew sandpipers at Langebaan Lagoon

Month	Energy ingested* A	Energy required for activity B	Balance A - B
March 1974	212,8	130,2	+ 82,6
April	194,8	163,3	+ 31,5
May	154,1	110,7	+ 43,4
June	116,0	122,6	- 6,6
July	108,7	121,3	- 12,6
August	92,1	119,0	- 26,9
September	130,8	119,0	+ 11,8
October	126,0	126,0	0
November	122,4	115,0	+ 7,4
December	138,7	115,8	+ 22,9
January 1975	142,3	125,3	+ 17,0
February	196,0	130,4	+ 65,6

* 80% assimilation efficiency

TABLE 4 Estimated percentage of gross annual production taken by curlew sandpipers feeding on marshes, in the "*Assiminea* zone" (0,5 m above LWS to HWN) and on the lower shore.

Month	Curlew sandpiper population[a] (no. birds)	Marsh (600 ha)			*Assiminea* zone (380 ha)			Lower Shore (1 200 ha)		
		Population energy intake[b] (1 000 kJ/ ha/month)	Estimated production (P)[c] (1 000 kJ/ ha/month)	% of P taken	Population energy intake[b] (1 000 kJ/ ha/month)	Estimated production (P)[c] (1 000 kJ/ ha/month)	% of P taken	Population energy intake[b] (1 000 kJ/ ha/month)	Estimated production (P)[c] (1 000 kJ/ ha/month)	% of P taken
March 1974	37 390	29	1 909	1,52	210	12 070	1,74	179	5 261	3,40
April 1[d]	31 500	44	1 800	2,44	35	13 126	0,27	63	5 295	1,19
April 2[d]	13 300	18	1 800	1,00	15	13 126	0,11	27	5 295	0,51
May	13 300	41	1 746	2,35	59	11 937	0,13	27	5 834	0,46
June	13 300	28	5 024	0,56	43	11 033	0,49	21	6 116	0,34
July	13 300	37	7 972	0,46	40	10 712	0,40	15	5 917	0,25
August	13 300	20	4 325	0,46	42	14 242	0,29	16	6 048	0,26
September	19 500	6	4 442	0,14	91	16 195	0,56	48	5 300	0,91
October	23 250	4	4 128	0,10	139	14 175	0,98	49	5 178	0,95
November	28 100	5	3 764	0,13	107	9 947	1,08	71	3 993	1,78
December	28 100	5	4 312	0,12	167	8 734	1,91	70	4 027	1,74
Jan. 1975	28 100	23	5 531	0,42	175	11 100	1,58	63	3 022	2,08
February	32 900	19	3 383	0,56	198	12 434	1,59	116	3 512	3,30
TOTAL				10,26			11,13			17,17

[a] Pringle & Cooper (1976) and author's extrapolations.

[b] Based on values in Table 2.

[c] Energy content of prey organisms and P : B ratios given in Appendices 1 and 2. Biomass of prey from Part 1.

[d] First and second fortnights in April respectively.

results are reviewed by King (1974). I consider that the energy requirements of curlew sandpipers as reported in the present study are fairly reliable, since the agreement between mean estimated energy requirement and energy intake (125 and 144 kJ per day) is good. However, exact absolute values are of no greater importance than the indications they give of the efficiency of time and energy partitioning in free-living birds. The relatively high energetic cost of increased foraging in autumn (Table 1) is negligible when compared with the advantage (and necessity) of accumulating a fat store prior to migration. Although birds appeared to have a negative energy balance in winter, they did not spend all available time foraging then (Part 3). The deficit was possibly a short-term one, corresponding to short-term fluctuations in body mass.

Energy ingested in late summer and autumn far exceeds the birds' immediate energy requirements, and this energy is available for fat deposition and for moult. Adult curlew sandpipers undergo a post- and pre-nuptial moult between September and February (Elliott _et_ _al_. 1976) during which the birds produce 4,5g (dry weight) of feathers (Summers 1977). The minimum energy cost to the birds (i.e. the energy content of the feathers alone) is 24,75 kcal (103,6 kJ), assuming that feathers are composed chiefly of keratin with an energy content of 5,5 kcal/g (Siegfried _et_ _al_. 1976). Very little information is available on the energetic cost of feather synthesis (King 1974), but the positive energy balance shown by the birds during September - February indicates a possible change in energy partitioning, or at least in time partitioning, to compensate for the energy cost of moult.

The tide acts as an important temporal regulator of the availability of foraging space to the birds. Hence, although exploitation by the birds of the lower intertidal zone is 50% greater than of the marsh and *Assiminea* zones (Table 3), the lower zone is only exposed for a relatively short time each tidal cycle. The marsh and *Assiminea* zones were exploited equally by the birds. Thus, the marshes do not merely serve as a supplementary foraging area when the flats are covered, but also apparently provide an indispensable proportion of the birds' diet.

Curlew sandpipers are not only an important numerical constituent of the Langebaan Lagoon avifauna but they also play an important role in the energetics of the lagoon ecosystem as a whole. They took 12,9 ± 3,8% (± S D) of the estimated gross annual production of benthic invertebrates potentially available to them, or 91,0 ± 26,7 kJ/m^2 (± S D) per year in 1974. This is slightly more than the 20,8 kcal/m^2 per year (87,1 kJ) estimated by Summers (1977) for the total wader population in 1975. However, Summers multiplied the BMR by a factor of four, which was conservative, to obtain estimates for free-living birds. Also, the curlew sandpiper population in 1975 was much lower than in 1974.

The percentage (12,9%) of the estimated gross annual production of prey taken by curlew sandpipers appears to be relatively small. However, not all gross annual production is available to predators, since part of this is utilised by the prey species themselves for growth, reproduction and metabolic activities. The proportion taken by the birds would be much higher if expressed as a percentage of nett production. I do not know what percentage of nett production of the benthic invertebrates at Langebaan can 'safely' be taken by the birds before the standing crop of prey populations would be permanently affected. Milne & Dunnet (1972) found that the entire gross production of Mytilus at the Ythan estuary is accounted for in winter by predation and metabolic requirements, suggesting that the mussel bed is being maximally cropped. It is not clear at this stage whether the carrying capacity of Langebaan Lagoon for wading birds has been reached, and only studies of the productivity of prey and of the energy requirements of other predators including fish are likely to provide a definitive answer. However, it seems possible that the lagoon's carrying capacity for curlew sandpipers has not been reached, with respect to food, since at no time during the year do the birds spend all their daily time foraging (Part 3); agonistic behaviour was infrequent both intra- and interspecifically (pers. obs.); and, potential foraging areas do exist which are not exploited during the whole period that they are accessible (e.g., the Assiminea zone is not used by curlew sandpipers when the sandflats below it are uncovered by the tide). Food may not, of course, be the single limiting factor for curlew sandpipers at Langebaan Lagoon. Other factors, such as the availability of suitable roosting sites, are also likely to be important.

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APPENDIX 1 Mean energy content (kJ/g dry mass) of some of the main prey organisms taken by curlew sandpipers at Langebaan Lagoon. Energy content was determined using a Phillips microbomb calorimeter

Species	Energy content
Assiminea globulus	12,84
Ceratonereis erythraensis	17,65
Cleistostoma edwardsii	11,30
Urothoe grimaldi	17,75
Stratiomyid larvae (O. Diptera)	10,78

APPENDIX 2 P : B ratios used to provide estimates of gross annual production of the intertidal invertebrates available to curlew sandpipers at Langebaan Lagoon

Zone	Food Item	P:B Ratio	Source
Marsh	_Assiminea globulus_	4,96	Part 1
	Stratiomyid larvae (O. Diptera)	3,00	Estimate
Assiminea	_A. globulus_	4,96	Part 1
	Ceratonereis erythraensis	3,00	Chambers & Milne (1975) for _Nereis diversicolor_
Lower shore	_C. erythraensis_	3,00	As above
	Urothoe grimaldi	3,20	Mean of 1,36 (Part 1) and 5,00 Sanders (1956 in Burke & Mann 1974)
	Cleistostoma edwardsii	3,20	As for _U. grimaldi_

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SUMMARY

1. The food available to the curlew sandpiper *Calidris ferruginea* at Langebaan lagoon (33^{o}S, 18^{o}E) is described, together with the diet of curlew sandpipers feeding there, aspects of the birds' foraging behaviour, and the impact of their foraging on the benthic fauna.
2. Spatial and temporal changes in the distribution of food organisms available to curlew sandpipers was studied during February 1974 - March 1975. The gastropod *Assiminea globulus*, comprising 62,5% of the total biomass, was distributed between high water springs and high water neaps; it was the most abundant species on *Arthrocnemum* marsh areas also. Polychaete worms, crabs, amphipods and bivalves were distributed below high water neaps. The fauna showed spring and autumn peaks in biomass and numbers at sandy sites and winter peaks at sites containing *Spartina*, *Zostera* and *Arthrocnemum*.
3. Nereid worms (mainly *Ceratonereis erythraensis*) and *A. globulus* were the most important prey items throughout the year. Other important items were the amphipod *Urothoe grimaldi* and the crabs *Hymenosoma orbiculare* and *Cleistostoma edwardsii* and dipteran larvae (Stratiomyidae). Changes in the food items taken by the birds largely reflected changes in those that were available to them. Immature curlew sandpipers took smaller prey items than adult birds. The diet of male and female birds differed in the proportion, size and

range of prey items taken.

4. Adult curlew sandpipers spent 55-65% of daylight hours foraging in spring and summer. They foraged faster and more successfully in autumn than in spring and summer, and this, together with foraging on the marshes at high tide when the sandflats were no longer exposed, enabled them to accumulate fat reserves for migration in mid-April. Immature birds spent up to 80% of daylight hours foraging in winter, and they also foraged faster then. They foraged more slowly and less successfully than adults, which may explain why they overwinter in the southern hemisphere.

5. The birds' foraging and success rate, and biomass taken per unit time, all accorded with Royama's (1971) profitability hypothesis. A feature not occurring in the model was that small prey sizes may have reduced the birds' foraging and success rates by decreasing profitability at high prey densities. Birds foraged more successfully in groups than birds foraging alone. Higher levels of aggression when the birds were closer together counteracted an increase in bird density.

6. Female curlew sandpipers foraged faster and more successfully than males. Sexual segregation of foraging birds occurred and intrasexual aggression was low. It is suggested that competition on the breeding rather than on the wintering grounds favours the sexual dimorphism which exists in the species.

7. Mean estimated energy requirement of free-living birds was 125 kJ per day. Mean energy intake was 180 kJ per day, with 144 kJ assimilated at an assumed assimilation efficiency of 80%. The estimated gross annual production of benthic invertebrates potentially available to the birds was 705 kJ/m^2 per year; the curlew sandpiper population took 12,9% of this, or 91 kJ/m^2 per year. It appears that the carrying capacity of Langebaan Lagoon has not been reached for curlew sandpipers with respect to food, but food is unlikely to be the only limiting factor.

CONCLUSION

This dissertation, on the food, aspects of the feeding ecology, and the energetics of curlew sandpipers at Langebaan Lagoon, has attempted to contribute information useful in understanding trophic relationships within the lagoon ecosystem. However, many aspects affecting resource utilization by curlew sandpipers in the south-western Cape still remain to be elucidated.

Prey behaviour has mostly been neglected as a crucial component in predator/prey relationships where the prey has comprised invertebrate species. In particular, very little is known about the behaviour of benthic invertebrate prey species, although prey behaviour has been shown to influence the potential availability of prey to avian predators (Goss-Custard 1969, Vader 1964). The relatively small size of most of these organisms makes studies of their behaviour particularly difficult but the effect of prey behaviour on curlew sandpiper foraging and diet has been shown in the present study. The behaviour of benthic invertebrates at Langebaan needs investigation, especially in relation to tidal fluctuations and in relation to the presence of predators.

Estimates of curlew sandpiper energy intake and of the population's impact on the estimated gross annual production of benthic invertebrates in this study have given some indication that a potential surplus of food exists at Langebaan. The importance of an accurate assessment of the lagoon's carrying capacity to the maintenance of wader populations in the south-western Cape has already been stressed in this study (cf. Introduction). In order to determine whether or not the carrying capacity of the lagoon with respect to the wader community has been reached, investigation is needed in three crucial 'areas'. Firstly, annual production of the major prey species should be quantified from population studies of these species including such factors as growth, reproduction, energy metabolism, mortality, etc. Secondly, the energy requirements of other predators, including fish, should be estimated. Finally, the importance of limiting factors which are not food-related, such as the availability of suitable roosting areas, the degree of human disturbance or interference due to activities such as boating, fishing, etc., require investigation. The findings presented in this study apply only to one of the secondary consumers in the lagoon ecosystem. There will obviously be no clear understanding of trophic relationships within the ecosystem nor of resource partitioning among secondary and tertiary consumers until the resource utilization of the most abundant species, both producers and consumers, is elucidated.

Since 90% of the benthic community comprises deposit feeders, the cycling of detritus is important to higher trophic levels, especially fish and birds.

Assiminea globulus, for example, which comprises over half (62,5%) of the diet of curlew sandpipers and which is numerically the most abundant benthic invertebrate at Langebaan, is a detritus feeder. A study of the detritus cycle, including detritus-associated bacteria, within the lagoon and especially in the intertidal and marsh areas would contribute to an understanding of the biology of this important species.

Although this study has attempted to elucidate several aspects of prey selection by curlew sandpipers, it is still not clear why the birds in general appear to feed on smaller numbers of larger organisms (e.g. polychaete worms) rather than on many smaller ones (e.g. snails and amphipods). Laboratory experiments in which curlew sandpipers are presented with choices among several prey items under varying conditions of item size, frequency and sequence of item presentation may show the relative profitability of different prey items and whether or not the birds' preference for particular items reflects the profitability of the same items. Throughput times and the relative digestibility of different prey items should be studied in conjunction with these experiments, since these factors are likely to influence the relative profitability of prey items. The study of curlew sandpiper foraging behaviour in relation to prey density in the light of Royama's (1971) profitability theory revealed a feature not incorporated in the model. This was that smaller prey size may have affected foraging and success rates at high prey densities. This requires further testing by determining the spatial distribution of different size classes of more of the prey species, and the birds' response to this, since the evidence presented in this study that prey size and prey density were negatively correlated only applied to two prey species. The birds' responses could perhaps be tested experimentally.

The suggestion that competition outside the wintering areas favours sexual dimorphism in curlew sandpipers (Part 5) conflicts with the conclusion made by Baker & Baker (1973) that resource partitioning among waders in North America was greatest in wintering areas and that food was limiting there rather than in the breeding areas. Studies already suggested above should indicate whether or not food is in fact not limiting at Langebaan Lagoon, and the status of food in the rest of the wintering area should also be examined with Baker & Baker's (1973) conclusion in mind. Furthermore, aspects of the breeding biology which would elucidate this problem include patterns of incubating behaviour, the energy cost of incubating, the degree of sexual dimorphism among congenerics and the effect of this on the foraging success in these species. In addition, monitoring the relative rate at which male and female curlew sandpipers accumulate fat reserves before migration from the wintering areas should indicate whether or not females were at a selective advantage in the wintering areas by virtue of their larger size.

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APPENDIX A

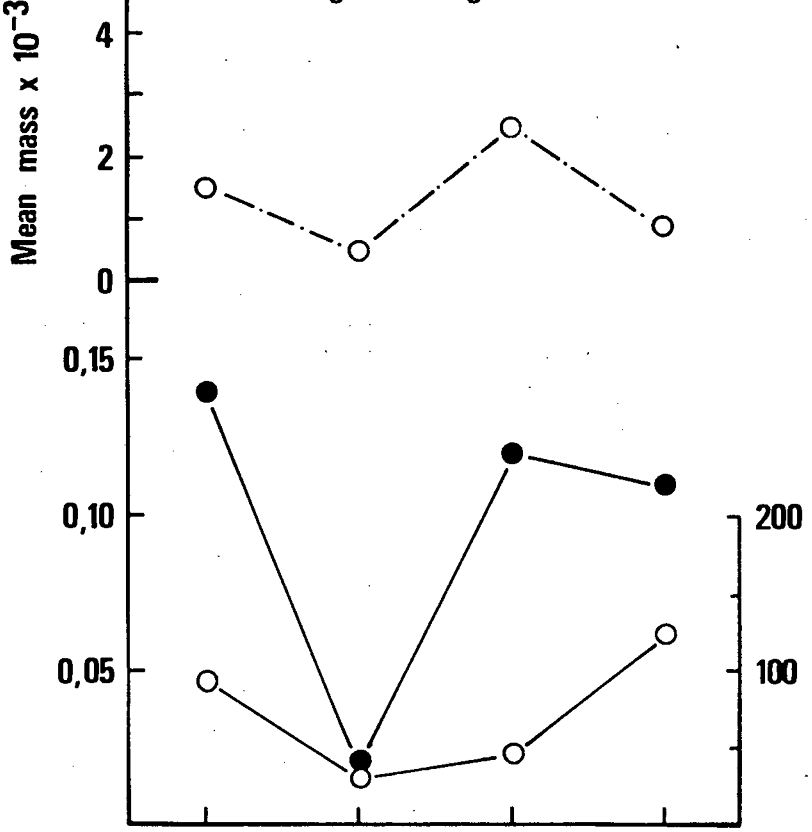
Figure 1. Mean biomass (g dry mass per m^2) (dots) and mean numbers (per m^2) (circles), and mean mass (x 10^{-3}g) (top), of Marginella capensis in autumn (A), winter (W), spring (Sp) and summer (S).

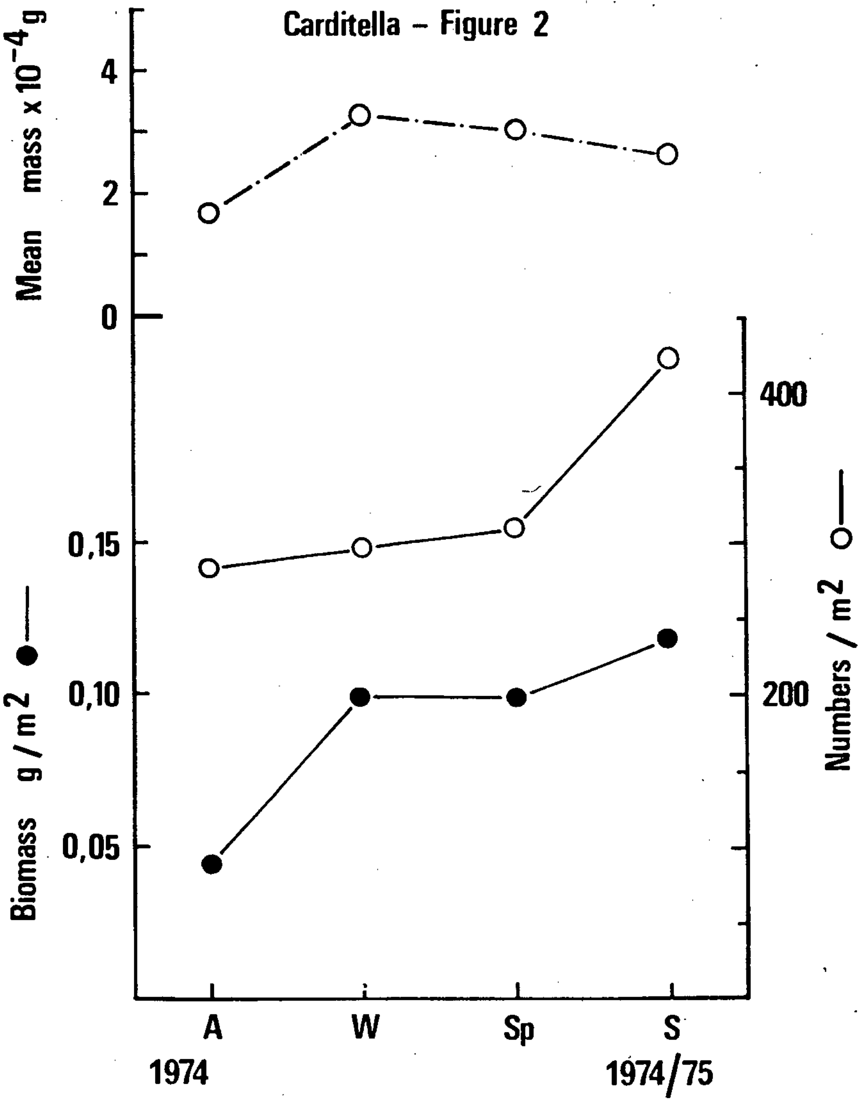
Figure 2. Mean biomass (g dry mass per m^2) (dots), and mean numbers (per m^2) (circles), and mean mass (x 10^{-3}g) (top), of Carditella rugosa in autumn (A), winter (W), spring (Sp) and summer (S).

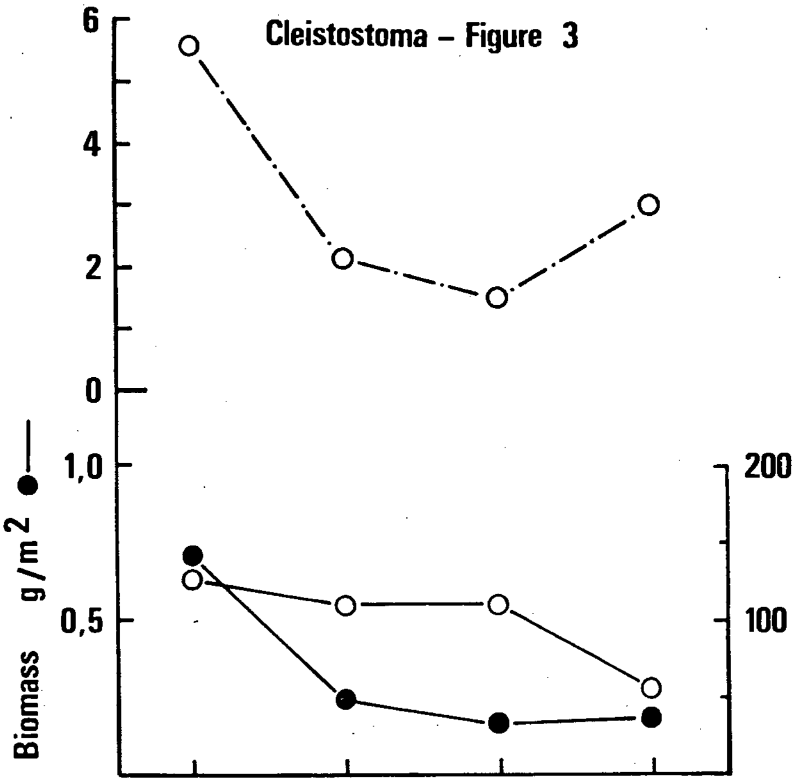
Figure 3. Mean biomass (g dry mass per m^2) (dots) and mean numbers (per m^2) (circles), and mean mass (x 10^{-3}g) (top), of Cleistostoma edwardsii in autumn (A), winter (W), spring (Sp) and summer (S).

Figure 4. Mean biomass (g dry mass per m^2) (dots) and mean numbers (per m^2) (circles), and mean mass (x 10^{-3}g) (top), of Hymenosoma orbiculare in autumn (A), winter (W), spring (Sp) and summer (S).

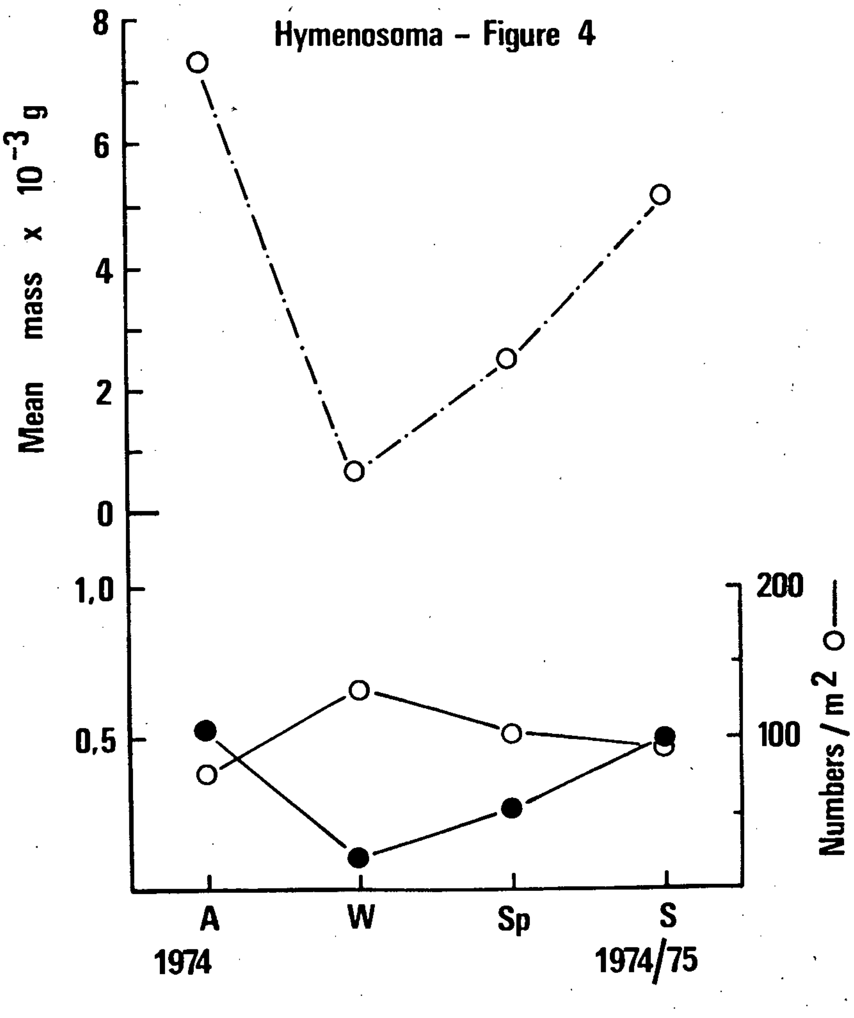
Figure 5. Mean biomass (g dry mass per m^2) (dots) and mean numbers (per m^2) (circles), and mean mass (x 10^{-3}g) (top), of *Ceratonereis erythraensis* in autumn (A), winter (W), spring (Sp) and summer (S).



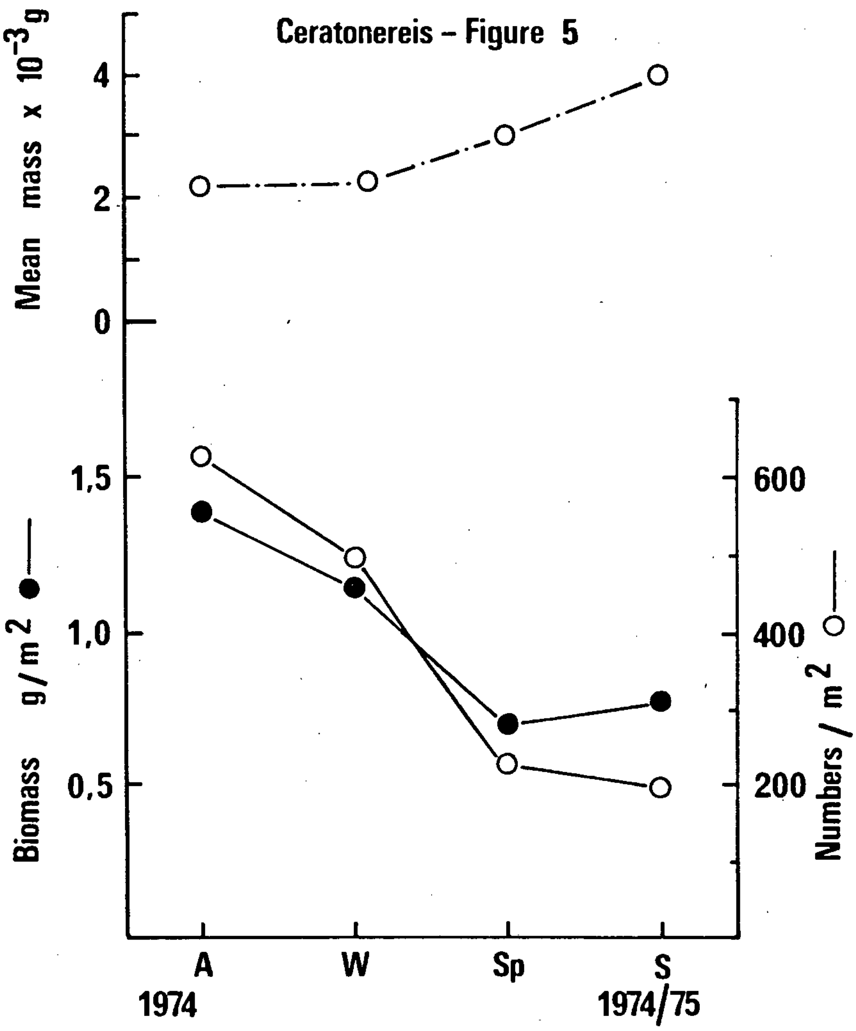

Carditella – Figure 2



Cleistostoma – Figure 3



Hymenosoma – Figure 4


Ceratonereis - Figure 5
Mean mass x 10^{-3} g
4
2
0
Biomass g / m^2 ●
1,5
1,0
0,5
Numbers / m^2 ○
600
400
200
A
1974
W
Sp
S
1974/75

APPENDIX B

Composition of curlew sandpiper diet based on 248 samples (see Part 2). ('+' < 0,1%)

Sandflats stomachs

Food item	% Mass	% Number	% Occurrence
Mollusca : Gastropoda			
Assiminea spp.	0,62	8,98	25,30
A. globulus	0,64	11,50	31,93
A. knysnaensis*	+	1,90	11,45
Coriandria cf. gisia	+	1,71	8,43
Marginella capensis	0,32	2,27	25,30
Turritella capensis	+	0,30	6,63
Nassa speciosa	+	+	1,81
N. kraussiana	0,71	+	4,22
Natica genuana	+	+	1,20
Littorina sp.	+	+	1,20
Turbonilla sp.		+	0,60
Siphonaria capensis	+	+	1,81
Tellimya sp.	+	0,15	1,81
Nucula sp.	0,18	3,61	29,52
Carditella rugosa	+	1,28	11,45

Annelida : Polychaeta			
Orbinidae	+	+	9,04
Eunicidae	12,72	12,18	21,08
Nereidae	55,82	31,36	37,35
Glyceridae	9,05	6,22	35,54
Nephtys sp.			0,60
Crustacea : Amphipoda			
Urothoe grimaldi	0,96	3,27	23,49
Ampelisca palmata	6,33	2,46	14,46
Melita zeylanica	0,26	0,75	4,22
Cymadusa filosa	0,25	0,64	3,01
Paramoera capensis	+	0,28	2,41
Orchestia sp.	+	+	+
Lemboides sp.	+	0,24	4,82
Crustacea : Isopoda			
Cirolana sp.	+	+	+
Exosphaeroma sp.	+	0,17	3,61
Crustacea : Mysidacea			
Unident sp.	0,20	0,15	3,01
Crustacea : Macrura			
Hippolyte kraussiana	+	+	1,20

Crustacea : Anomura			
Upogebia africana	+	+	+
Crustacea : Brachyura			
Cleistostoma edwardsii	8,87	1,71	33,93
Hymenosoma orbiculare	0,29	0,71	13,25
Crustacea : Copepoda			
Harpacticoidea	+	+	1,20
Crustacea : Ostracoda			
Cylindroleberis sp.	+	0,17	2,41
Unident sp.	+	0,32	6,02
Insecta : Diptera			
Chironomidae (Larvae)	1,19	1,00	2,99
Marsh stomachs			
Coleoptera			
Hydraenidae	0,24	1,08	11,85
Dytiscidae	0,19	0,27	4,35
Curculionidae	0,31	1,29	8,70
Carabidae		0,22	4,35
Hydrophilidae	+	0,99	8,06
Berosus sp. (larva)	3,11	8,48	14,90
Berosus sp. (adult)	+	0,22	6,20

Diptera			
Tendipedidae	1,85	1,16	5,00
Chironomidae	0,30	0,14	1,70
Ephydridae (adult)	+	0,37	6,20
Ephydridae (pupa)	0,19	1,55	10,85
Dolichopodidae (adult)	+	0,35	5,35
Dolichopodidae (larva)	0,47	0,81	7,40
Anthomyiidae	+	0,60	1,70
Stratiomyiidae (larva)	86,04	33,63	71,48
Hemiptera			
Saldidae	+	0,90	16,76
Amphipoda			
Austrochiltonia capensis	+	0,27	1,85
Orchestia sp.	0,19	0,47	1,85
Brachyura			
Cleistostoma edwardsii	0,40	0,34	6,20
Isopoda			
Exosphaeroma sp.			1,85
Gastropoda			
Assiminea spp.	1,54	12,52	42,22
Other			
Salicornia sp. (seeds)	3,45	7,80	21,20
Acarina	+	0,34	3,70
Araneida	0,12	0,39	13,70
Formicidae		0,41	5,56

Zygoptera	+	+	1,85
Orthoptera		0,47	1,85
Flats oesophagi			
Mollusca : Gastropoda			
Assiminea spp.	2,33	8,24	14,94
A. globulus	2,46	10,73	
*A. knysnaensis**	0,34	2,87	8,04
Coriandria cf. *gisia*	0,11	1,53	3,45
Marginella capensis	0,24	2,11	9,20
Turritella capensis	0,03	0,38	2,30
Nassa speciosa	0,08	0,19	1,15
Littorina sp.	0,11	0,96	4,60
Mollusca : Bivalvia			
Tellimya sp.	0,16	2,11	4,60
Nucula sp.	0,82	4,79	10,34
Carditella rugosa	0,24	0,76	1,15
Annelida : Polychaeta			
Ceratonereis erythraensis	4,21	0,38	1,15
Scoloplos johnstonei	0,82	0,19	1,15
Nephtys sp.	1,79	0,38	2,30
Terebellidae	5,16	0,19	1,15
Glyceridae	5,36	1,92	10,34
Nereidae	16,66	2,87	12,64

Crustacea : Amphipoda			
Ampelisca palmata	6,52	9,00	10,34
Urothoe grimaldi	7,47	22,99	10,34
Melita zeylanica	0,52	0,57	1,15
Cymadusa filosa	4,97	3,06	2,30
Paramoera capensis	2,85	12,07	10,34
Orchestia sp.	0,14	0,19	1,15
Lemboides sp.	0,21	0,19	1,15
Crustacea : Brachyura			
Cleistostoma edwardsii	29,35	2,87	10,34
Hymenosoma orbiculare	2,70	4,41	16,09
Crustacea : Anomura			
Callianassa krausii	0,20	0,19	1,15
Other			
Ostracoda	1,10	0,57	3,45
Pycnogonida	+	0,19	1,15
Mysidacea	1,41	0,95	1,15
Harpacticoidea		0,38	1,15
Crustacea : Isopoda			
Exosphaeroma sp.	0,91	1,53	6,80

Marsh oesophagi			
Coleoptera			
Berosus sp. (larva)	2,92	3,08	11,11
Hydraenidae		1,54	11,11
Curculionidae		4,62	22,20
Diptera			
Stratiomyidae (larva)	66,91	24,62	38,89
Ephydridae (adult)	0,55	1,54	5,56
Hemiptera			
Saldidae	0,18	7,68	22,20
Amphipoda			
Orchestia rectipalma	3,77	6,14	22,20
Austrochiltonia capensis	0,79	3,08	11,00
Isopoda			
Deto sp.	11,86	4,62	11,00
Salicornia sp. (seeds)	11,01	27,69	16,67

**Assiminea knysnaensis* (Krauss 1848) was previously identified as *Assiminea isosceles* (Puttick 1977). However, this species should be placed in the genus *Hydrobia* (G.M. Davis pers. comm.).

APPENDIX C

Mean sizes of <u>Assiminea globulus</u> (mm ± S.D., n in parentheses = number of objects measured) in stomach samples of curlew sandpipers collected while feeding on sandflats, and mean sizes of those potentially available. (See Part 2).

	Number of birds	Food sample	Available
March 1974	10	2,96 ± 0,78 (56)	
April	1	1,72 ± 0,15 (4)	1,87 ± 0,30 (4 612)
May	10	2,53 ± 0,72 (73)	1,57 ± 0,27 (3 958)
June	0		1,66 ± 0,24 (3 394)
July	8	2,64 ± 0,29 (21)	1,68 ± 0,18 (2 566)
August	12	2,30 ± 0,72 (57)	1,79 ± 0,30 (3 786)
September	17	1,84 ± 0,63 (43)	1,90 ± 0,19 (5 864)
October	14	1,44 ± 0,58(304)	1,52 ± 0,22 (3 846)
November	16	1,76 ± 0,79(124)	1,80 ± 0,28 (3 819)
December	33	1,34 ± 0,51(153)	1,71 ± 0,23 (3 010)
January 1975	19	2,06 ± 0,68 (57)	1,48 ± 0,43 (5 780)
February	0		1,57 ± 0,43 (6 012)
March	19	2,08 ± 0,41(234)	1,72 ± 0,42 (4 592)

APPENDIX D

Mean sizes of Urothoe grimaldi (mm ± S.D., n in parentheses = number of objects measured) in stomach samples of curlew sandpipers collected while feeding on sandflats, and mean sizes of those potentially available. (See Part 2).

	Number of birds	Food sample	Available
April 1974	1	3,18 ± 1,05 (22)	3,41 ± 0,85 (46)
May	10	4,42 ± 1,21 (57)	3,97 ± 1,24 (36)
June	0		3,63 ± 0,88 (57)
July	8	5,70 ± 0,57 (10)	4,21 ± 0,66 (39)
August	12	4,25 ± 1,26 (46)	3,61 ± 0,81 (64)
September	17	3,77 ± 0,87 (66)	3,69 ± 0,95 (40)
October	14	3,70 ± 0,85 (14)	3,81 ± 1,01 (58)
November	16	3,40 ± 0,09 (59)	3,88 ± 1,06 (42)
December	33	4,53 ± 0,97 (14)	2,94 ± 0,79 (64)

APPENDIX E

Mean sizes (mm ± S.D., n in parentheses) of main prey items taken by curlew sandpipers and mean sizes of those available. (See Part 2).

	Food sample	Available
Marginella capensis		
Autumn	2,46 ± 0,73 (22)	3,29 ± 0,85 (19)
Winter	2,55 ± 0,47 (20)	2,93 ± 0,52 (13)
Spring	2,34 ± 0,65 (59)	3,09 ± 0,87 (37)
Summer	2,15 ± 0,47 (42)	3,64 ± 1,36 (22)
Nucula sp.		
Autumn	1,76 ± 0,18 (17)	1,88 ± 0,45 (145)
Winter	1,78 ± 0,55 (32)	1,84 ± 0,35 (141)
Spring	1,83 ± 0,42 (113)	1,58 ± 0,39 (415)
Summer	1,80 ± 0,42 (57)	1,62 ± 0,33 (314)
Cleistostoma edwardsii		
Autumn	4,95 ± 1,72 (23)	2,76 ± 1,19 (31)
Winter	4,30 ± 1,49 (14)	3,08 ± 1,46 (36)
Spring	3,51 ± 1,69 (33)	2,30 ± 1,42 (63)
Summer	3,75 ± 1,78 (49)	2,55 ± 1,46 (13)
Ampelisca palmata		
Autumn	5,51 ± 1,46 (113)	3,67 ± 1,11 (82)
Winter	4,91 ± 1,48 (21)	5,67 ± 1,43 (61)
Spring	5,18 ± 1,18 (24)	4,19 ± 1,23 (236)
Summer	5,67 ± 0,92 (23)	4,13 ± 2,20 (3)

Stratiomyid larvae		
Autumn	12,67 ± 4,60 (356)	8,11 ± 3,92 (65)
Winter	13,98 ± 4,39 (145)	10,63 ± 4,08 (69)
Spring	12,11 ± 3,29 (52)	17,10 ± 3,93 (20)
Summer	12,23 ± 3,79 (46)	7,00 ± 4,06 (70)
Nereid jaws	1,01 ± 0,37(1668)	0,43 ± 0,32 (98)
Glycerid jaws	0,63 ± 0,15 (418)	0,59 ± 0,29 (33)

ACKNOWLEDGEMENTS

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ADDENDUM

Part 1

Page 13. Line 23, sentence should read: The birds took an estimated 8,6; 11,2 and 16,3% of the nett production potentially available to them on the marshes, the *Assiminea* zone and the lower shore respectively. Thus they took an estimated mean of 12,0% annually, or 84,6 kJ/m^2 per year, which is slightly lower than the estimated 87 kJ/m^2 per year taken during 1975 by the total wader population at Langebaan lagoon (Summers 1977).

Page 14. Second sentence from top should read: The percentage (12,0%) of the estimated nett annual production of prey taken by Curlew Sandpipers appears to be relatively small. Not all gross annual production is available to predators, since part of this is utilised by the prey species themselves in the respiration required for growth, reproduction and other metabolic activities. Delete sentence following.

Page 19. Insert two lines from bottom: Studies in which prey populations have been sampled to a greater depth suffer from the bias of giving an over-estimate of food potentially available.

Page 21. Fig. 2 caption should include: Animal densities are expressed as numbers per m^2.

Page 30. Captions to Tables 3 and 4 should include: ... using Crisp's (1971) method as modified by Chambers and Milne (1975a).

Part 2

Page 57. Insert at foot of page: Digestion correction factors were not calculated, firstly since the proportions of hard and soft prey represented in individual birds appeared to vary too widely to allow meaningful extrapolation to all gizzard contents and secondly because the diet of the Curlew Sandpiper appeared to be far more heterogeneous than that of redshank (Tringa totanus) for which a correction factor was successfully obtained (Goss-Custard 1969).

Page 58. Fig. 2 caption should include: ... as represented by oesophagus and stomach contents combined.

Page 61. "STOM." and "OES." should be transposed in Fig. 9.

Part 3

Page 70. Insert in line 2: This method of measuring foraging rate may have given a consistent overestimate because the gap between the final measured peak and the subsequent one is not included in the interval.

Page 70. Insert in line 4: Prey handling times for worms and crabs were measured by direct timing of foraging birds. Handling times for snails were too short to measure directly and were calculated from the difference between unsuccessful foraging bouts and those in which one snail was captured.

Page 84. Table 5 caption should read: Seasonal changes in the diversity of prey taken by Curlew Sandpipers on sandflats and marsh (based on percentage by number of prey items represented in stomach samples). Data taken from Part 2.

Page 85. Second sentence should read: Prey handling times are short (Table 6) so that it is to be expected that increased prey handling time at higher success rates would not be of great importance.

Page 85. First sentence of last paragraph should read: Curlew Sandpipers foraged significantly faster at the same level of the beach on incoming than on outgoing tides in five of the seven months when comparisons could be made (Table 8).

Page 90. Last sentence of top paragraph should read: The number of prey taken per min. decreased significantly from upper to lower shore and was lowest about 100 m from the low water mark on the incoming tide ($r_s = 0,81$, $p < 0,01$) (Figure 13).

Page 91. Figure 12 insert 95% of confidence limits from left to right as follows: 2,85; 3,72; 5,37; 3,70, 4,23; 4,78; 6,89.

Page 92. Insert at top: Personal observation of night feeding was attempted in Autumn (March and April) and winter (June and July) at full moon periods. No birds were found or heard calling on the feeding areas during at least eight visits of up to an hour each.

Page 92. Point (3) should read: (3) A quarter of the total Curlew Sandpiper population always foraged on the marshes at low water when they could have been foraging on the adjacent sandflats, which did not have high densities of birds there.

Page 94. Second sentence should read: Elliott _et_ _al_. (1976) have shown that the overwintering population of Curlew Sandpipers at Langebaan are made up of immature birds and suggest that they are unable to deposit the necessary fat reserves for migrating.

Part 4

Page 106. Second paragraph should read: The foraging rate of Curlew Sandpipers increased significantly with increasing prey density ($r_s = 0{,}9$, $t = 13{,}54$, $p < 0{,}001$) until a density between 30 000 and 40 000 prey per m^2 was reached (Fig. 2). Foraging rate appeared to decline slightly at higher prey densities. A similar relationship was found between the success rate of foraging birds and prey density (Fig. 3), where the initial increase was also significant ($r_s = 0{,}68$, $t = 8{,}94$, $p < 0{,}001$). The biomass appeared to show a slight increase with increasing availability of prey biomass (Fig. 4), although the probability of this occurring by chance was high ($r = 0{,}22$, $p > 0{,}1$). The curves in Figures 2 and 3 were fitted by eye.

Page 110. Sentence half-way down should read: At intermediate relative worm densities (0,15 - 0,4), the birds obviously took none since none were available in this range. There was no apparent increase or decrease in the proportion of "small prey" taken with increasing proportion available (Fig. 6).

Page 111. Fig. 5 caption should include: The increasing trend was statistically significant ($r_s = 0{,}96$, $p < 0{,}001$) while the decreasing trend was not ($r_s = 0{,}21$, $p > 0{,}1$).

Page 115. Paragraph 2 should read: The density of foraging Curlew Sandpipers increased significantly with increasing prey density ($r_s = 0{,}58$, $t = 3{,}10$, $p < 0{,}005$) until a density of between 25 000 and 35 000 prey per m^2 was reached (Fig. 12). Bird density appears to decline slightly at higher prey densities. Foraging success rate was correlated with bird density ($r = 0{,}68$, $p < 0{,}001$), increasing initially but levelling off at higher densities (Fig. 13). Although it is recognised that partial correlation analysis may have shown whether the association between success and bird density arises because both were correlated with prey density, partial correlation analysis was not possible because these measurements did not come from the same body of data.

Page 122. Insert after 3rd sentence in Discussion: Results are not expressed in terms of biomass consumed related to prey density since direct observation of prey size taken (and hence of prey mass taken) was impossible due to the small size of the birds and of their prey, and the usual distance at which observations could be made at all. Royama (1971) applies the the profitability model in terms of percentage predation (that is prey numbers taken). Hence prey numbers taken appear to be an acceptable measure of profitability.

Page 122. Last sentence should read: However, I observed the responses of Curlew Sandpipers to variations in prey density within three different prey spectra, and, combined, these show a foraging-prey density relationship consistent with Royama's hypothesis, although the model was developed for a preferred-prey situation.

Page 129. Last sentence should read: Conceivably, birds must sample a wider area when they begin to encounter smaller prey at higher densities, and this would reduce their success rate; also the biomass of individual prey taken would be reduced.

Page 131. Figure 18 caption should read: Bird density and foraging success in relation to the density of prey. Curves are based on those in Figures 3 and 12. At A social factors start to operate and begin to reduce bird density. At B birds begin to encounter smaller prey and profitability is thereby reduced.

Part 5

Page 143. Insert in line 7: The frequency of agonistic behaviour (Table 5) should be examined in relation to the frequency of observed segregation into groups (Table 4). A X^2 test showed that the frequency of agonistic interactions observed differed significantly from that expected on the basis of segregation frequency ($X^2 = 10{,}6$, df = 2, $p < 0{,}05$). Delete following sentence.

Page 146. Table 5 caption should read: A total of 39 aggressive interactions was observed.

Page 152. Paragraph 2, sentence 3 should read: Hence, although prey density was high at Kommetjie, bird densities were also high (up to 15 birds per m^2) because the total foraging area available at Kommetjie was small; this may have accounted for the incidence of spatial segregation as a means to reduce competition for food in a relatively small foraging area.

Part 6

Page 156. Sentence 5 lines from bottom should read: The birds took 12% of this, or 84,6 kJ/m^2 per year.

Page 161. Third paragraph should read: Estimation of the percentage of the benthic invertebrate standing crop taken by the birds (Table 4) makes full allowance for month-to-month fluctuations in bird population numbers; it does have the disadvantage of cumulatively incorporating remaining biomass from month to month. The population took an estimated 8,6, 11,2 and 16,3% of the nett production of the benthic invertebrates potentially available to them on the marshes, the Assiminea zone, and the lower shore respectively (Table 5).

Thus they took an estimated mean of 12,0 ± 3,9% (± S.D.) annually, or 84,6 ± 27,5 kJ/m^2 (± S.D.) per year.

Page 162. Insert at end of first paragraph: Maximum and minimum ingestion values were obtained by combining the maximum and minimum values respectively (given by S.D.'s) of foraging rate, success rate, diet composition and prey mass in the above calculation.

Page 166. Insert at end of first paragraph: The apparent deficit varies between 5 and an exceptional 20% of the total energy requirement, a percentage error which I consider to be acceptable for an estimate of this sort.

Page 165. Table 4 has been amended and should read as Table 4 appended to the addendum.

Page 165a. Insert between pp. 165 and 166.

Page 167. Sentence 7 lines from bottom should read: They took 12,0 ± 3,9% (± S.D.) of the estimated nett annual production of benthic invertebrates potentially available to them, or 84,6 ± 27,5 kJ/m^2 (± S.D.) per year in 1974. This is slightly less than the 20,8 kcal/m^2 per year (87,1 kJ) estimated by Summers (1977) for the total wader population in 1975.

Page 168. Sentence half-way down should read: Milne and Dunnet (1972) found that the entire gross production of Mytilus at the Ythan estuary is accounted for in winter by predation and metabolic requirements, and they suggest that the mussel bed is being maximally cropped.

Page 168. Sentence 4 lines from top should read: The percentage (12,0%) of the estimated nett annual production of prey taken by Curlew Sandpipers appears to be relatively small. Not all gross annual production is available to predators, since part of this is utilised by the prey species themselves in the respiration required for growth, reproduction and other metabolic activities.

Delete sentence following.

TABLE 4. Estimated percentage of standing crop of prey taken by curlew sandpipers feeding on marshes, in the "*Assiminea* zone" (0,5 m above LWS to HWN) and on the lower shore.

Month	Curlew sandpiper population[a] (no. birds)	Marsh (600 ha)			*Assiminea* zone (380 ha)			Lower Shore (1 200 ha)		
		Population energy intake[b] (1 000 kJ/ha/month)	Mean standing crop(B)[c] (1 000 kJ/ha/month)	%of B taken	Population energy intake[b] (1 000 kJ/ha/month)	Mean standing crop (B)[c] (1 000 kJ/ha/month)	% of B taken	Population energy intake[b] (1 000 kJ/ha/month)	Mean standing crop (B)[c] (1 000 kJ/ha/month)	% of B taken
March 1974	37 390	29	477	6,08	210	3 033	6,92	179	1 686	10,62
April	22 400	31	450	6,89	25	3 298	0,76	45	1 697	2,65
May	13 300	41	437	9,38	59	2 999	1,97	27	1 870	1,44
June	13 300	28	1 256	2,23	43	2 772	1,55	21	1 960	1,07
July	13 300	37	1 993	1,86	40	2 691	1,49	15	1 896	0,79
August	13 300	20	1 081	1,85	42	3 578	1,17	16	1 938	0,83
September	19 500	6	1 111	0,54	91	4 069	2,24	48	1 699	2,83
October	23 250	4	1 032	0,39	139	3 562	3,90	49	1 660	2,95
November	28 100	5	941	0,53	107	2 499	4,28	71	1 280	5,55
December	28 100	5	1 078	0,46	167	2 194	7,61	70	1 291	5,42
Jan. 1975	28 100	23	1 383	1,66	175	2 789	6,27	63	969	6,50
February	32 900	19	846	2,25	198	3 124	6,34	116	1 126	10,30
TOTAL				34,12			48,49			50,95

[a] Pringle & Cooper (1976) and author's extrapolations.

[b] Based on values in Table 2.

[c] Energy content of prey organisms given in Appendix 1. Biomass of prey from Part 1.

Table 5. Percentage of estimated nett annual production taken by Curlew Sandpipers feeding on marshes, in the "*Assiminea* zone" (0,5 m above LWS to LWN) and on the lower shore.

	Marsh	*Assiminea* zone	Lower shore
% of standing crop (B) taken[a]	34,12	48,49	50,95
% of estimated nett production (P) taken[b]	8,57	11,18	16,30

[a] From Table 4

[b] By simple proportion (if say $^{P}/B = 4$, $B = {}^{P}/4$). Mean P:B ratio used given in Appendix 2.