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EFFECTS OF CHANGES OF LAND USE ON SOME
ANIMAL POPULATIONS

P. J. KNIGHTS, B.Sc. (DUNELM)

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being a thesis presented in candidature for the degree
of Doctor of Philosophy in the University of Durham,
1979

A B S T R A C T

Effects of changes of land use on some animal populations.

P. J. Knights.

Two examples are considered: (1) The effects of organotin agricultural fungicides on soil Acarina; (2) The effects of reclamation of intertidal land on overwintering shorebirds at Seal Sands, Teesmouth.

The effect of triphenyltin acetate and triphenyltin hydroxide was examined by field experiments and the results are discussed in relation to the dose level, regime and season of treatment. Numbers of soil Acarina were reduced by both chemicals when applied in autumn at recommended doses. The Mesostigmata and an abundant Prostigmatid, Tarsonemus floricolus, were particularly affected and the magnitude of reductions was related to the quantity of chemical applied. Not all species of mites were affected and treatment of half the recommended dose resulted in an increase in some families of Prostigmata. Seasonal changes in the abundance of mites are described and compared with the results of studies elsewhere in Britain. Suitable laboratory culturing techniques were devised for small Prostigmatid mites.

Reclamation of Seal Sands between 1972-74 resulted in a loss of feeding area and reduced feeding time. The effects of reclamation are considered in relation to the overwintering numbers of five waders: Grey Plover (Pluvialis squatarola), Curlew (Numenius arquata), Godwit (Limosa lapponica), Redshank (Tringa totanus) and Dunlin (Calidris alpina) and to the Shelduck (Tadorna tadorna). Monthly counts of each species are described and compared with counts in previous winters. Changes in numbers are discussed in relation to progressive reclamation. The relative importance of the reduction in feeding area and feeding time in determining the overwintering numbers after reclamation is considered by examination of: (a) the time spent feeding, and (b) the foraging behaviour and diet. The waders overwintered in lower numbers than previously but Shelduck numbers were unchanged. To satisfy their food requirements, Grey Plovers adapted by feeding at night while the other waders fed on adjacent fields in mid-winter. Shorebirds did not change their diet or foraging behaviour. Reduction in numbers was related to the reduced feeding area and food resources available, but for Dunlins loss in feeding time was more important.

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The study of the effects of organotins on soil sites was supported by a research assistantship from the Natural Environment Research Council, while my work at Teesmouth was funded by the Institute of Terrestrial Ecology and by the Royal Society for the Protection of Birds.

My special thanks to my wife, Sheila, for her skill and endurance in typing the thesis. Throughout its preparation she was invaluable.

Facilities for typing were kindly made available by Mr. N. J. Wheeler, National Park Officer of the Pembrokeshire Coast National Park.

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P R E F A C E .

The work undertaken and described in this thesis arose from two separate projects, neither of which could be funded for a full three-year period. The two projects have nothing in common except that they both deal with changes in land use and their effects on animal populations.

The first part of the thesis examines the side effects of two agricultural chemicals on soil Acarina and assesses whether these effects occurred by direct toxicity or indirectly, by the destruction of potential food. Additionally, I followed the seasonal fluctuations in the numbers of soil mites in the recently established grassland which comprised the study area and discuss changes in the species composition of mite communities associated with the cessation of cultivation.

The second project considers the effects of reclamation of intertidal mudflats on the numbers of overwintering shorebirds in the Tees estuary and examines the relative importance of loss of feeding sites and reduction in feeding time in determining the numbers of birds which wintered there after reclamation.

Because the two projects were not directly linked, they are presented separately.

PART 1.

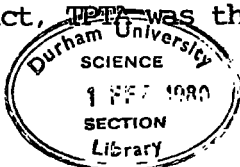
THE EFFECTS OF ORGANOTIN AGRICULTURAL
CHEMICALS ON SOIL ACARINA.

THE HISTORICAL DEVELOPMENT OF ORGANOTINS AS AGRICULTURAL CHEMICALS.

Organotin compounds were first synthesised in the mid nineteenth century (Lowig, 1852; Frankland, 1853 and 1854), but apart from the establishment of some industrial applications and a few biological applications, for example mothproofing (Farbenid, 1930; Miller et al., 1931), systematic investigation of their properties and potential uses began almost a century later. Renewed interest in organotin compounds was initiated in the early 1950's by the International Tin Research Council (now the Tin Research Institute) and research was initially carried out at the Institute of Organic Chemistry, T.N.O., Utrecht.

Subsequently the momentum of research in this field increased. While some new uses were industrial, for example as stabilizers of vinyl resins, plastics and polymers, considerable emphasis in research has been towards the utilization of the biocidal properties, particularly as agricultural chemicals. The success of this research is reflected in the sharp rise in production of organotins for agricultural use from a few hundred tons in the mid 1950's to over 100,000 tons in 1968 (Van der Kerk, 1970). In 1968 approximately 25% of the British potato crop was protected by triphenyltin fungicides (Thomas and Tann, 1971).

Van der Kerk and Luijten (1954) first established the fungicidal properties of various organotin compounds including triphenyltin acetate (henceforth referred to as TPTA). In fact, TPTA was the basis for the first commercially



available organotin fungicide, a formulation registered as Brestan and produced by Faberwerke Hoechst (Hartel, 1958 and ^{Kaas-}/Sijpesteijn, 1959) in 1959. Subsequently triphenyltin hydroxide (TPTH), the hydrolysis product of TPTA, was introduced for the control of the same fungal diseases (Pieters, 1962). The vast amount of research and development concerned with various aspects of fungicidal activity in organotin compounds are discussed in depth in a number of reviews (Kaas-
/Sijpesteijn et al. in Torgeson, 1967; and Poller, 1970).

In Britain and Europe, and more recently in the U.S.A., TPTA and TPTH have become firmly established in agricultural use for the control of potato blight (Phytophthora infestans), yellow blight (Cercospora beticola) on sugar beet and leaf spot (Septoria apii) on celery (Poller, 1970). While the triphenyltins are not the most strongly fungitoxic of the organotin chemicals, their phytotoxicity is far less than that of aliphatic tin compounds. In situations where phytotoxicity is of no consequence Tributyltin oxide (TBTO) is very widely used, for example in wood preservation, since it is highly toxic to fungi (Hof and Luijten, 1959). Thus, the use of triphenyltins in agriculture is a compromise.

The International Standards Organisation has designated the triphenyltins as Fentins - TPTA as fentin acetate and TPTH as fentin hydroxide. These two compounds are now marketed in Britain under a variety of brand names (see Appendix 1). In these formulations TPTA is always combined with the dithiocarbamate, Maneb, TPTA being present as a 20% active ingredient. TPTH is not combined with Maneb and usually occurs as a 60% active ingredient. The solubility in water of both TPTA and TPTH is low so they are prepared as wettable powders and applied in aqueous suspension. The inclusion of Maneb with TPTA formulations is related to reduction of phytotoxicity rather than improvement of the fungicidal properties (Tin Research Institute, pers. comm.).

As pesticides, organotin chemicals have a major advantage over most other

organometallic compounds, namely that they break down to inorganic tin which is one of the least toxic metal ions to man.

THE TOXICOLOGY OF TRIPHENYLTIN COMPOUNDS.

Triphenyltins appear not to be systemic, since radioactively labelled TPTA is not absorbed by plants through either roots or leaves (Herok and Götte, 1963). However, residues may remain on the surface of plants and a number of studies have aimed at determining the potential hazard to human beings from contaminated foodstuffs, on the basis of toxicity to laboratory mammals. Investigations by Stoner (1966) concluded that an acceptable daily intake for man was in the order of 0.001 mg/kg of TPTA or TPTH, a considerably lower level than first suggested by Harlow et al. (1962). Evidence of TPT residues in and on potatoes indicate that such levels are unlikely to be reached in current agricultural practice (Thomas and Tann, 1971; Lloyd et al., 1962).

Verschuuren et al. (1966) confirmed the findings of Stoner (1966) and demonstrated various sub-lethal effects such as growth retardation. Despite initial evidence of an accumulative action of TPT's (Scholz, 1965), subsequent investigation indicates that it is only partially cumulative, with a half-life of around 50 days in guinea pigs (Stoner and Heath, 1967).

A comprehensive radiometrical study (Barth et al., 1964) to determine possible effects on ruminants of TPTA ingested on silage found that most of the compound passed directly through the alimentary system. The small portion which was absorbed was quickly broken down and after a few weeks no residues could be detected. Earlier radiometrical estimates by Herok and Götte (1962) found that

unchanged TPTA or its hydroxide had a half-life of 20 hours in the tissues of cattle, the resulting metabolites having a half-life of 8 - 70 days. The acute toxicity of TPTA and TPTH to various laboratory mammals is summarized by Ben-Dyke (1970).

At a cellular level the activity of trialkyltins, notably trimethyltin and triethyltin compounds, has attracted extensive study since it was found that these chemicals provided a useful tool in attaining an insight into the mechanism of oxidative phosphorylation (Aldridge and Rose, 1969). Their value in this context was due to their high biological specificity, both trialkyltins apparently inhibiting oxidative phosphorylation through the binding of these chemicals with a specific site in the mitochondria (Aldridge and Street, 1971; Gremer, 1968; and Selwyn et al., 1970).

Triphenyltins have been studied in less detail but the published information which does exist suggests that these compounds also have a direct inhibitory effect on oxidative phosphorylation (Stockdale et al., 1970; Byington, 1971; Byington et al., 1974). These investigations were similarly undertaken to establish the use of organotin compounds as a tool in determining the mechanism of oxidative phosphorylation.

Additionally, histopathological examinations have been conducted as part of insect anti-feedant studies (Abo-Elghar and Radwan, 1971) and for the determination of mammalian toxicity (Stoner, 1966; Verschuuren, 1966) and sub-lethal effects, such as reduced fertility (Newton and Hays, 1968). These effects are summarized by McCollister and Schober (1975) in a review of toxicological properties of organotins.

While TPT's appear to be broken down photochemically on exposed plant and mineral surfaces, breakdown within the soil itself is due to microbial activity (Barnes et al., 1971 and 1973). Furthermore, the breakdown of TPTA was not preceded by a marked lag period, suggesting a rapid adaptation of the soil microflora. Tributyltin oxide (TBTO), generally a more toxic chemical than the TPT's,

was also found to have little effect on various activities of the micro-flora, such as ammonification, nitrification and sulphur oxidation (Bollen and Tu, 1972). This evidence suggests that the less toxic organotinns may have little effect on soil fertility provided that organic breakdown to particle sizes small enough for microbial action to start is not prevented by toxicity to the macro-fauna. The exact mechanism of biodegradation remains to be determined. Barnes et al. (1971) determined a half-life of TPTA in the soil of 140 days and noted rapid adsorption of TPTA to soil particles such that 70% of the compound remained in the top 4 cm. of soil. It was concluded that pollution of ground water by TPTA was unlikely.

Systematic investigation of potential insecticidal activity of organotinns began in the early 1960's. Kotchkin (1964) demonstrated the toxicity of TPT's to houseflies (Musca domestica) while Kenaga (1965) found that both TPTA and TPTH sterilized adult houseflies at sub-lethal concentrations and suppressed reproduction in the German cockroach (Blatella germanica) and the flour beetle (Tribolium confusum). Several studies have confirmed the chemosterilant property of TPTA and TPTH towards houseflies (Kissim and Hays, 1966; Hays, 1968) and shown that other groups of insects are similarly susceptible, for example, tobacco bollworm (Heliothis zea - Lepidoptera: Noctuidae) (Wolfenburger, 1968) and Japanese beetle (Popilla japonica - Coleoptera: Scarabidae) (Ladd, 1968).

TPT's generally act as stomach poisons rather than as contact insecticides (Gardiner and Poller, 1964). Direct toxicity in this manner has been proved effective against cotton leafworm (Spodoptera littoralis) (Abo-Elghar and Radwan, 1971; Findlay, 1970) and the pink bollworm (Pectinophora gossypiella) (El Sebae and Ahmed, 1963). At sub-lethal concentrations an anti-feedant effect is shown by these and related pest species (Asher and Rones, 1964; Asher and Nissim, 1964 and 1965; Findlay, 1970). However, conflicting with these numerous field and laboratory studies is the rather erratic efficiency of TPT's against the bollworm, (Heliothis zea), described by Graves et al (1965).

Acaricidal properties have also been investigated. Both TPTA and TPTH have

been found to provide effective control of, for example, citrus rust mite (Phyllocoptruta oleivora) (Bullock and Johnston, 1968) and pink rust mite (Aculus pelekassi) (Asher and Nissim, 1964; Sternlight, 1966). Generally, TPTH appears to be more effective than TPTA but both are inferior to the new extensively used acaricide Plictran (reg). The active constituent of this is tricyclohexyltin hydroxide and has been evaluated in a number of studies (Allison et al., 1968; Downing and Moilliet, 1970).

While several early studies suggested that TPTA was considerably toxic to certain mollusca, for example Astralorbis glabratus (Hopf and Muller, 1962; Deschiens and Floch, 1962), more detailed work (Frick and Jimenez, 1964) has shown that the toxicity of TPTA is inferior to that of TBTO. TBTO is now of considerable importance in attempts to eradicate the snail vectors of Schistosomes (bilharzia) (Evans, 1971), a situation in which its phytotoxicity is of minor importance.

Despite the considerable volume of literature relating to screening tests and possible applications of organotins as biocides, little information is available on toxicity to non-target animal species. The major exception to this is the standard assessment of the effects to man and domestic animals, detailed above.

In view of the variation in performance of TPT's towards target species, prediction of their effect on non-target organisms is likely to be unreliable. This led to the work to be reported in this thesis.

AIMS OF THE STUDY.

The primary aim of this study was to determine the effects, if any, of commercially available triphenyltin fungicides on population levels of certain soil invertebrates when the fungicides are applied at dose levels used in current agricultural practice.

The need to identify the soil organisms studied to a reasonably fine taxonomic level (and preferably to species) in broad spectrum toxicological studies has been demonstrated by many workers, for example Sheals (1957). It was particularly necessary in my study since, as detailed in the introduction, organotins generally show remarkable variations in toxicity between different groups of animals and even between different species of the same group. Since it was impractical to identify all the invertebrate fauna in agricultural soils to this level, soil Acarina alone were selected for counting and identification. This choice was dictated largely by numerical abundance within the study area available.

Fungicide applications were made and samples taken during a virtually continuous programme from September 1972 to July 1974. The results of these trials are presented in pages 30 - 65.

Another aim of my study, subsidiary to the toxicological work, was to determine the seasonal changes in population levels of the principal orders of soil mites and of some particularly abundant species. These observations are presented in pages 77 - 95.

An attempt was made to complement the results obtained in field trials by culturing certain mite species in the laboratory and carrying out direct toxicity studies. A successful means of culturing several species was eventually achieved but no systematic laboratory trials could be initiated during the two year period of the study. The culturing techniques used are described in pages 66 - 76.

THE STUDY AREA.

Although more realistic effects of the fungicides would have been obtained by setting trial plots in arable land under normal agricultural use, such an area was not available.

The study area chosen comprised recently established grassland which had been seeded with coarse lawn grass mixture after several years' cultivation. Final rotavation had occurred eighteen months before the present trials commenced. Although the grass had been mown regularly since sowing, this area had received no other treatment or use. In particular, no agricultural chemicals had been applied to the area for at least two years before the study began and no organotin compounds had ever been used there.

In the following sub-sections the soil, vegetation and general climatic influences are briefly described.

SOIL CHARACTERISTICS.

The soil of the study area was developed on boulder clay, typical of most of lowland County Durham. This generally heavy soil had been modified by the incorporation of considerable solid debris including old pottery, brick fragments and clinker which was derived from the construction and subsequent removal of a nearby railway track.

The soil structure was broadly similar to that of cultivated soils,

containing no distinct litter layer. The distinction between A and B horizons was difficult to determine. The mineral component was therefore dominant with generally low humus levels. No detailed analysis of the soil was carried out.

Drainage of the soil was slow, the clay component retaining water well. When dry, the soil became extremely solid.

The surface of the site had a slight slope of approximately 8° .

VEGETATION.

The dominant component of the vegetation cover was rye grass (Lolium perenne), this having been seeded in the first instance. Clover (Trifolium repens) and dandelion (Taraxacum vulgaria) had become established subsequently.

However, even the rye grass cover was sparse, and closer examination showed the immediate soil surface of the gaps between rye grass clumps to be covered by mosses (primarily Pottia and Phascum spp.).

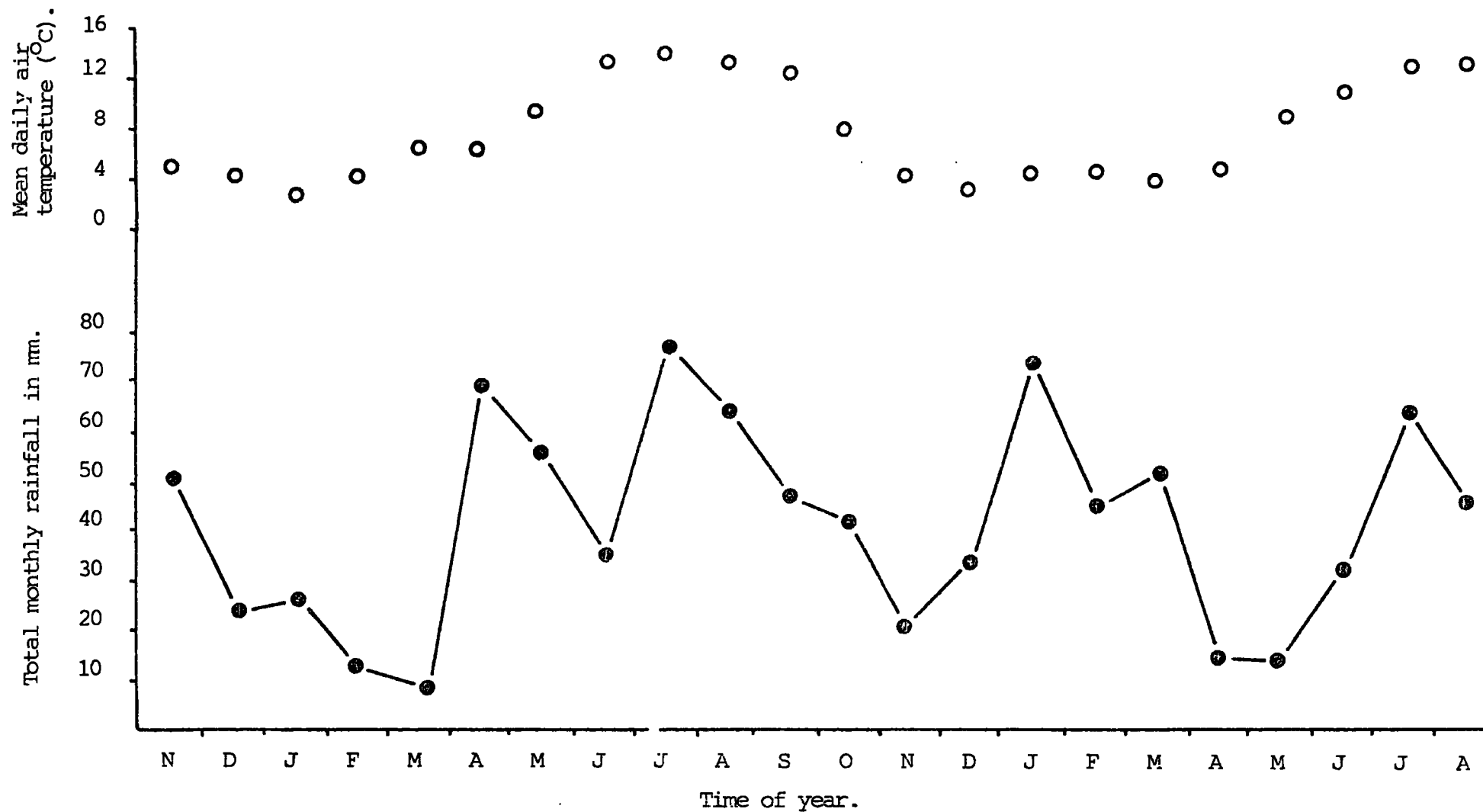
The majority of root development occurred in the top 3 - 4 cm. of the soil; certainly the roots of rye grass penetrated very little below this.

No gradients in soil fertility were visible in the form of variable vegetation growth.

CLIMATE.

The site was open but at the same time afforded some protection by adjacent woodland. The climate is typical of that in the vicinity of Durham City, being generally moderate with respect to many parts of north-east England. Thus, in any year, air temperatures range from around 10°C in December to 27°C in August. The number of ground frosts are generally over 100 per year. Average annual rainfall is 650 mm., there being between 180 - 200 days with rain - the highest rainfall occurring between the months of April and August. In an average year snow falls on only 7 - 14 days, whilst snow cover may remain for over two weeks.

FIGURE 1 : THE SEASONAL VARIATION IN TEMPERATURE AND RAINFALL AT DURHAM.



N.B. These data are extracted from the reports of the Durham University Observatory.

Detailed records of climatic variation were not made at the study site since more comprehensive measurements were made at the Durham University Observatory located about a mile from the study area in a very similar situation and altitude.

The variation in rainfall and temperature recorded by the Observatory during the two years of my study are summarized graphically in Figure 1.

METHODS OF STUDY,

PROGRAMME OF FIELD TRIALS.

Two triphenyltin fungicides, Duter (TPTH) and Brestan (TPTA with Maneb) were used in the trials. The recommended dosages for agricultural use are $1\frac{1}{4}$ lbs./Acre (1.4 kg./ha) and 7 oz./acre (0.5 kg./ha), respectively, these dosages being repeated up to six times at 10 - 21 day intervals for each product. Both are wettable powders, being sprayed in suspension in 20 - 100 gallons (91 - 455 litres) of water.

In this study, five series of trials were undertaken, involving a total of seven different levels of treatment. These were as follows:-

- Series A 4 x recommended dosage TPTH (single application).
- Series B 2 x recommended dosage TPTH (single application).
- Series C Agricultural dosage TPTH (repeated 4 times at 10 - 14 day intervals).
- Series D/1 2 x recommended dosage TPTA (single application).
- D/2 Agricultural dosage TPTA (repeated 4 times at 10 - 14 day intervals).
- D/3 2 x recommended dosage TPTA (repeated 3 times at 10 - 14 day intervals).
- Series E/1 4 x recommended dosage TPTA (single application).
- E/2 Agricultural dosage TPTH (repeated 4 times at 10 - 14 day intervals).
- E/3 2 x recommended dosage TPTH (single application).

Treatments E/2 and E/3 were repeats of trial series C and B respectively, but were carried out at different times of year. In all cases, each dosage was prepared immediately before treatment.

The lay-out of trial plots.

Treatment series A, B and C were laid out in strips, two experimental and two control for each series, these being arranged alternately with a distance of 30 cm. between each strip. Within each strip eight individual plots, 60 cm. by 60 cm., were separated from adjacent plots by a distance of 30 cm. of untreated ground. This free ground enabled easy access for sampling and spraying, and at the same time reduced the risk of lateral movement and contamination of adjacent plots. In view of the lack of substantial leaching demonstrated by Barnes et al. (1971), this distance would be an adequate, if not unnecessary, provision.

The alternating arrangement of control and experimental strips was intended to reduce the influence of any gradients in soil quality, vegetation or soil water which might have affected the distribution of Acarina.

In series D and E, a 4 x 8 latin square design of plots was adopted, this scheme being more usual in toxicological field trials. It enabled three separate treatments to be incorporated in each series and at the same time reduced further any errors due to various environmental gradients. Each treatment had eight replicates which, along with control plots, provided a total number of thirty-two samples on each occasion. This overall total was determined purely by the capacity of the apparatus available for extracting Acarina from soil cores. The size of plots in both series D and E was 90 cm. by 90 cm., each plot being separated from adjacent plots by a distance of 45 cm.

In all series the size of plots chosen was related to the anticipated number of samples to be taken while allowing considerable distances between successive samples. The lay-out of trial plots is shown in Figs. 2 and 3.

FIGURE 2 : THE ARRANGEMENT OF TRIAL PLOTS IN SERIES A, B AND C OF THIS STUDY.

In this alternating arrangement, experimental or treated plots are designated 'T', while control or untreated plots are designated 'C'.

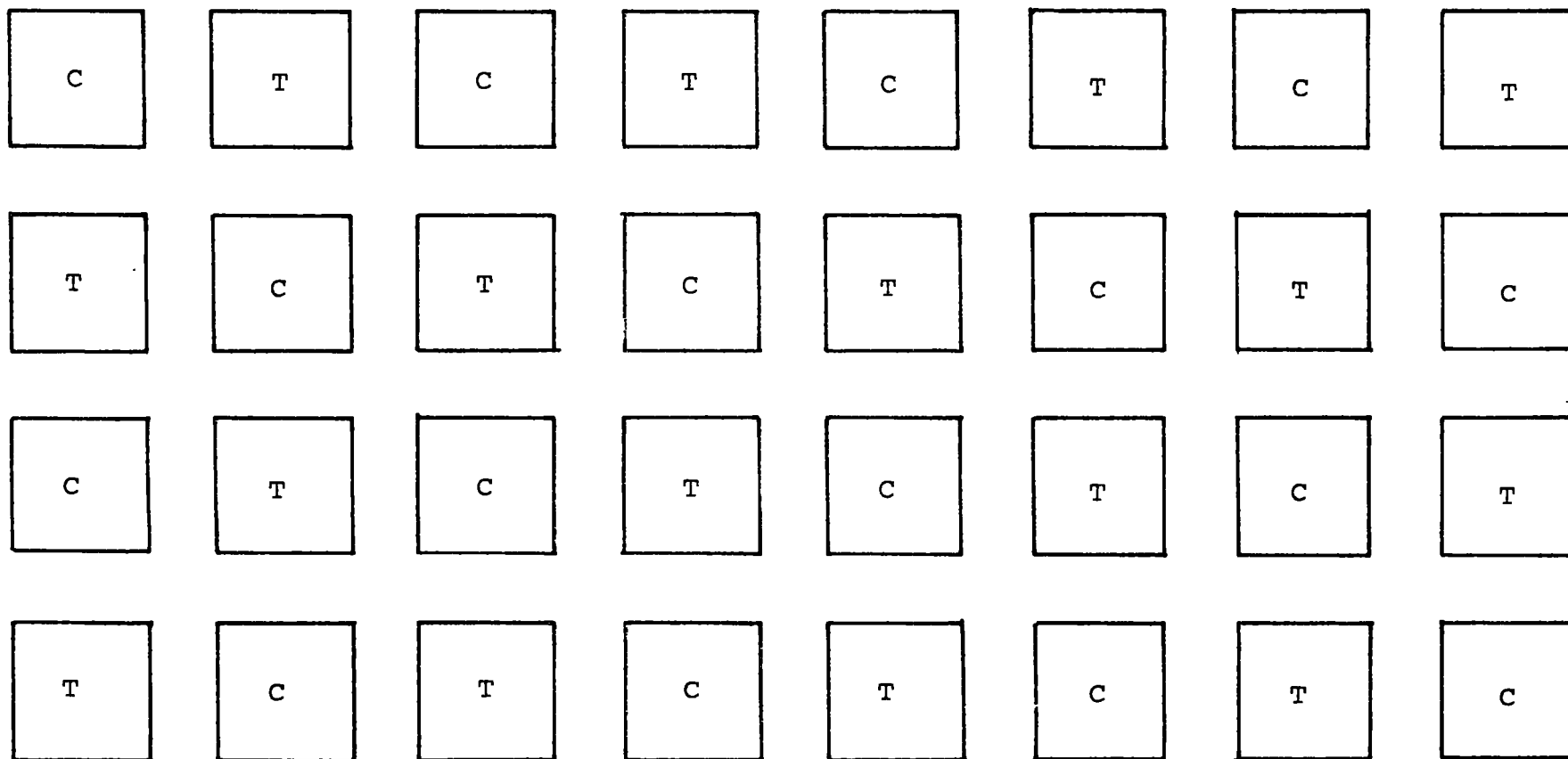


FIGURE 3 : THE ARRANGEMENT OF TRIAL PLOTS IN SERIES D AND E OF THIS STUDY.

In this latin square design, treated plots are designated by their number, while control plots are designated 'C'.

C	D/3,E/3	D/2,E/2	D/1,E/1	C	D/3,E/3	D/2,E/2	D/1,E/1
D/1,E/1	C	D/3,E/3	D/2,E/2	D/1,E/1	C	D/3,E/3	D/2,E/2
D/2,E/2	D/1,E/1	C	D/3,E/3	D/2,E/2	D/1,E/1	C	D/3,E/3
D/3,E/3	D/2,E/2	D/1,E/1	C	D/3,E/3	D/2,E/2	D/1,E/1	C

Sampling Regime.

For each series of trials a set of pre-treatment samples were taken.

Sampling of series A was carried out for a period of three months between November 1972 - January 1973 inclusive. In series A, emphasis was placed on frequent sampling immediately after treatment to identify accurately any rapid changes in abundance. Samples were taken at 4, 8, 12, 16 and 28 days after initial treatment and subsequently at monthly intervals.

Series B and C ran approximately concurrently from February 1973 to August 1973, the first sample being taken two weeks after initial treatment and further samples at monthly intervals.

Since no marked rapid changes occurred amongst soil Acarina in series A, B and C, sampling in series D and E was undertaken only at monthly intervals from October 1973 to January 1974. Since in each of these series a given treatment was replicated only eight times, two sets of samples were taken from each plot each month. This gave a total of 16 samples for each treatment in each month (the second samples were taken three days after the first to allow extraction of the latter).

To provide a useful sequence of samples for study of population changes amongst soil Acari, an additional series of samples was taken during intervals between the various trial series, and for a seven month period after completion of the final trial series; otherwise the control samples within each series were used for this purpose.

Preparation and Treatment of Plots.

The general study area was fenced off a month before each sampling programme was begun, thereby excluding any human activity which might have affected the results. The sample plots themselves were marked out with bamboo canes and string, care being taken during this procedure not to trample on the future

trial plots - an important precaution in view of their small size.

Before spraying, the grass on all plots was clipped to approximately 1 cm. in height to allow maximum penetration of the spray to the soil surface. Spraying was carried out at least ten days after this, to allow both fauna and vegetation some time to adapt to the new conditions. Immediately before spraying, superficial litter, such as dead grass and leaves, was removed since these would also interfere with penetration of the spray.

In series A, B and C the dosages were applied in 300 ccs. of tap water to each plot, these being equivalent to the quantity of liquid per hectare suggested for agricultural application. This quantity appeared to provide even coverage of each plot without waterlogging the soil (which would have increased the chances of immediate run-off).

In series D and E, one litre of water was used as carrier for each plot. Once again this is equivalent to the amount of liquid recommended for agricultural use. In no series was the amount of water added to trial plots considered so large as to require equivalent amounts of water to be applied to control plots.

Spraying was carried out under damp weather conditions as far as possible to facilitate penetration of the fungicide particles into the soil. Under dry conditions, it seems likely that penetration would be poor and a substantial proportion of each dose would remain very near the surface where it might be subject to more rapid photochemical degradation. Under extremely wet conditions, on the other hand, the fungicide might be moved appreciably within or on top of the soil; therefore such conditions were also avoided. Spraying was carried out always in late afternoon, at which time the study area received no direct sunlight. This was again a precaution to allow reasonable penetration of the fungicide.

A small hand-held sprayer (manufactured by Gromess Co. Ltd.) was used

throughout the study. This provided a narrow spread of fine spray, enabling even dispersal of the fungicide. Being hand pressured, the rate of delivery could be easily adjusted. The sprayer was held such that the nozzle was 14 - 16 cm. above the soil surface, providing accurate coverage and avoiding breaking up the soil surface.

When the study was first planned it was hoped to measure the amount of each dose actually reaching and penetrating the soil and subsequently to monitor its progressive degradation by polarographic analysis. Attempts to do so, however, were defeated by the tenacity with which triphenyltin adsorbs to clay particles. No solvent has yet been found to provide the complete recovery of organotins from soil necessary for meaningful analysis.

SAMPLING AND EXTRACTION TECHNIQUES.

The sampling equipment and method.

In all five trials series, cylindrical core samples were taken, 3.8 cm. in diameter with a surface area of 11.5 square cm. Preliminary sampling had indicated that this size of sample contained sufficient mites to provide useful data while at the same time allowing reasonably quick sorting.

Cores were taken to a depth of only 3 cm. Important factors determining this choice depth were as follows:

(a) Mites were separated from soil by means of a high gradient extractor. Macfadyen (in Murphy, 1962) recommends the use of cores 3 cm. in depth - the depth of samples affecting the gradients of temperature and humidity within it, and possibly, therefore, movement of some species. For deeper samples, it would have been necessary to divide each core, a process which would have increased effects due to soil compression, particularly in view of the clayey nature of

the soil.

(b) The extractors available held a total of 32 samples only. If division of cores had been adopted, it would have been necessary to reduce the number of treatments possible to maintain adequate replication of each.

(c) With the sampling equipment available, it was difficult to obtain good quality samples consistently below 3 cm., since the soil was so stony. In the dense clay soil, compression was more evident in samples deeper than 3 cm. Problems of compression are generally more marked with a small size of core (Murphy, 1962), as used here.

(d) In most soils 70% of total soil Acari are found within this depth (Wallwork: in Burges and Raw, 1967) and preliminary sampling within the present programme found around 80% to be present in the top 3 cm. This is perhaps not surprising in view of the shallow penetration and development of roots. Only a relatively small number of mite groups occurred consistently below 3 cm. - for example Pyemphorus sp. and Rhodocarellus sp.

(e) The study was intended to detect proportionate changes in abundance rather than an absolute measure of density.

(f) Barnes et al. (1971) found that 70% of a TPTA dosage remained in the upper 4 cm. of soil.

The type of corer used was similar to that employed and described by Block (1965) and Springett (1965). The manner of use followed that outlined in these previous studies and will not be described here, but several aspects of sampling procedure are worth emphasis.

Before each set of samples were collected, the cutting edge of the sampler was sharpened to minimize compressional effects. Sampling under conditions when the soil was waterlogged was avoided, since compression of the sample was then more frequent and severe, and smearing of the surface occurred. Furthermore, during extraction, wet samples tended to shrink considerably, and a gap would form between the core and canister which held the core. This disturbed the correct temperature and humidity gradients.

Sampling was carried out in the first half of the morning, before 10.00 hours, so as to exclude, in part at least, variation due to any diurnal vertical migration of animals within the soil. Within each plot samples were taken on a stratified, random design, i.e. the co-ordinates of sample site were determined by random numbers, as used by Davis (1963). Samples which showed evident compression, perhaps due to a large stone contained within the core, were rejected and replaced in the plot. Under normal circumstances no replacement cores were provided for those removed. The area of each plot was adequate to allow several centimetres around each previous sample hole for the anticipated number of samples to be taken.

Canisters containing cores were stored individually with appropriately numbered slips of paper. On all occasions samples were loaded into the extractor within two hours of sampling.

Extraction.

Samples were extracted using a modified Macfadyen high gradient extractor. Although this system has been found to be inferior to Tullgren funnels for the extraction of most groups of Acari from mineral soils (Edwards and Fletcher, 1971), the Tullgren funnels available at Durham were not suitable for the extraction of small core sizes. Furthermore, preliminary use of Tullgren funnels was found unsatisfactory, as much debris fell into the collecting vessels, a factor which greatly increased the time taken to sort samples,

particularly those containing the smaller Acarina.

Block (1965 and 1966) described the construction of the extractor used in this study, the development of temperature/humidity gradients and the rates of extraction of different groups of mites from mineral soils. Although no check of extraction efficiency was made in the course of this study, Block found that the equipment extracted 76% of Acarina from mineral soils.

The extractor held a total of 32 samples, an important determining factor in the arrangement of plots, the number of replicates in each treatment etc. as already noted.

Following Block's findings, I adopted the following heating regime:

18 hours at 60 volts

24 hours at 100 volts

24 hours at 140 volts

Thus, including sampling and loading of the extractor, a complete sequence of extraction required three days.

The treatment of samples before and after extraction.

Before loading the cores into the extractor, care was taken to clip and remove surface vegetation very close to the soil surface but without actually disturbing the soil itself. The presence of surface vegetation could quite easily form hiding places and ultimately traps for the mites, and might have interrupted the development of temperature and humidity gradients.

It was found important to mount the core above the collecting vessel with the minimum of disturbance to reduce the quantity of debris falling into the vessel. Similarly, care was taken when removing the dry cores after extraction was complete.

After completion of the extraction, samples were washed from collecting

vessels with 90% alcohol into plastic screw topped containers of 100 ml. capacity. Together with the small amount of water initially in the collecting vessel, this gave a final storage fluid of approximately 75% alcohol. Since storage times before sorting were relatively short, possibly a month, no glycerol was added, as is recommended for storage over a longer term, Evans et al. (1961).

The sorting of samples.

For counting and identification, samples were flushed from storage containers with 70% alcohol into a fine sieve. This sieve comprised a perspex ring with an internal diameter of 5 cm., and across one end was glued a fine nylon mesh, a method developed by G. Robertson (pers. comm.). The perspex ring was obtained by cutting an 8 mm. wide section of perspex tube. The nylon mesh had a pore size sufficiently fine to retain adults of all species of interest, yet enabling reasonably rapid flow of fluid and the escape of finer debris. Care was taken to ensure good adhesion of the mesh to the perspex.

The mesh surface was demarcated for easy searching by china-graph pencil. Despite the necessity to remark at frequent intervals, perhaps every sixty samples or so, the pencil was not soluble in alcohol as were several markers tested.

Because of the gradual accumulation of very fine debris amongst strands of the nylon mesh, and consequent darkening of the background, the mesh was renewed regularly.

For examination, the sieve was placed on a white filter paper disc in a petri dish. The filter paper enabled specimens to be kept moist easily and provided a good bright background for separating mites from debris. Using this system, sorting and identification of mites was a comparatively simple process.

For counting and the bulk of identification, a Zeiss binocular microscope with 10 x 1.4 - 6 (zoom) magnification proved most convenient. During initial

identification, and subsequently for checking doubtful specimens, temporary slides were made for examination under high power magnification. Highly sclerotized species, for example various Gamasids and Cryptostigmata, were first cleared in warm 5% acetic acid before mounting in D.P.X. Cavity slides were necessary only for the larger Mesostigmata. In general, I followed procedures outlined by Evans et al. (1961).

Mites for each sample series were removed from the sieve as they were counted and identified and stored in two by one inch vials in case further, or more detailed, identification was necessary. The storage fluid used was 70% alcohol plus glycerol.

Mites were manipulated with a micro-spatula (the flattened end of a strand of copper wire set in a glass rod) or a fine paint brush.

TAXONOMY.

Both for the identification of major groups of soil Acari in the initial phase of this study and for subsequent identification to family level, "An Introduction to Acarology" (Baker and Wharton, 1952) proved of greatest use. Identifications were confirmed by K.H. Hyatt of the British Museum and D. Macfarlane of the Commonwealth Institute of Entomology, but responsibility for checking these against the bulk of specimens is mine.

Preliminary sampling of the study area indicated that Prostigmata were dominant, conforming with the findings of Loots and Ryke (1967), Edwards and Lofty (1968) and Phillon and Gibson (1962) that in cultivated soils Prostigmata are far more numerous than Cryptostigmata. In fact, at the beginning of the study no Cryptostigmata were found. This contrasts strongly with the abundance of these groups in permanent pastures, and confirms the close similarity of the study area with agricultural land.

Although a complete species list was not prepared for my study area, it was evident that relatively few species comprised the bulk of Acarina present. For the present study the major groups of Acari were separated as also were a small number of the more abundant species.

Below, the general diversity within each of the four commonly occurring orders of the sub-class Acari is briefly outlined. This basic classification follows Evans et al. (1961).

1. Prostigmata.

On the basis of numerical abundance two species, Tarsonemus floricolus (Canestrini and Fanzago) and Scutacarus (Variatipes) montanous (Paoli) were separated as also was the genus Pygmephorus of which two species were probably present. T. floricolus has not previously been reported in the north-east of England and was not recorded by Hull (1916), in his major work "Terrestrial Acari of the Tyne Province".

Identification and information concerning the ecology of these genera was obtained from Stammer (Ed.) (1959: Karafiat, Scutacaridae; Krczal, Pyemotidae; Schaarschmidt, Tarsonemidae). Apart from a comprehensive taxonomic study of the family Tarsonemidae by Beer (1954) recent interest in these three groups has been shown primarily by European workers. Further information relating to the Tarsonemidae was obtained from Karl (1965), Schaarschmidt (1963) and Mahunka (1970). For the Scutacaridae, Rack (1965) and Mahunka (1965) provided most information.

Those Prostigmatids which are generally more abundant in established pasture occurred in relatively small numbers in my study area, but representatives of the Eupodidae and Tydeidae were regular components of samples throughout the study.

2. Mesostigmata.

Throughout the study Rhodacarellus epigynalis, Sheals, and an unidentified Pachylaelaps species were the most abundant representatives of this order. The large Mesostigmatid, Pergamasus longicornis, Berlese, was less frequent, but nonetheless regular in occurrence. Of the Uropodina a single species, Dinychopsis appendiculata, Berlese, occurred regularly but at no time was common.

3. Cryptostigmata.

During preliminary sampling within my study area, no Cryptostigmata were

found. Subsequently, however, small numbers of one species, Tectocephus velatus (Michael), appeared during sampling of trial series, and in series B and C an unidentified Oppia sp. also became a regular component of the population. Towards the end of my study, a third species Nanhermannia nana (Nicolet) began to appear regularly.

4. Astigmata.

Astigmatids were generally uncommon in the study area with the exception of a single species (unidentified) belonging to the genus Schwiebea.

These details of species are summarized in Table 1.

TABLE 1 : A SPECIES LIST OF ACARINA WITHIN THE STUDY AREA AT DURHAM.

<u>Order</u>	<u>Family</u>	<u>Genus or Species</u>
Prostigmata	Tarsonemidae	Tarsonemus floricolus (Canestrini and Fanzago)
		Tarsonemus talpae (Canestrini and Fanzago)
	Pyemotidae	Pygmephorus spp.
	Scutacaridae	Scutacarus sp.
		S. (Variatipes) montanus (Paoli)
	Eupopidae	Eupodes sp.
	Tydeidae	(Unidentified)
	Stigmaeidae	Eustigmaeus sp.
Mesostigmata	Rhodacaridae	Rhodacarellus epigynialis, Sheals .
	Parasitidae	Pergamasus longicornis, Berlese .
	Pachylaelapidae	Pachylaelaps sp.
	Uropodidae	Dinychopsis appendiculata, Berlese .
Cryptostigmata	Tectocepheidae	Tectocepheus velatus (Michael)
	Oppiidae	Oppia sp.
	Nanhermanniidae	Nanhermannia nana (Nicolet)
Astigmata	Acaridae	Schwiebea sp.
	Acaridae	Tyrophagus sp.

N.B. Small numbers of Prostigmata were found which were not ultimately identified even to family level, but for other orders the representation of families given here is complete.

THE RESULTS OF FIELD TRIALS.

CHOICE OF ANALYSIS.

In common with many studies of soil invertebrate populations, even within plots of a few metres square, the variance of numbers in replicate samples was frequently found to be as great as the mean (Snedecor, 1966). In these circumstances simple comparison of means is unsatisfactory in assessing the results of fungicide treatments on the soil Acarina.

Although some experiments were carried out using a latin square design (series D and E), analysis of variance of the results is valid only if the data comply with a model which assumes the additivity of variance, together with normal and independent distribution of error and homogeneity of variance (Snedecor, 1966). Suitable transformation can provide variances which are independent of the means and are additive, but Bartlett's test for homogeneity indicated that in my study variances were heterogeneous, a feature which simple transformation cannot resolve.

A non-parametric method, the Wilcoxon two sample test, was therefore chosen for analysis of field trial data in this study, since it makes no assumptions about the nature of the frequency distributions of numbers between samples.

PRESENTATION OF RESULTS.

The effects of triphenyltin fungicides are considered in relation to counts of total Acarina, two principal orders, the Prostigmata and Mesostigmata, and a single species of Prostigmata, Tarsonemus floricolus. Excluded from the group 'Prostigmata' is the genus Pygmephorus in all trial series and the species Scutacarus (Variatipes) montanus also in series D and E. These were analysed separately because of their increasing abundance in the sampling area in 1973. However, treatment with fungicides had no consistent effects on these groups, so they are not discussed further below, but median densities after various treatments are included in Appendix 2.

For each series of trials the median numbers of each taxonomic group per square metre are plotted in histogram form (Figs. 4 - 13). A complete inventory of median densities and the total range of observed densities within sample groups is provided in Appendix 2 . The results of analyses by Wilcoxon two sample tests are provided in Tables 2 - 10 . In each table, values represent the level of significance of differences between control and treatment populations on the same sampling date. The direction of the difference is expressed by an arrow, for example $0.001 \downarrow$ indicates that the density of mites in the treated plots is significantly lower than that recorded in corresponding control plots. Differences with $p > 0.05$ are considered not significant and represented in each table by the abbreviation "Ns". In Tables 11-19, the differences in numbers of mites between control and treated plots is expressed as a percentage of the median densities in control plots for each sampling occasion. Thus "75 $\downarrow$ " indicates that the density of mites in treated plots is 75% lower than the density in the corresponding control plots, the direction of change again being indicated by an arrow.

FIGURE 4: CHANGES IN DENSITY OF ALL SOIL ACARINA AND MESOSTIGMATA DURING TREATMENT SERIES A.

The date of treatment is indicated by the letter T↑.
A significant ($p = < 0.05$) difference of density in treated and control plots is marked thus: ↓

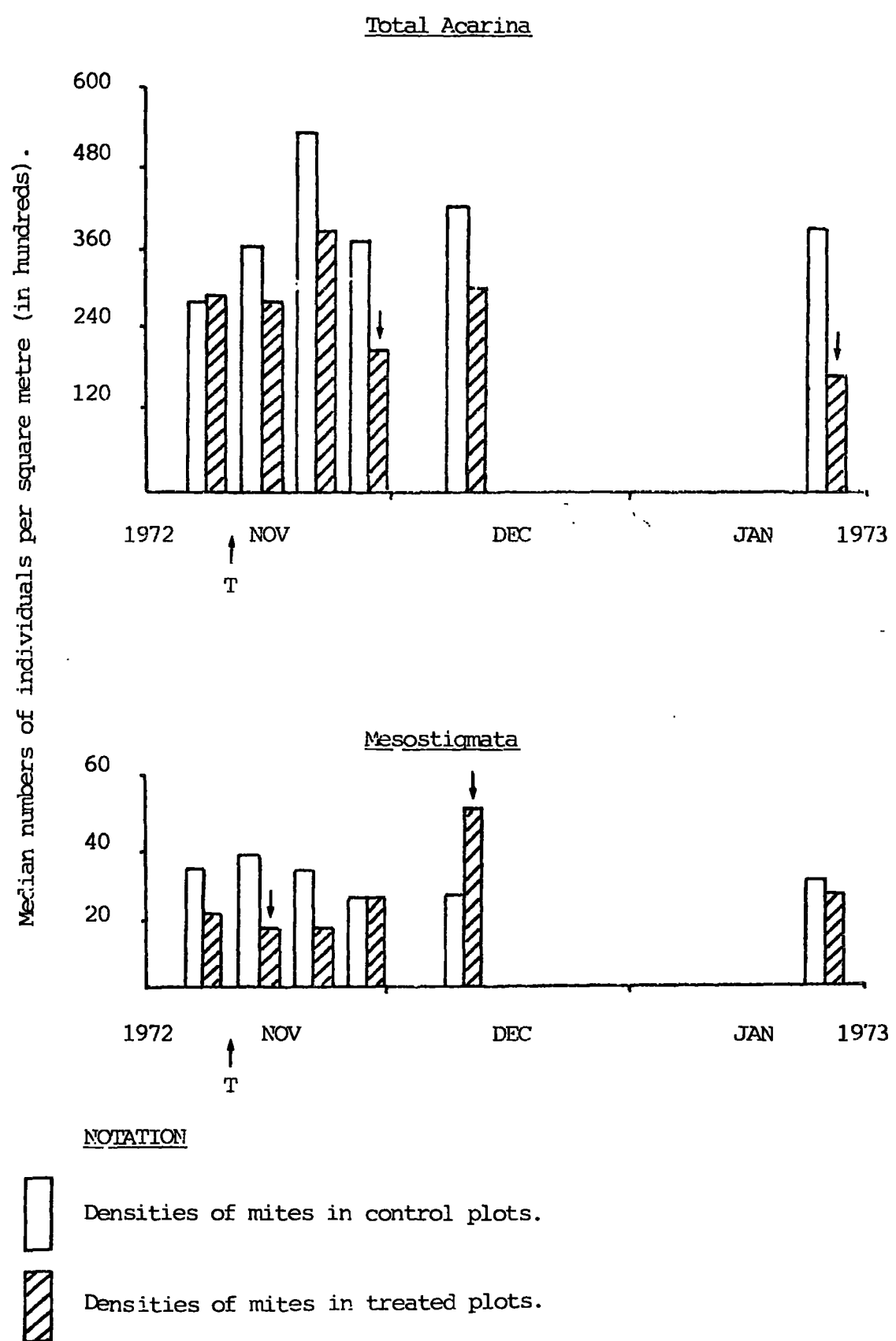
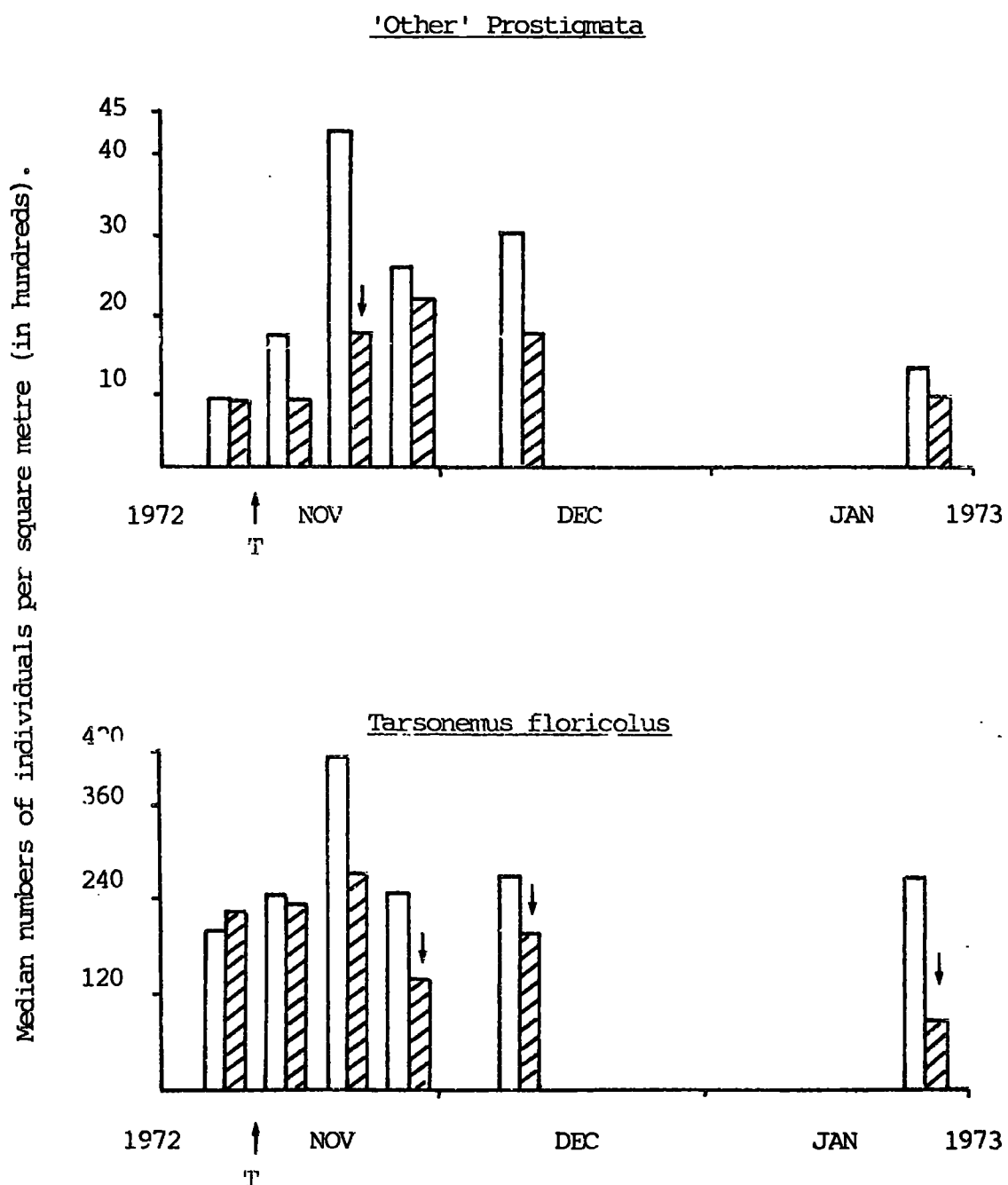


**FIGURE 5 : CHANGES IN DENSITY OF 'OTHER' PROSTIGMATA AND
TARSONEMUS FLORICOLUS DURING TREATMENT SERIES A.**

The date of treatment is indicated by the letter T↑.
A significant ($p = < 0.05$) difference of density in
treated and control plots is marked thus: ↓



NOTATION



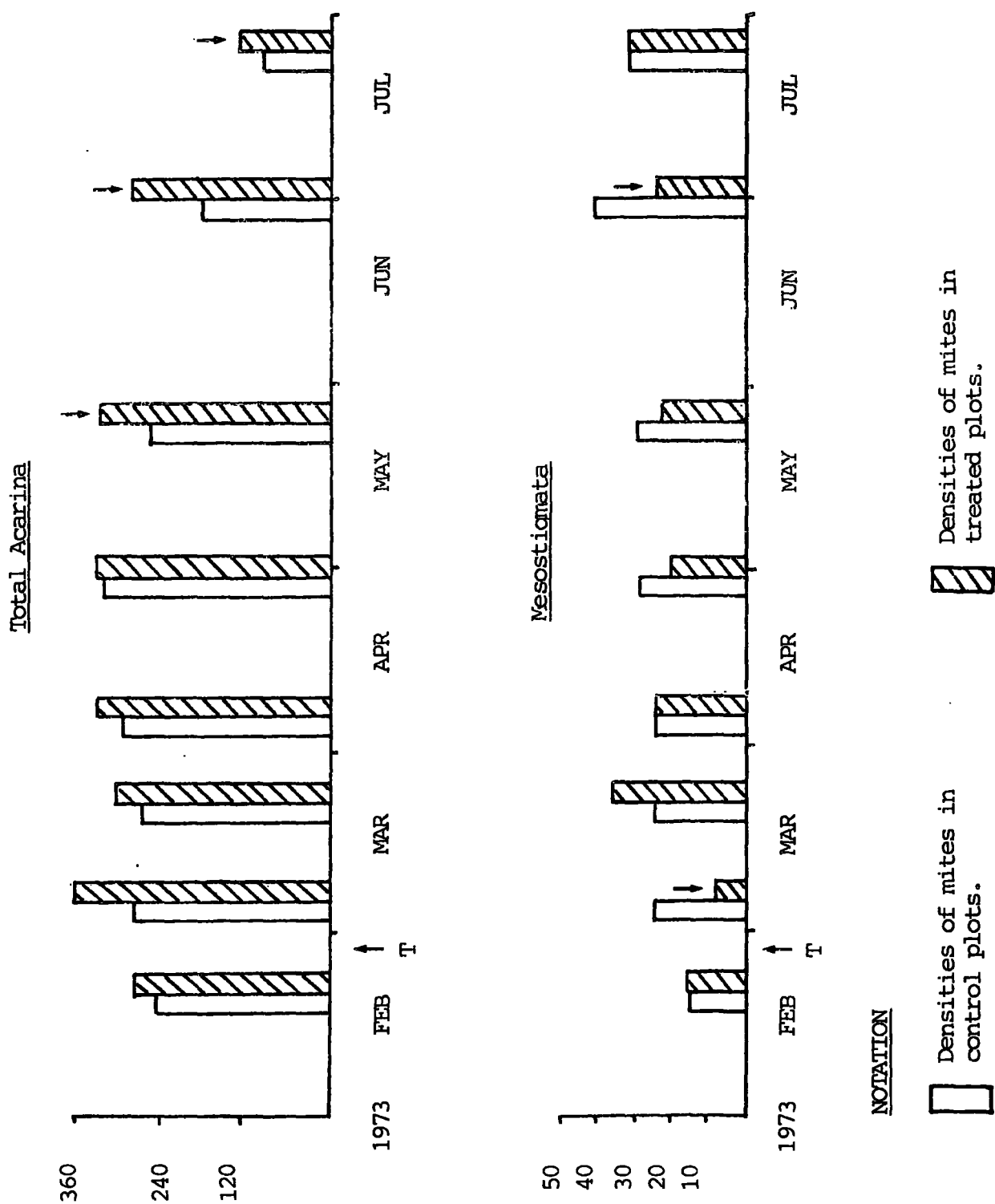
Densities of mites in control plots.



Densities of mites in treated plots.

FIGURE 6 : CHANGES IN DENSITY OF ALL SOIL ACARINA AND MESOSTIGMATA DURING TREATMENT SERIES B.

The date of treatment is indicated by the letter T↑.
A significant ($p = < 0.05$) difference of density in treated and control plots is marked thus: ↓



Median numbers of individuals per square metre (in hundreds).

FIGURE 7 : CHANGES IN DENSITY OF 'OTHER' PROSTIGMATA AND
TARSONEMUS FLORICOLUS DURING TREATMENT SERIES B.

The date of treatment is indicated by the letter T ↑
A significant ($p = \leq 0.05$) difference of density in
treated and control plots is marked thus: ↓

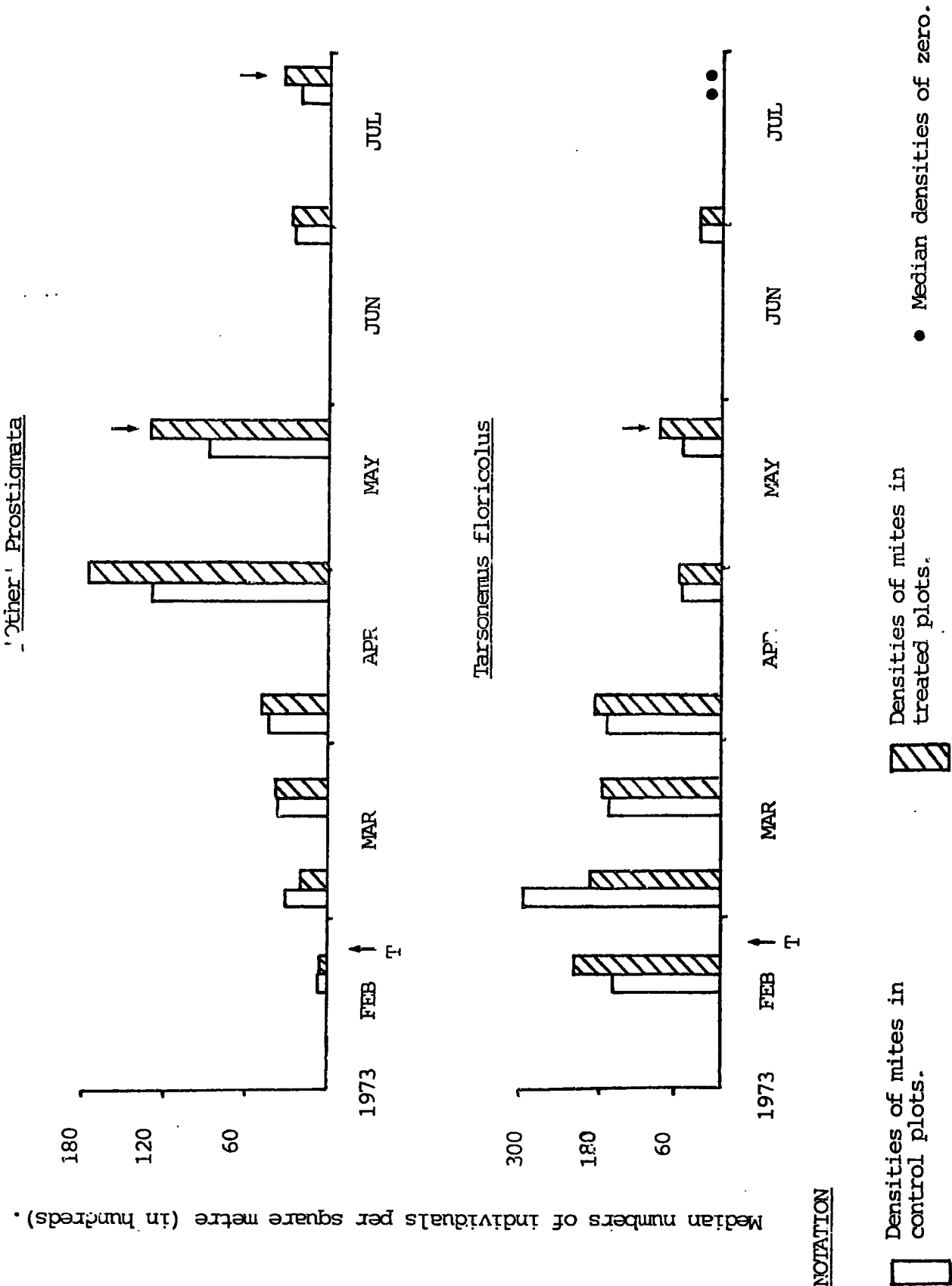


FIGURE 8 : CHANGES IN DENSITY OF ALL SOIL ACARINA AND MESOSTIGMATA DURING TREATMENT SERIES C.

The date of treatments is indicated by the letter T ↑.
A significant ($p = < 0.05$) difference of density in treated and control plots is marked thus: ↓

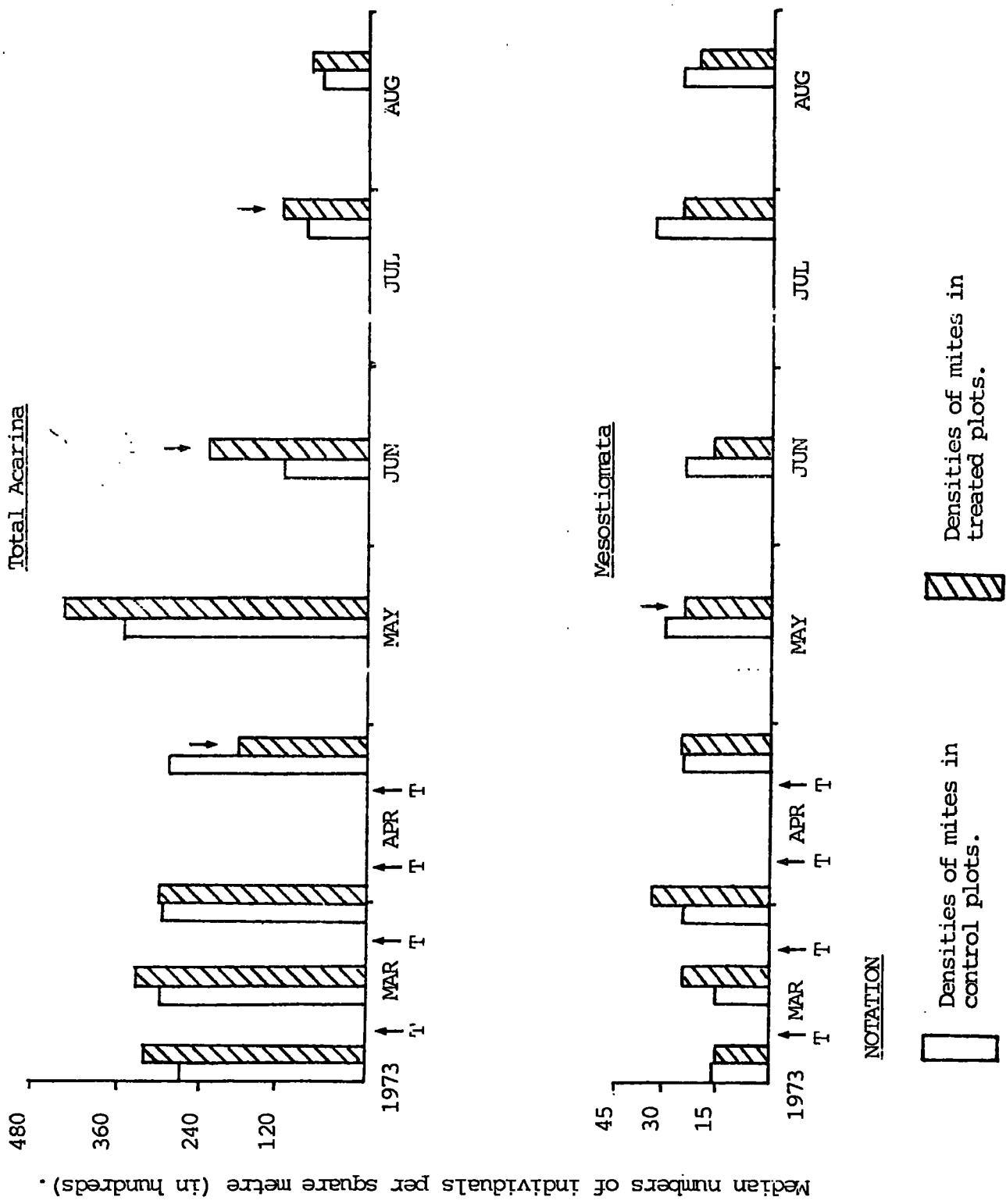


FIGURE 9 : CHANGES IN DENSITY OF 'OTHER' PROSTIGMATA AND
TARSONEMUS FLORICOLUS DURING TREATMENT SERIES C.

The date of treatments is indicated by the letter T↑.
A significant ($p = < 0.05$) difference of density in
treated and control plots is marked thus: ↓

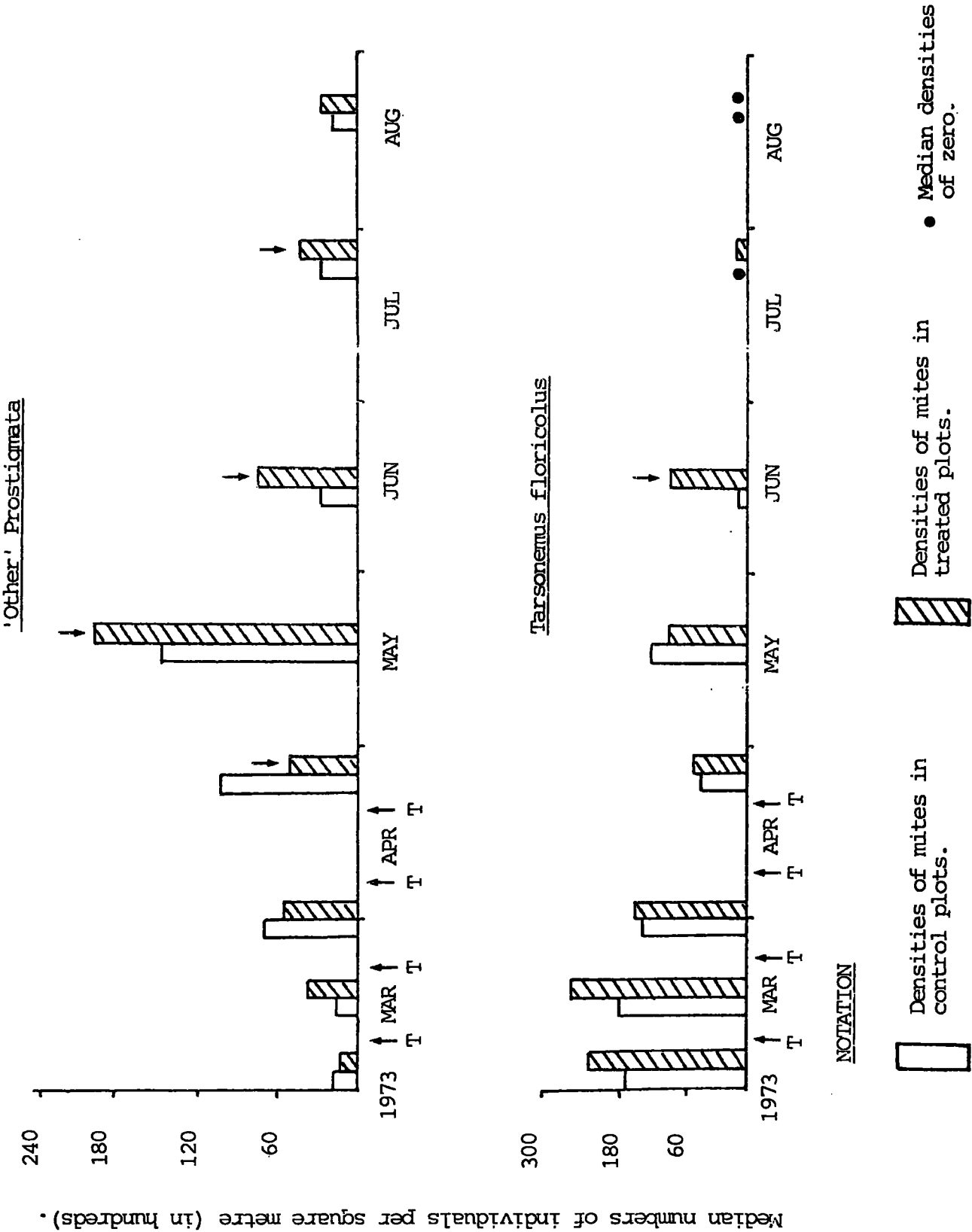


FIGURE 10 : CHANGES IN DENSITY OF ALL SOIL ACARINA AND

MESOSTIGMATA DURING TREATMENT SERIES D.

The date of treatments is indicated thus: D/1↑ , D/2↑ , D/3↑ .
A significant ($p = \leq 0.05$) difference of density in treated and control plots is marked thus: ↓

NOTATION

The density of mites in each trial is distinguished as follows:

- Median densities of zero.

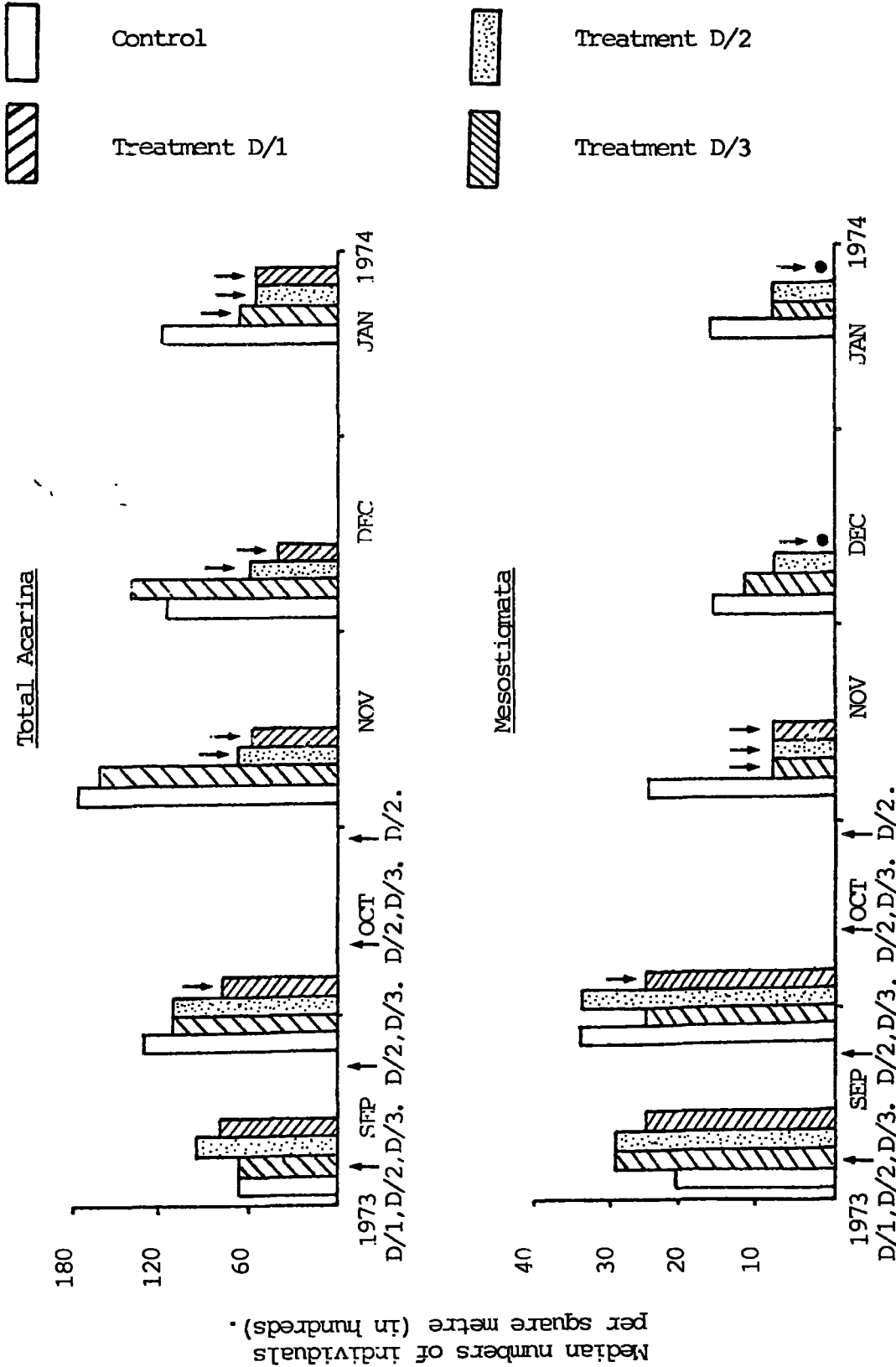


FIGURE 11 : CHANGES IN DENSITY OF 'OTHER' PROSTIGMATA AND
TARSONEMUS FLORICOLUS DURING TREATMENT SERIES D.

The date of treatments is indicated thus: D/1 ↑ , D/2 ↑ , D/3 ↑ .
A significant ($p = \leq 0.05$) difference of density in
treated and control plots is marked thus: ↓

NOTATION

The density of mites in each trial is distinguished as follows:

- Median densities of zero.

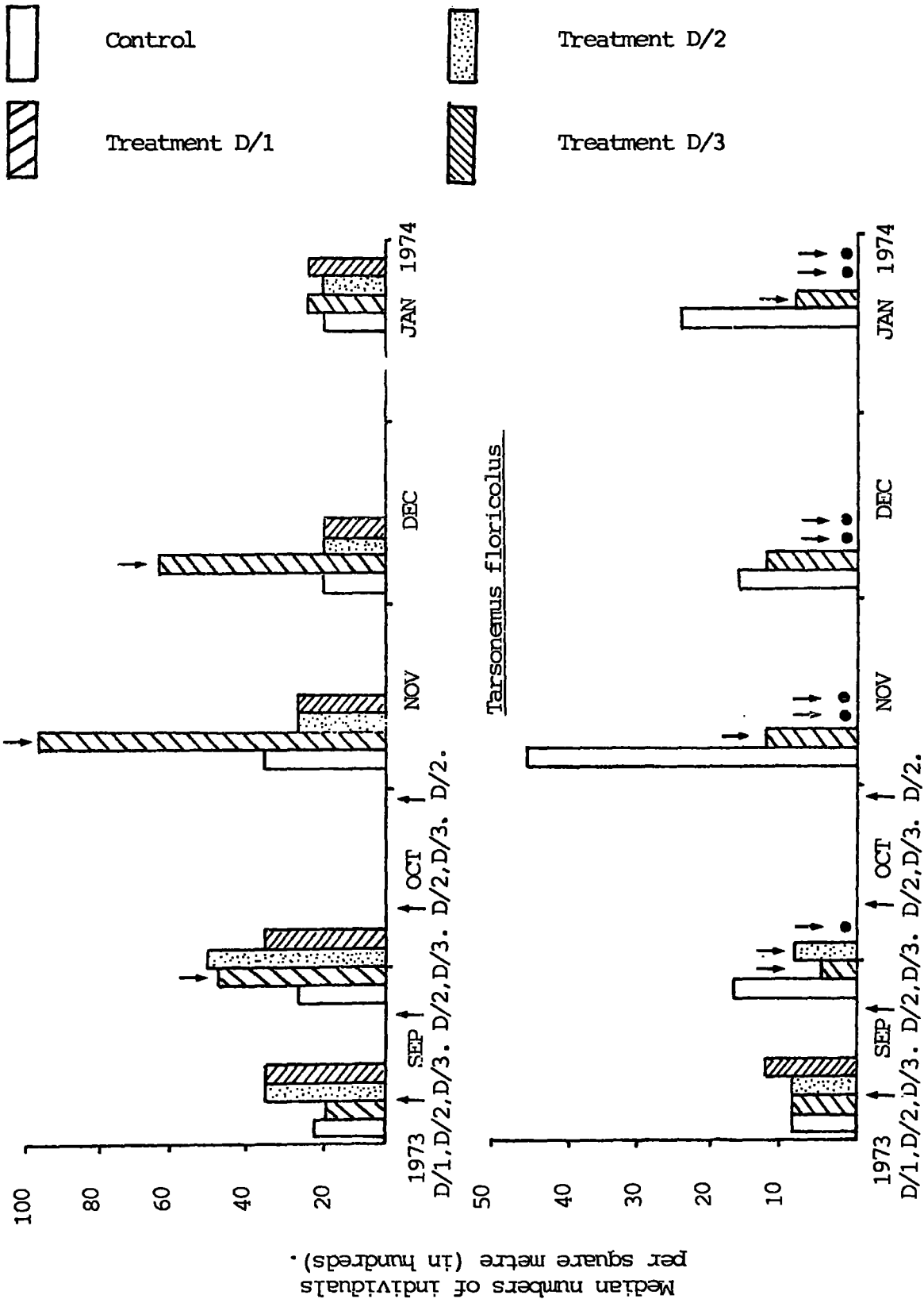


FIGURE 12 : CHANGES IN DENSITY OF ALL SOIL ACARINA AND MESOSTIGMATA DURING TREATMENT SERIES E.

MESOSTIGMATA DURING TREATMENT SERIES E.

The date of treatments is indicated thus: E/1↑, E/2↑, E/3↑. A significant ($p = <0.05$) difference of density in treated and control plots is marked thus: ↓

NOTATION

The density of mites in each trial is distinguished as follows:

- Median densities of zero.

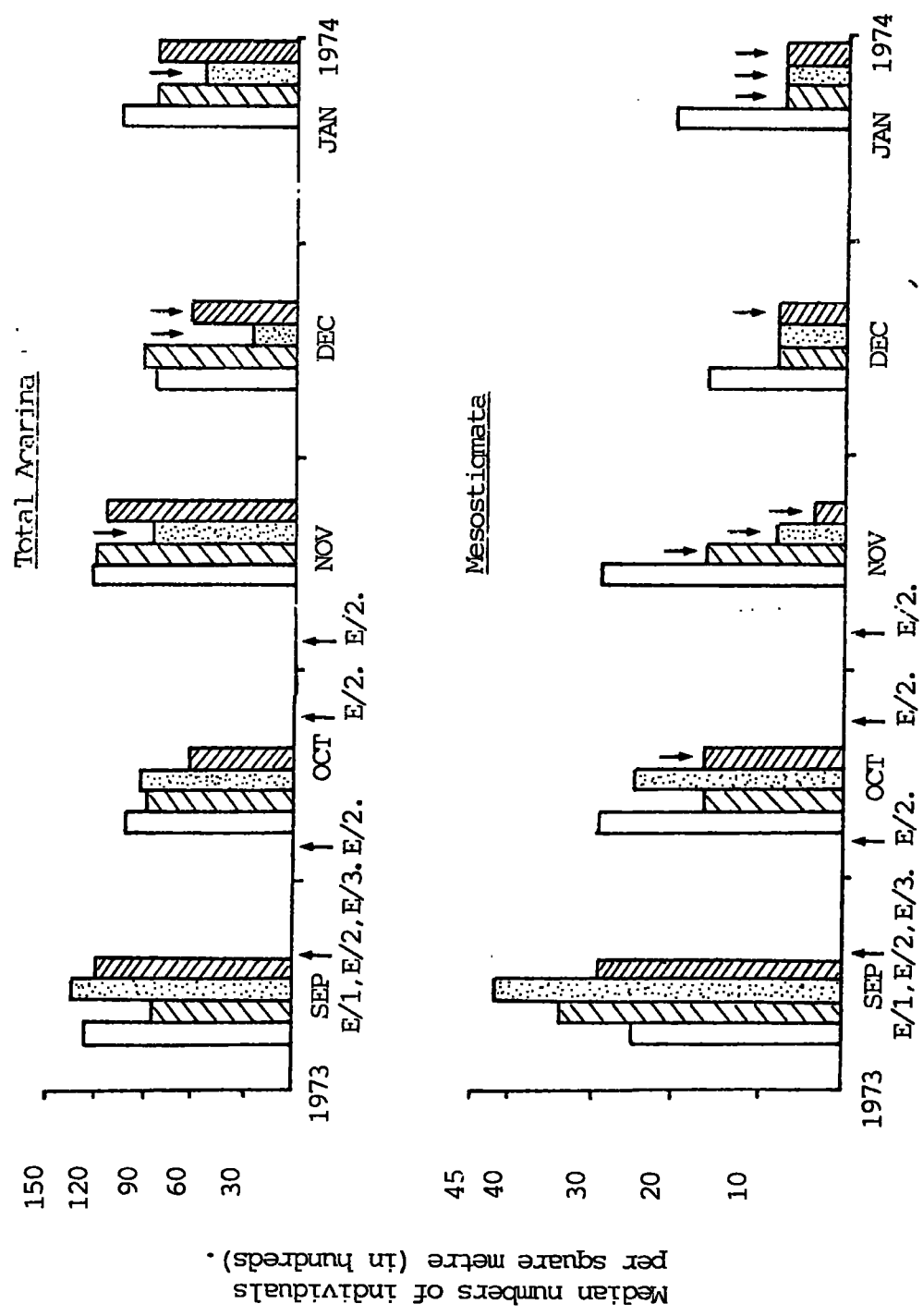
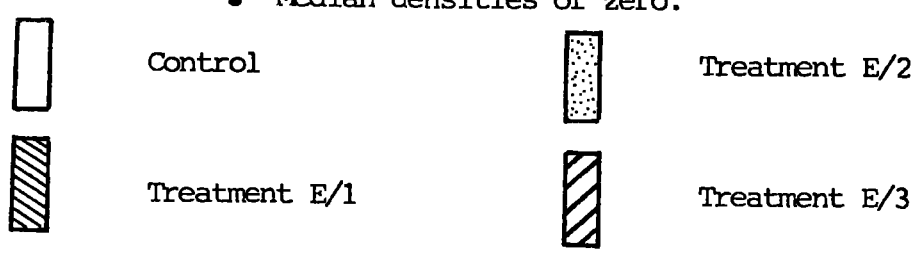


FIGURE 13 : CHANGES IN DENSITY OF 'OTHER' PROSTIGMATA AND

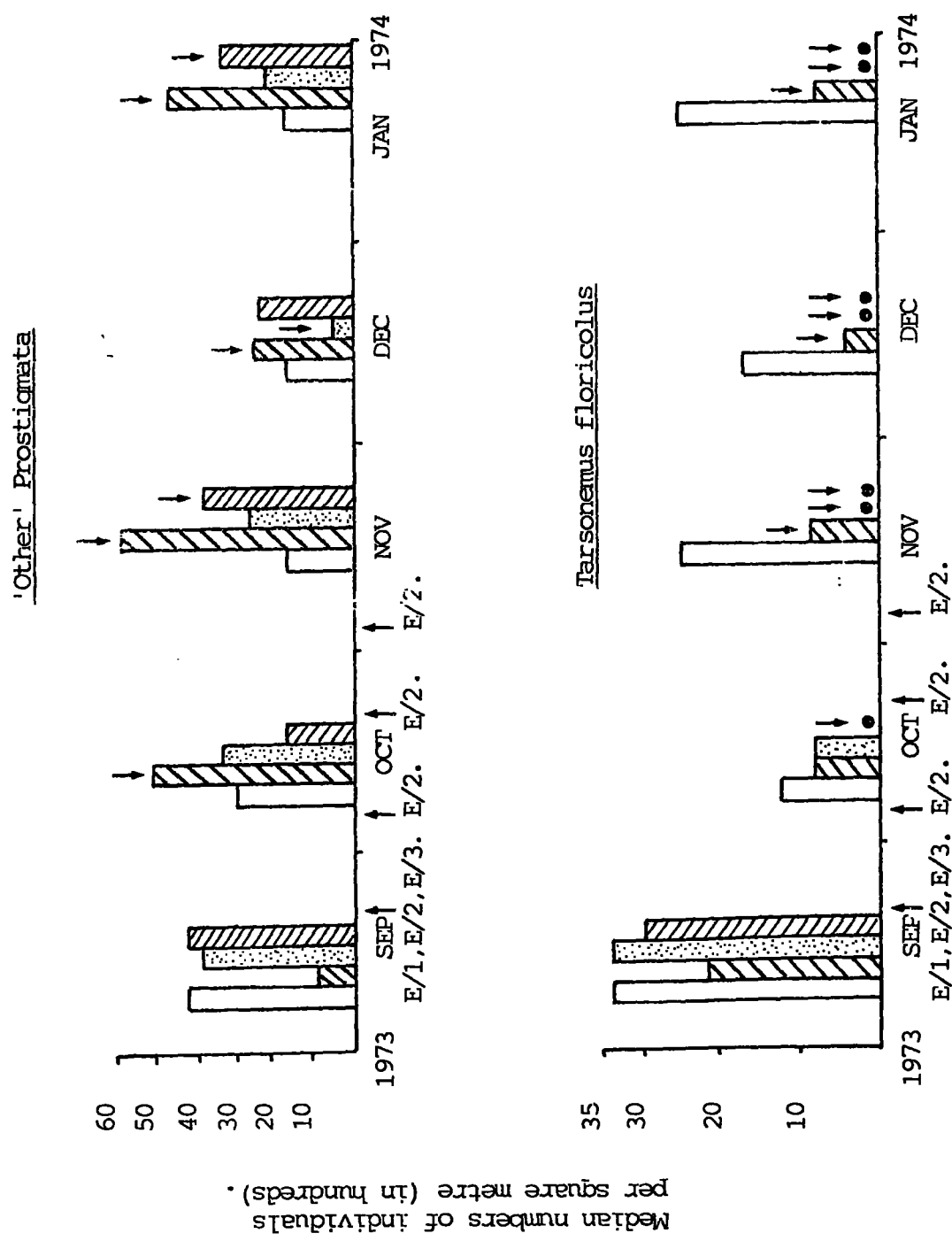
TARSONEMUS FLORICOLUS DURING TREATMENT SERIES E.

The date of treatments is indicated thus: E/1 ↑, E/2 ↑, E/3 ↑. A significant ($p = < 0.05$) difference of density in treated and control plots is marked thus: ↓

NOTATION

The density of mites in each trial is distinguished as follows:

- Median densities of zero.



TABLES 2 - 10:

THE SIGNIFICANCE LEVELS OF POPULATION CHANGES IN GROUPS OR SPECIES OF SOIL
ACARINA AFTER TREATMENT OF PLOTS WITH ORGANOTIN FUNGICIDE.

Each value in the following tables represents the level of significance of differences between control and experimental populations on the same sampling date. The direction of change with respect to the population of control plots is indicated by an arrow - thus 0.001 ↓ indicates a fall in numbers of Acari within treated plots which is significant at the 0.001 level. The lowest level of significance recorded is 0.05; a non-significant record is abbreviated thus - "Ns".

Trial series A, B, C, E/2 and E/3 comprise treatments of triphenyltin hydroxide, while trials D/1, D/2, D/3 and E/1 comprise triphenyltin acetate treatments.

TABLE 2: Series A comprising four times the recommended agricultural
dose of TPTH (single application).

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
8.11.72	12.11.72	Ns	Ns	0.05 ↓	Ns
	17.11.72	Ns	0.05 ↓	Ns	Ns
	23.11.72	0.025 ↓	Ns	Ns	0.025 ↓
	08.12.72	Ns	Ns	0.025 ↑	0.025 ↓
	27.01.73	0.001 ↓	Ns	Ns	0.025 ↓

TABLE 3: Series B comprising twice the recommended agricultural dose of TPTH (single application).

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
23.02.73					
	06.03.73	Ns	Ns	0.05 ↓	Ns
	21.03.73	Ns	Ns	Ns	Ns
	04.04.73	Ns	Ns	Ns	Ns
	28.04.73	Ns	Ns	Ns	Ns
	22.05.73	0.005 ↑	0.001 ↑	Ns	0.005 ↑
	29.06.73	0.005 ↑	Ns	0.05 ↓	Ns
	26.07.73	0.01 ↑	0.001 ↑	Ns	Ns

TABLE 4: Series C comprising the recommended agricultural dose of TPTH repeated four times at approximately 2 week intervals.

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
06.03.73					
17.03.73	17.03.73	Ns	Ns	Ns	Ns
03.04.73	31.03.73	Ns	Ns	Ns	Ns
16.04.73	25.04.73	0.05 ↓	0.001 ↓	Ns	Ns
	17.05.73	Ns	0.025 ↑	0.05 ↓	Ns
	25.06.73	0.001 ↑	0.005 ↑	Ns	0.001 ↑
	23.07.73	0.01 ↑	0.025 ↑	Ns	Ns
	21.08.73	Ns	Ns	Ns	Ns

TABLE 5: Series E/2 comprising the recommended agricultural dose of TPTH repeated four times at approximately two week intervals.

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
14.09.73					
05.10.73					
20.10.73	9/15.10.73	Ns	Ns	Ns	Ns
06.11.73	16/19.11.73	0.025 ↓	Ns	0.001 ↓	0.001 ↓
	11/14.12.73	0.001 ↓	0.001 ↓	Ns	0.001 ↓
	21/24.01.74	0.005 ↓	Ns	0.001 ↓	0.001 ↓

TABLE 6: Series E/3 comprising twice the recommended agricultural dose of TPTH (single application).

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
12.09.73					
	9/15.10.73	Ns	0.025 ↑	Ns	Ns
	16/19.11.73	Ns	0.005 ↑	0.001 ↓	0.05 ↓
	11/14.12.73	Ns	0.025 ↑	Ns	0.01 ↓
	21/24.01.74	Ns	0.01 ↑	0.001 ↓	0.05 ↓

TABLE 7: Series D/1 comprising twice the recommended agricultural dose of TPTA (single application).

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
03.09.73					
	27.9/3.10.73	Ns	0.01 ↑	Ns	0.05 ↓
	6/12.11.73	Ns	0.001 ↑	0.05 ↓	0.001 ↓
	5/08.12.73	Ns	0.001 ↑	Ns	Ns
	13/17.01.74	0.05 ↓	Ns	Ns	0.001 ↓

TABLE 8: Series D/2 comprising the recommended agricultural dose of
TPTA repeated four times at 2 - 3 week intervals.

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
04.09.73					
18.09.73					
08.10.73	27.9/03/10.73	Ns	Ns	Ns	0.001 ↓
29.10.73	6/12.11.73	0.001 ↓	Ns	0.005 ↓	0.001 ↓
	5/08.12/73	0.005 ↓	Ns	Ns	0.001 ↓
	13/17.01.74	0.005 ↓	Ns	Ns	0.001 ↓

TABLE 9: Series D/3 comprising twice the recommended agricultural dose
of TPTA repeated three times at 2 - 3 week intervals.

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
04.09.73					
18.09.73					
08.10.73	27.9/03.10.73	0.01 ↓	Ns	0.025 ↓	0.001 ↓
	6/12.11.73	0.001 ↓	Ns	0.001 ↓	0.001 ↓
	5/08.12.73	0.001 ↓	Ns	0.001 ↓	0.001 ↓
	13/17.01.74	0.001 ↓	Ns	0.025 ↓	0.001 ↓

TABLE 10: Series E/1 comprising four times the recommended agricultural
dose of TPTA (single application).

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
12.09.73					
	9/15.10.73	Ns	Ns	0.05 ↓	0.005 ↓
	16/19.11.73	Ns	0.05 ↑	0.001 ↓	0.001 ↓
	11/14.12.73	0.05 ↓	Ns	0.005 ↓	0.001 ↓
	21/24.01.74	Ns	0.025 ↑	0.005 ↓	0.005 ↓

TABLES 11 - 19:THE PERCENTAGE CHANGE IN MEDIAN DENSITIES OF SOIL ACARINA FOLLOWING ORGANOTIN TREATMENT.

Each value in the following tables represents the percentage by which densities of mites in treated plots differ from that of the equivalent control plots (100%). The direction of this difference is indicated by an arrow; for example, 50 ↓ shows that the median density of the treated plots was 50% lower than that of respective control plots.

Trial series A, B, C, E/2 and E/3 comprise treatments of triphenyltin hydroxide, while trials D/1, D/2, D/3 and E/1 comprise triphenyltin acetate treatments.

TABLE 11: Series A comprising four times the recommended agricultural dose of TPTH (single application).

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
08.11.72	12.11.72	20.7 ↓	50 ↓	55.5 ↓	2 ↓
	17.11.72	29.5 ↓	60 ↓	50 ↓	35 ↓
	23.11.72	42 ↓	16.6 ↓	0	43 ↓
	08.12.72	29 ↓	43 ↓	100 ↑	26.5 ↓
	27.01.73	57 ↓	33.3 ↓	14 ↓	68 ↓

TABLE 12: Series B comprising twice the recommended agricultural dose of TPTH (single application).

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
24.02.73	06.03.73	30 ↓	100 ↑	67 ↓	35 ↓
	21.03.73	12 ↑	12.5 ↑	50 ↑	8 ↑
	04.04.73	10 ↑	10 ↑	0	18 ↑
	28.04.73	4 ↑	36 ↑	29 ↓	0
	22.05.73	33 ↑	41 ↑	14 ↓	64 ↑
	29.06.73	53 ↑	0	67 ↓	0
	26.07.73	36 ↑	60 ↑	12 ↑	0

TABLE 13: Series C comprising the agricultural recommended dose of TPTH administered on four separate occasions at approximately two week intervals.

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
06.03.73					
17.03.73	17.03.73	10 ↑	125 ↑	50 ↑	33 ↑
03.04.73	31.03.73	1 ↑	19 ↓	30 ↑	8 ↑
16.04.73	25.04.73	35 ↓	52 ↓	0	13 ↑
	17.05.73	23 ↑	35 ↑	14 ↓	18 ↓
	25.06.73	100 ↑	200 ↑	33 ↓	1300 ↑
	23.07.73	43 ↑	60 ↑	25 ↓	100 ↑
	21.08.73	25 ↑	50 ↑	17 ↓	0

TABLE 14: Series E/2 comprising the recommended agricultural dose of TPIH administered on four separate occasions at approximately two week intervals.

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
14.09.73					
05.10.73					
20.10.73	9/15.10.73	8 ↓	14 ↑	17 ↓	33 ↓
06.11.73	16/19.11.73	31 ↓	50 ↑	71 ↓	100 ↓
	11/14.12.73	68 ↓	75 ↓	50 ↓	100 ↓
	21/24.01.74	46 ↓	25 ↑	60 ↓	100 ↓

TABLE 15: Series E/3 comprising twice the recommended agricultural dose of TPIH (single application).

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
19.09.73					
	9/15.10.73	13 ↓	71 ↑	43 ↓	33 ↓
	16/19.11.73	4 ↓	250 ↑	43 ↓	67 ↓
	11/14.12.73	11 ↑	50 ↑	50 ↓	75 ↓
	21/24.01.74	17 ↓	175 ↓	60 ↓	67 ↓

TABLE 16: Series D/1 comprising twice the recommended agricultural dose of TPIA (single application).

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
03.09.73					
	27.9/03.10.73	16 ↓	83 ↑	25 ↓	75 ↓
	6/12.11.73	7 ↓	188 ↑	67 ↓	73 ↓
	5/08.12.73	22 ↑	275 ↑	25 ↓	25 ↓
	13/17.01.74	45 ↓	25 ↑	50 ↓	67 ↓

TABLE 17: Series D/2 comprising the recommended agricultural dose of TPTA repeated four times at 2 - 3 week intervals.

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
04.09.73					
18.09.73					
08.10.73	27.9/3.10.73	16 ↓	100 ↑	0	50 ↓
29.10.73	6/12.11.73	61 ↓	25 ↓	67 ↓	100 ↓
	5/08.12.73	48 ↓	0	50 ↓	100 ↓
	13/17.01.74	52 ↓	0	50 ↓	100 ↓

TABLE 18: Series D/3 comprising twice the recommended agricultural dose of TPTA repeated three times at 2 - 3 week intervals.

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
04.09.73					
18.09.73					
08.10.73	27.9/3.10.73	42 ↓	33 ↑	25 ↓	100 ↓
	6/12.11.73	66 ↓	25 ↓	67 ↓	100 ↓
	5/08.12.73	63 ↓	0	100 ↓	100 ↓
	13/17.01.74	52 ↓	25 ↑	100 ↓	100 ↓

TABLE 19: Series E/1 comprising four times the recommended agricultural dose of TPTA (single application).

Treatment Date	Sample Date	Total Acarina	'Other' Prostigmata	Mesostigmata	T. floricolus
12.09.73					
	9/15.10.73	38 ↓	43 ↓	43 ↓	100 ↓
	16/19.11.73	7 ↓	125 ↑	86 ↓	100 ↓
	11/14.12.73	21 ↓	50 ↑	50 ↓	100 ↓
	21/24.01.74	17 ↓	100 ↑	60 ↓	100 ↓

INTERPRETATION OF RESULTS.

In the following sub-sections the reaction of soil Acarina to each of the two fungicides was considered separately and then similarities in observed changes are discussed.

Treatments are considered to have had an effect on the numbers of soil Acarina only where results followed a developing pattern or trend. Where an apparently significant difference occurred in the absence of such a pattern, it was usually only at the 1 in 20 level and probably arose as an artefact of the small sample sizes.

The effect of triphenyltin hydroxide (TPTH) treatments.

(Trials A, B, C, E/2 and E/3).

(i) Effects on *T. floricolus*.

In each of the autumn/winter trial series A, E/2 and E/3 there was a significant and progressive fall in the numbers of *T. floricolus* in treated plots. While the percentage reduction in the numbers of this species appears similar after a single application of both the lowest (trial E/3) and highest (trial A) dose levels, in trial E/2 - in which the total quantity of fungicide administered was the same as for trial A - a considerably greater reduction was recorded. Although treatment on four separate occasions in trial E/2 (rather than as a single application in trial A) might be responsible for the greater effect in this trial, it is also possible, perhaps more likely, that the magnitude of changes in the two years cannot be compared directly. This might be the case if the populations being studied in the two years were in a different state, perhaps containing more or less individuals vulnerable to treatment, thus for example giving age differences in mortality as found for mollusca by Frick and Jimenez (1964). Furthermore, the differing weather conditions during these

trial periods may have affected the efficiency of triphenyltin, its uptake by fungi and therefore availability, through feeding, to the mites. Clearly there will be many more variables of this nature which are beyond the scope of this study. Comparison of trials E/2 and E/3, which were conducted concurrently and therefore not subject to these variables to the same degree, certainly indicates a relationship between the level of dose and response of T. floricolus.

In series B and C which were carried out during spring and early summer, no dose response effect was evident.

(ii) Effects on 'Other' Prostigmata.

In series E/3, the lowest level of DITH treatment, a significantly higher number of Prostigmatids was recorded from treated plots on all sampling occasions. This did not occur consistently, however, in the earlier trial at this dose level, trial B, although a similar reaction of this group was suggested under the higher dose levels in trial C. In contrast, there is no indication on any occasion of sampling that a similar increase in 'Other' Prostigmatids occurred under the highest dose levels in trials E/2 and A. In the latter, in fact, percentage changes suggest a decline in this group.

Once again there is difficulty in relating the responses of mites to similar dose levels between the two years in which trials were conducted. Some variables which might contribute to this have been mentioned in consideration of the changes in the numbers of Tarsonemids, but there is the further possibility here that the species composition varied between years.

(iii) Effects on Mesostigmata.

Following treatment in trials E/2 and E/3, consistently lower median densities of Mesostigmata were recorded. Although this reduction in numbers was significant only in the second and fourth months post treatment, a real

effect of treatment is suggested on the basis of percentage change in median densities. A similar response is not evident in series A, but in series B and C median densities of Mesostigmata in treated plots were lower than densities in control plots over periods of 3 and 4 months respectively. These differences were, however, rarely significant.

(iv) Effects on Total Acarina.

The contrasting changes in densities outlined above are reflected in different responses of total Acarina. In the two autumn trials, A and E/2, which involved a treatment equal to the total recommended agricultural dose, although differing in the regime of treatment, a fall in the total number of Acarina in treated plots was recorded. In contrast, the same level of treatment in series C, which was conducted in spring, was followed by an increase in total Acarina.

Similarly, differences in response according to season were shown at lower levels of fungicide application. An increase in total Acarina followed treatment in spring (trial B) whereas treatment in autumn (trial E/3) produced no change in the total numbers of mites.

The effect of triphenyltin acetate treatment. (Series D/1, D/2, D/3 and E/1).

Since all TPTA treatments were carried out at the same time of year, under similar edaphic conditions, the results are more directly comparable than for the TPTH trials and can be interpreted more briefly.

(i) Effects on T. floricolus.

In each trial series the densities of T. floricolus were reduced in treated plots. These reductions continued after the treatment until numbers reached very low levels. Under the highest dose rates, only occasional individuals

survived four months after treatment. At the lowest dose levels (D/1) the reduction in numbers was less severe and on one sampling occasion was not significant.

(ii) Effects on 'Other' Prostigmata.

The numbers of 'Other' Prostigmata increased markedly following the lowest level of TPTA treatment (D/1). A suggestion of such an increase was also obtained after the highest single dosage application (E/1), but not after the same absolute dose level given as four separate treatments (D/2) and not at the highest level of treatment (D/3).

(iii) Effects on Mesostigmata.

In trials D/3 and E/1 there was a significant reduction in the numbers of Mesostigmata following treatment, but in trials D/2 and D/1, although there were percentage reductions in numbers which were consistent, the differences were significant on only one occasion in each trial.

(iv) Effects on Total Acarina.

As noted in relation to the effect of TPTA treatment, the total numbers of mites recovered in samples from TPTA treated plots depends on the relative abundance of different groups and the manner and degree to which they are affected. In general, small doses of TPTA which produce a modest yet significant decline in numbers of T. floricolus and the Mesostigmata, rarely produce a significant decline in total Acarina since there is a compensating increase in the group 'Other' Prostigmata. At higher levels of TPTA treatment where the numbers of 'Other' Prostigmata do not change significantly, the fall in T. floricolus and the Mesostigmata is reflected directly in a significant decline in the total numbers of mites.

THE EFFECTS OF ORGANO TIN AGRICULTURAL
CHEMICALS ON SOIL ACARINA - DISCUSSION
AND CONCLUSIONS.

THE EFFECTS OF TPTA AND TPTH WHEN SPRAYED AT RECOMMENDED CONCENTRATIONS AND
REGIMES OF TREATMENT.

Results from my field trials at Durham demonstrate that both TPTA and TPTH may reduce the total numbers of Acarina occurring in autumn in agricultural soils if applied at levels of dosage recommended by manufacturers and the Ministry of Agriculture. In this sub-section, the action of TPTA and TPTH as autumn treatments only is discussed (namely, treatments E/2 and D/2 respectively), since these provide comparable data from which to generalise. An equivalent treatment with TPTH in spring (trial C) is considered in a subsequent sub-section of this discussion. However, it is important to recognize that summer treatment is more likely in agricultural practice and, therefore, none of my trials precisely correspond with this use.

Partial separation of the Prostigmata revealed that although certain species (namely, Scutacarus (v) montanus and the two unidentified species belonging to the genus Pygmephorus) appeared to be unaffected by administration of TPTA and TPTH in autumn, the small fungiferous mite Tarsonemus floricolus disappeared completely from some samples within two months of treatment beginning. To both

chemicals, therefore, the reaction of this species was very rapid. Other Prostigmata, chiefly comprising Eupodidae and Tydeidae, which amounted to some 20% of all Prostigmata by numbers during autumn trials D and E, were as a group unaffected. Conceivably, however, this group might have included some species adversely affected by treatment while others might have increased, thus compensating and maintaining overall densities no different from those in the control plots.

Reductions in excess of 60% in the numbers of Mesostigmata were recorded from plots treated with both chemicals in autumn. Since the Mesostigmata were considered as a group without separation to species level, it is not known whether TPTA and TPTH affected only one or two species or all species.

The Cryptostigmata and Astigmata occurred at densities too low to allow adequate detection of any effect of treatment.

In general, the changes in densities of soil mites following the recommended treatments with both TPTA and TPTH appear broadly similar and this is perhaps not surprising, since it is likely that TPTA when in the soil might be converted quite quickly to its hydrolysis product, namely TPTH. It might be that my trials with the two chemicals were in practice identical but I am not aware of the rate of hydrolysis and, therefore, how likely this is.

Since TPTA and TPTH may not affect all species of mites in the same way, nor to the same degree, their influence on the total numbers of soil Acari will depend directly on the relative abundance of susceptible species. At other sites treatment with these chemicals might produce a greater or lesser change in numbers than occurred at Durham. Furthermore, environmental factors which may modify the effect of organotin, e.g. the adsorption to different types of soil particles, climate, etc., will also differ from site to site.

THE INFLUENCE OF LEVEL OF DOSE ON THE EFFECT OF TRIPHENYLTLINS.

The autumn series of treatments with TPIH (E/2 and E/3) and TPTA (D/1, D/2 and D/3) enable comparisons to be made between the effect of the full recommended agricultural dose and a dose of half this quantity, and also in the case of TPTA of $1\frac{1}{2}$ times the recommended dose. Although the spring trials B and C are identical to E/3 and E/2 respectively and might be expected to contribute to this comparison, the degree of seasonal difference in the responses of those groups and species which were separated does not permit this and they are considered in the next sub-section.

For both TPIH and TPTA a dose-related response is evident in the post treatment fall in numbers of T. floricolus and also in the post treatment increase in numbers of 'Other' Prostigmata. In the case of T. floricolus, treatment with the full recommended agricultural doses of both chemicals brought about almost complete extinction, with only occasional individuals occurring in samples after the completion of treatment. In contrast, after treatment with only half the recommended dose, the density of this species in both TPTA and TPIH treated plots remained above 500/m². Since the full recommended dose of both TPTA and TPIH in trials D/2 and E/2 did not affect the numbers of 'Other' Prostigmata significantly, it seems reasonable, in the first instance, to assume that treatments had no effect on numbers of constituent species. However, since treatment with half the recommended dose of both TPT's produced significant increases in the numbers of the 'other' group, the constituent species may be responding differently when subject to different concentrations of organotins in the soil. It seems possible that there may be a balance between (a) the benefits of treatment to some species, which tend to inflate the numbers of the group, and (b) the toxicity of TPT's to the same or different species within the group. The increase in numbers of soil fauna under low doses of a more usually toxic chemical is not infrequent and possible reasons why this might arise are

discussed later (p. 63).

The Mesostigmata appeared to be affected to an equal degree by both half and full doses of both TPTA and TPTH, the percentage reduction in treated populations in each case being around 65--70% of control populations. However, 'mortality' may be related to the quantity of chemical administered, for TPTA at least, since in trial D/3 $1\frac{1}{2}$ times the recommended dose depressed the population far more than the full dose. Only occasional individuals were present in samples three months after treatment in this trial.

From studies with other agricultural chemicals (Edwards, 1969) it seems likely that the effect of TPT's will not be proportional to the dose but more nearly logarithmic.

THE EFFECT OF SEASON UPON THE ACARICIDAL ACTIVITY OF TPTH.

Only for TPTH have I comparable records for treatments in spring as well as in autumn (autumn series E/3 and E/2 are identical to B and C in spring). Over the four month post-treatment period for which each trial was studied, the overall impression was that in spring population changes in experimental plots were erratic and differences with respect to control populations less marked, compared with their autumn counterparts. This may be illustrated, for example, with respect to the Mesostigmata. In both the autumn series E/2 and E/3, significantly lower numbers of this order were collected from treated plots in the second, third and fourth months after treatment, whereas in the spring trials B and C a similarity in terms of consistently lower densities in treated plots was significant on only two occasions in trial B and on one occasion in trial C.

A particularly conspicuous contrast in the results of these replicate trials was provided by the response of T. floricolus which, although having shown a marked fall in numbers after treatment in the preceding autumn (series A), failed to show a decline in spring - in fact, there was a suggestion of a rise in the

population in treated plots, although this was not significant. However, in the following autumn, in series E/2 and E/3 the numbers of this species dropped drastically after treatment, confirming the preliminary findings.

Conversely, spring series C showed changes not evident in its autumn replicate E/2, namely a significant increase in the numbers of 'other' Prostigmata in several months, rather than the absence of effects noted in series E/2. The reaction in trial C was similar, therefore, to that in trial E/3 when half the recommended agricultural dose was administered. This raises the possibility that the effective toxicity of TPTH was for some reason less in spring than in autumn. This is supported by the fact that (1) there is a dose-related response affecting Prostigmata including T. floricolus and (2) that the responses of all groups was rather less definite, as already noted, trends being suggested by percentage changes rather than by a series of significantly different levels of population. In contrast to the difference between trials E/2 and C, with respect to the 'Other' Prostigmata, the response of this group in E/3 and B is closely similar, and this detracts from the notion that spring application is less toxic than in autumn as it does also, of course, from the idea of a dose-related response. However, since it is likely that the relationship between effect and dose level is not linear, there may be a plateauing in the beneficial effect of TPTH which treatment levels in both E/3 and B have reached.

The reaction of Mesostigmata fits less well into the hypothesis that spring treatment is less effective than autumn since this is the only group which responds similarly at both levels of treatment in the different seasons. However, differences do exist, notably that the degree of reduction in density is consistently less in spring and there is not the progressive change which is conspicuous in autumn.

Lower activity of TPTH in spring may be attributable to seasonal differences in climate and vegetation since these are known to change the effectiveness of other organic pesticides (Harris and Sans, 1972), although this is not known for

TPT, at least against soil animals. Equally, however, the sensitivity of the animals to treatment may vary seasonally. For example, one feature associated with the lack of effect on T. floricolus populations in spring is that treatment then acted upon naturally declining populations, while in autumn and winter populations were stable or falling only slightly. Further examination of such seasonal associations is difficult in the absence of information about the general biology of the species involved. This may occur because mite populations differ in character, for example, in age structure or in physiological state, with individuals being, as a result, more or less sensitive.

THE EFFECT OF DIFFERENT REGIMES OF TREATMENT ON THE ACARICIDAL ACTIVITY OF TRIPHENYLTIINS.

The reaction of the 'Other' Prostigmata to TPTA treatment provides the only indication throughout this study that the regime of treatment (namely, whether a single large dose or repeated small doses) might have had some influence on the response of soil Acarina. This possibility is shown in the results of trials E/1 and D/2. In both trials, total applications were equivalent to the recommended agricultural dose but in the former the TPTA was applied only once, whereas in the latter four separate treatments were given. In trial E/1, a significant increase in the numbers of Prostigmata was recorded on two sampling dates, two months and four months after initial treatment, while in trial D/2 no significant difference in numbers occurred. Percentage changes in density support this, with increases recorded in the second, third and fourth months after treatment in trial E/1. The response of 'Other' Prostigmata in E/1 was thus akin to their response when subjected to half this dose, but differed in that in D/1 (half full dose of TPTA) the increase in Prostigmata after treatment was highly significant on all sampling occasions. The reason why this difference occurred is not known.

THE RECOVERY IN NUMBERS OF SUSCEPTIBLE SPECIES FOLLOWING TRIPHENYLTIN TREATMENT.

In each trial series (with the exception of series A) samples were taken for a period of four months following the commencement of treatment. This period was chosen because (1) the half life of TPT's in the soil is around 140 days (Barnes et al., 1971) and if there was an acaricidal effect it would develop within this period. (2) This was a convenient period allowing two treatment series in a year, i.e. spring and autumn, since each series took around six months, allowing for the preparation of plots, etc. As noted earlier (p. 9) time was a particularly limiting factor in this study.

Although the recovery in numbers of other soil animals after treatments with highly toxic chemicals, e.g. Aldrin, DDT, etc. can be slow (Coleman, 1966), I hoped, because of time limitations, this would not be so in respect of TPT treatments, in particular since immigration would probably be rapid in the system of small plots which I employed. Certainly I expected some indications that recovery was beginning during the four month period after treatment. Although I increased the sampling period following series A, delay in the analysis of subsequent samples from trial series B, C, D and E gave me no opportunity to extend the sampling period. The net result of these difficulties is that I am not able to establish the effective period of TPT treatments. All the recorded responses of soil Acarina, including the positive effect of treatment amongst 'Other' Prostigmata and the negative effect as shown in T. floricolus, are maintained throughout the four month sampling period, both at recommended dose levels and at half this level.

THE PROCESSES BY WHICH TRIPHENYLTINS AFFECTED SOIL ACARINA.

Two directly conflicting effects of TPT treatment on soil Acarina have been identified in this study: firstly, that treatment at recommended dosages may

reduce the numbers of some species, and secondly, that at low dosage it may bring about an increase in the numbers of other species. This phenomenon is not infrequently found in studies which attempt to assess the effect of agricultural chemicals on soil fauna. For example, Sheals (1957) noted that, in plots treated with DDT, the numbers of Collembola increased while the numbers of Mesostigmatid mites were considerably reduced.

While field trials demonstrate the existence of deleterious or beneficial effects of agricultural chemicals, a precise indication as to the mechanism through which these population changes occur can be obtained only in laboratory trials. In only a small number of studies has this two part approach been conducted and unfortunately time was not available to undertake laboratory trials in this study. Preliminary work to this end, namely the development of culturing methods for T. floricolus, was achieved and this is described later in this thesis.

In spite of the absence of supporting evidence from laboratory trials in my study, and the general scarcity of information from other studies, some of the more likely possible mechanisms are briefly outlined and discussed below.

The fall in numbers of T. floricolus and Mesostigmatid mites may be explicable in terms of:

(a) Direct toxicity, that is mortality occurring as the result of ingestion of and/or contact with the chemical. This might involve poisoning but could include an initial anti-feedant effect resulting in starvation.

or

(b) Indirect 'toxicity', whereby the treatment modifies the environment, e.g. reducing the availability of a particular food, thereby inducing those species which depend upon it to move or starve.

Since intoxication and death of mites through contact is known to require almost complete saturation with high concentrations of TPT's (Bullock and Johnston, 1968) and this is so also with respect to insects (Abo-Elghar and

Radwan, 1971), this direct toxicity through contact is most unlikely to have been the means by which reductions of mite populations in my study occurred.

However, TPT's act as stomach poisons, as has been established for a variety of invertebrates (Asher and Nissim, 1964) and this route of intoxication seems most likely in this study. That T. floricolus was particularly susceptible would perhaps be expected since the hyphal material of fungi upon which this species is believed to feed (Wallwork, 1967) would probably be heavily contaminated with TPT's.

Assuming that those species of Mesostigmata suffering a reduction in numbers after treatment were predacious, like the majority of this order, for direct toxicity to occur TPT's must have been ingested by way of contaminated prey. This raises the possibility that prey species, and in turn the predators themselves, were accumulating TPT's in body tissues, a feature which was not found to occur in vertebrates (Barth et al., 1964).

The possibility that the reductions in numbers which I recorded might be due to an indirect effect of treatment rather than direct toxicity is a very real possibility in view of the small size of trial plots which I used. Study of T. floricolus in the laboratory indicated that this is a very mobile species, capable of moving quickly from an adverse environment. It seems likely that treatment of soils with TPT's results in severe depletion of soil fungi and, therefore, a shortage of food for species such as T. floricolus. If the diet of this species is quite specific, emigration from treated plots could result in the decline of numbers collected in samples. Various herbicides are reported to operate in this way also (Edwards, 1969).

Similarly, species of Mesostigmata might move from an area depleted of prey species and the decline in numbers of T. floricolus - the most abundant of the Prostigmata present in the study area - may have caused a food shortage for predators, assuming of course that it was important in their diet.

With respect to the increase in numbers of 'other' Prostigmata also, both

direct and indirect action of TPT treatments might be responsible. It is known, for example, that small sub-lethal doses of some toxins may heighten fertility, thereby resulting in higher population levels after breeding (Hueck, cited by Sheals, 1957). However, this assumes that breeding and recruitment of young to the population was occurring during the sampling periods in both spring (series B and C) and autumn (D and E). While some mites do breed several times in a year, many soil inhabiting species breed only once annually. Promotion of higher breeding success, therefore, seems unlikely to account for the increase in numbers of Prostigmata, but this cannot be ruled out. Certainly increases only occurred at low dose levels of TPT and this conforms with this idea. Frequently, increases in numbers in similar circumstances have been attributed to diminished predation, for example by Sheals (1957), Edwards (1969) and Heugens (1968), by way of being an indirect effect of treatment. Thus, in my study the reduction of predaceous Mesostigmatid mites might be the cause of the increase in numbers of 'Other' Prostigmata. Such an increase might occur by way of greater recruitment of young (if breeding occurs during the sampling period) or by immigration. Since increases occur only at low dose levels of TPT's, it is necessary to assume that some member species within the group of 'Other' Prostigmata are affected by direct or indirect toxicity and that the observed increase in number in the group is a balance between toxicity and the effect of diminished predation. Reduced competition might also create conditions under which the 'Other' Prostigmata might increase. For example, the reduction in numbers of T. floricolus in my study would have allowed this if this mechanism was operating. Equally, however, members within the group of 'Other' Prostigmata might be declining, allowing a disproportionate increase of (an) other species. This would be hidden by the incomplete separation of the Prostigmata to species level.

A further possibility is that treatment in some way created an attractive environment for some species within this group and that, as a result, there was

immigration and numbers increased. Certainly treatment would have created an abundance of dead and disintegrating fungal material which for saprophytic species would be an attractive source of food. Increases in some species of soil fauna after treatment with DNOC were similarly attributed to increases in food supply by Karg (1964).

THE IMPLICATIONS OF THE ACTION OF TRIPHENYLSTINS ON SOIL MITES.

The direct toxicity of TPT's, including TPTA and TPTH, to various invertebrates and indeed to vertebrates, including man, was known at the beginning of my study. An acaricidal activity of these organotin compounds was also known, a single report of screening tests including TPTA and TPTH having been given by Bullock and Johnston (1968). However, in common with most research connected with the selection of pesticides, at least in preliminary stages, no information appears to have been gathered concerning the effects of these chemicals on non-target organisms in field situations. Regarding their effect on the functioning of soil ecosystems, I am aware of only the study of Bollen and Tu (1972) who found that administration had no effect on soil microbial respiration and nitrification.

My choice of soil Acarina to demonstrate the existence of organotin toxicity to non-target organisms was largely one of convenience. Perhaps on the basis of known susceptibility, molluscs might have been a more reasonable choice since several studies had demonstrated that very low levels of TPT's were effective against this group (Evans et al, 1971). On the other hand, so as to establish some circumstantial link with avian predators (these were to be the subject of a toxicological laboratory study as the second part of the original project) probably larger soil invertebrates, such as tipulid larvae, would have been more appropriate.

Notwithstanding these reservations, my work using soil mites has demonstrated

as an example, that soil invertebrates are susceptible to levels of organotin administration which are used in agricultural practice and there are indications that fungal feeders, and this includes a large number of species from a variety of phyla, are perhaps particularly susceptible. Furthermore, it is possible, in view of the toxicity of organotins to the mainly predacious mites of the order Mesostigmata, that these chemicals may accumulate in body tissues and are capable of transference through food chains. In this final possibility lies a link to larger predatory invertebrates and ultimately to avian predators.

Although the Acari are a numerically abundant group within soils and are an important link in the food web of the soil ecosystem (Ghilarov, 1965), their role in nutrient cycling being of particular importance (Butcher et al., 1971; Richle, 1977), it is likely that most agricultural chemicals have no appreciable effect on soil fertility. For example, Edwards (1969) in reviewing the effect on soil fertility of highly toxic chemicals, such as D.D.T. and Aldrin, concluded that they had a relatively small effect compared with agricultural practices such as cultivation, drainage and fertilizer application. Bearing in mind that it is in highly cultivated soils that organotins are used, it seems likely that their use in quantities recommended for agricultural treatment has no significant effect on soil fertility or nutrient-cycling in the soil.

THE CULTURING OF SOIL MITES.

When it was found in field trials that TPT's did have an appreciable effect on certain soil Acarina, a series of laboratory trials was proposed whereby some facets of the mode of action of TPT's toxicity might be distinguished, the aim being to recreate, under controlled and easily observed conditions, situations similar to those occurring in field trials. I was particularly interested to establish whether direct or indirect toxicity was operating in the field situation.

It was necessary first to develop a successful method of culturing soil mites which would facilitate their easy observation, counting and handling. Unfortunately, although this was eventually achieved, as described below, time did not permit a toxicological study to be undertaken.

THE CHOICE OF SPECIES FOR CULTURING.

On the basis of (i) its abundance during the early part of my study, and (ii) the indications in trial series A that it was adversely affected by TPTH, Tarsonemus floricolus was the obvious choice for attempts at culturing. Furthermore, the Tarsonemidae are considered primarily mycetophagus by Wallwork (in Burges and Raw, 1967), Karl (1965) and Evans et al. (1961) so that TPT's might be expected to act both directly and indirectly against this species.

This choice of species has drawbacks, however, notably its small size, a

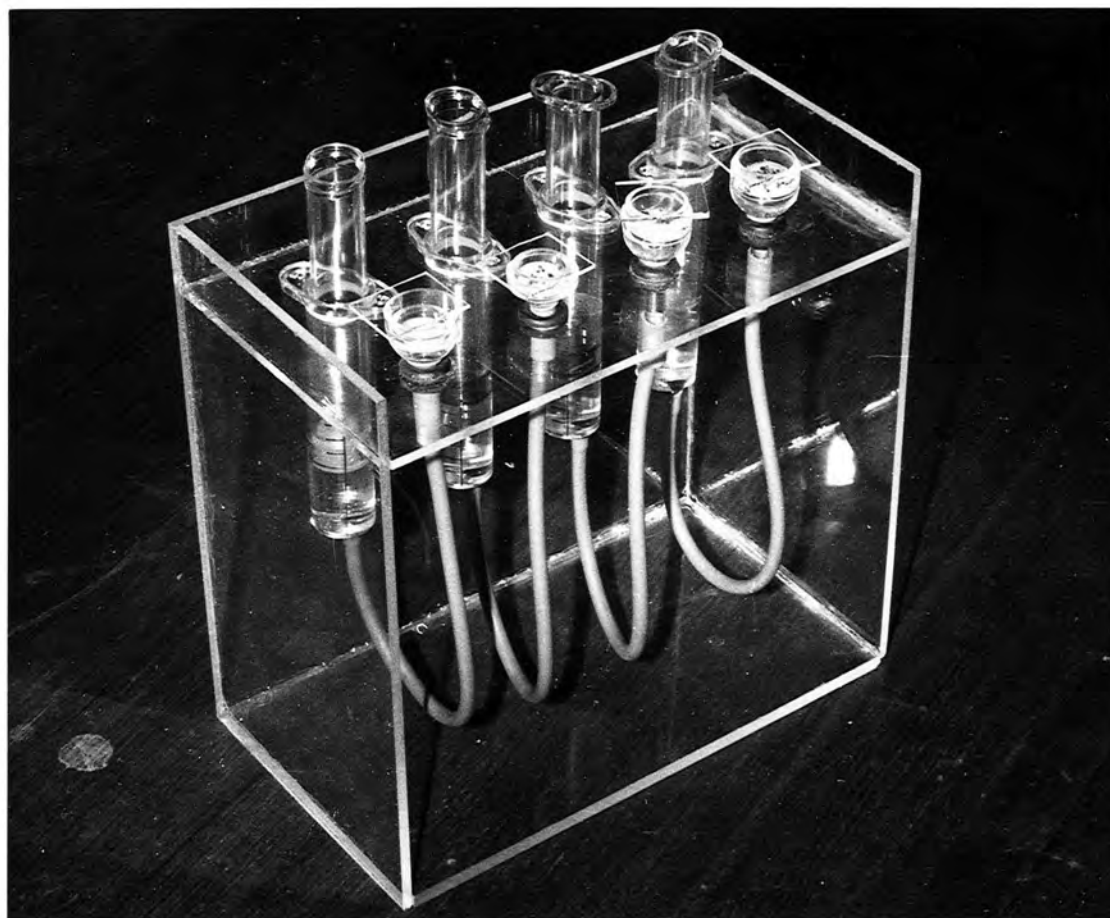
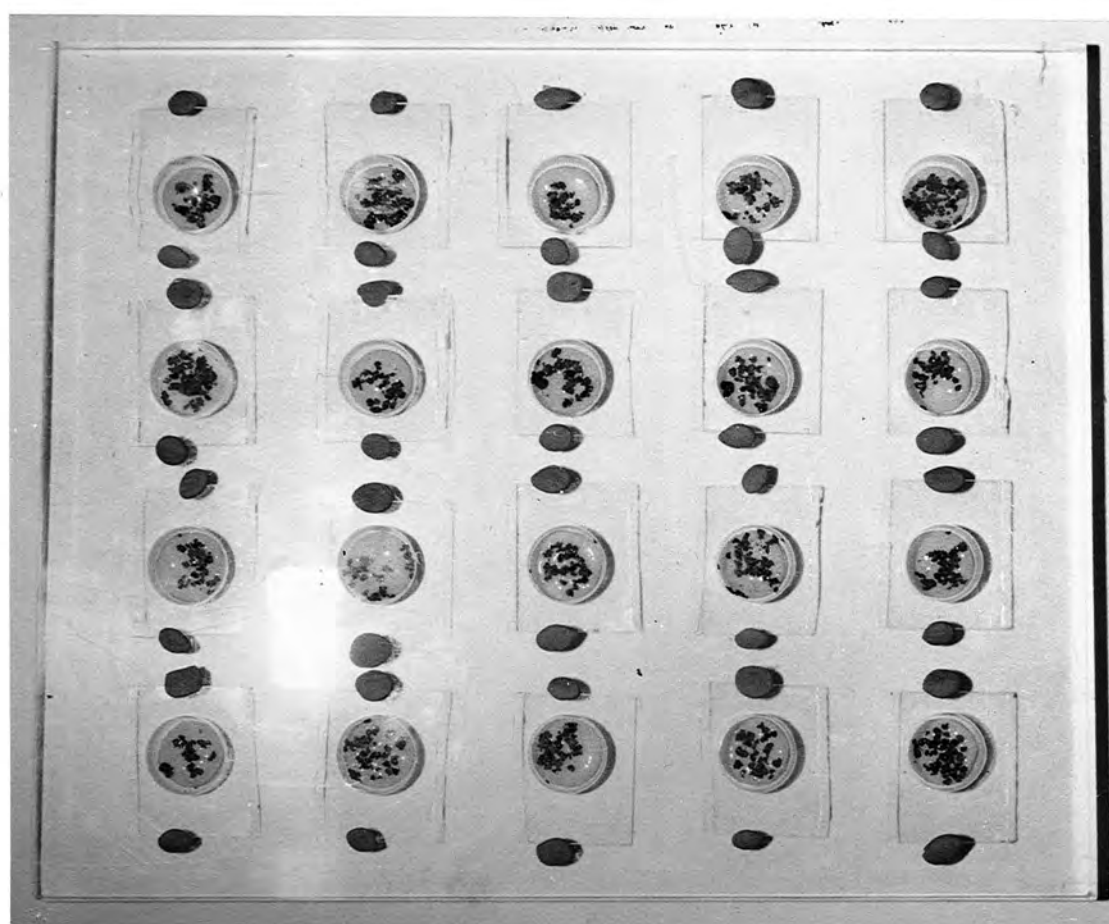


FIGURE 14 : Above - Micro-immersion culture cells
 Below - Perspex block culture cells



feature requiring modification of established culturing techniques and creating problems both in determining direct toxicity and in distinguishing toxicity due to ingestion from that due to contact with the chemical. Also, in common with a number of studies of direct toxicity to mites (Saba, 1971) only adult T. floricolus were reliably identified and, therefore, only these could be used for tests. No measurements are therefore possible of the effects of TPT treatment on pre-adult and egg stages, which may be the most susceptible stages of the life cycle. Successful long term culturing would, however, make this possible.

THE CULTURE CELLS.

Evans et al. (1961) review a number of methods suitable for culturing free living Acari, three of which were tested for this study.

The small size of adult T. floricolus, about 160 (μ) in length and 80 - 85 (μ) in width, demanded the use of a microscope even for counting, and established a number of criteria to be fulfilled by the culturing unit and individual culturing cells.

- (i) The cells had to be small, to save time searching for the mites, and to keep disturbance of their environment to a minimum.
- (ii) Cells had to have a sufficiently closely fitting seal to prevent escape, although not to prevent gaseous exchange.
- (iii) Where cells were grouped in a primary container unit, this also had to be convenient for frequent examination under the available low power microscope, and each cell had to be appropriately placed within it. For example, where the primary container unit was too large it was impossible for it to balance on the microscope stage while viewing all cells, and when square the central cells within a large container could not be viewed since the edge of the container

struck the trunk of the microscope.

(iv) The structure of individual culture cells had to permit the use of indirect lighting under the microscope stage (direct lighting causes excessive heating and fluctuations in the microclimate of the cells).

(v) The cells had to be sufficiently shallow to allow manipulation of the mites within the cell while under the microscope. A fine paint brush was generally used for this purpose.

These constraints, while not peculiar only to smaller mite species, are rather more rigid than those necessary for the culture of species of Cryptostigmata, for example. The following culture methods were used:-

(a) A method using a plaster-soil substrate.

Following a design developed by Edwards (in Kevan, 1955) and Rhode (1956), a unit of culture cells was made comprising a plastic storage container, 8 x 4 x 2 ins. (20.3 x 10.2 x 5.1 cm.) in which was laid a 2 : 1 plaster of Paris and soil substrate to a depth of $\frac{1}{2}$ inch (1.25 cm.). Individual cells comprised 1 x $\frac{1}{2}$ ins. (2.6 x 1.25 cm.) diameter plastic specimen tube, these being bisected with a hot knife, the bottom portion discarded and the top inserted $\frac{1}{4}$ inch (0.6 cm.) into the substrate. The plastic stoppers of each tube were perforated with holes of appropriate size. The lid of the storage container was also perforated.

An effective 100% humidity was maintained by periodically wetting the substrate between the individual cells. Each container accommodated two rows of eight cells.

(b) Micro-immersion filter culture cells.

Murphy and Doncaster (1957) developed a culture cell incorporating a micro-immersion filter for studying the behaviour of predatory soil helminths.

A similar system developed for this study is shown in Fig. 14.

The culture cells were made from a 5 mm. length of glass tubing of approximately 1 cm. in diameter, fixed at one end to a sintered glass disc with a porosity of 30 - 50 (μ). This formed the base of the cell. The upper end was ground with carborundum paste to give a tight seal with a glass cover slip or section of glass slide. The cells merely rested in shallow filter tubes and could, therefore, be removed easily for examination under the microscope. The filter tubes were secured firmly to the perspex framework by a rubber gromet to prevent any movement resulting from flexion of the rubber tube during irrigation. A plastic hypodermic syringe provided the water reservoir.

High humidity was maintained in each cell by keeping the water level in the filter tube just below the sintered glass base. This level was adjusted every two days to compensate for loss by evaporation.

(c) Perspex block technique.

Evans et al. (1961) describe the preparation of small cells drilled in a perspex block. This technique was modified somewhat in my study, with the following result.

Each unit comprised a perspex slab of 5 x 5 ins. (12.7 cm. square) and $\frac{1}{2}$ inch (1.25 cm.) deep, in which was drilled a number of holes forming the individual culture cells. The use of this thickness of perspex reduced the tendency of the material to warp. Each cell was around 6 cm. deep, 1 cm. in diameter and flat-bottomed. Four rows of four such cells were made in each block, an arrangement which allowed at least 1 cm. between each cell.

The substrate comprised a filter paper disc, cut with a cork-borer to be slightly smaller in diameter than the culture cell. The cells were sealed by portions of glass microscope slides, anchored by plasticine. These were sufficiently non-airtight to provide for gaseous exchange. A complete unit is

shown in Fig. 14.

Four perspex blocks were stacked on wire shelves in a dessicator. The base of the de siccator was filled with water and this provided a humidity around 100%. The vent in the lid of the de siccator was sealed with bolting silk so as to reduce the rate of evaporation while maintaining adequate circulation of air.

The filter paper discs were periodically wetted with distilled water to ensure a high humidity was maintained within the cells. The use of filter paper as a substrate for culturing small arthropods has been criticised since it also provides a good medium for fungal growth which can, if unchecked, overwhelm the culture cell. Edwards (in Kevan, 1955) recommends use of a 1 : 10,000 terpinol solution to prevent fungal growth, while the original perspex block technique (Evans et al., 1961) dispensed with the use of filter paper. In my study, however, no undue proliferation of filamentous fungi was seen and it seems likely that any growth simply provided additional feeding for T. floricolus. Globular, mucilagenous fungal growths did cause occasional cells to be abandoned but not often enough to require the use of fungicide, which would have complicated the proposed feeding experiments.

PRECAUTIONS COMMON TO ALL CULTURE METHODS.

In all trials the culture units were stored in a constant temperature cabinet at 10°C. This approximates to the soil temperatures near the soil surface during the day in most of spring and autumn and is assumed, therefore, to represent acceptable if not near-optimum conditions. The light regime, while perhaps of no great significance, was maintained at eight hours light in every 24 hours, approximately mid-winter conditions and a photoperiod unlikely to initiate changes in behaviour.

The maintenance of constant temperature reduced the problem of condensation within culture cells, a problem which occurred with each method, although

considerably less often with the immersion filter technique. T. floricolus was vulnerable to becoming trapped in droplets of condensation on the walls of culture cells, although in practice this occurred infrequently since if a suitable food was provided the mites rarely strayed from it. Some reduction of condensation was achieved by the use of de-misting or water repellant coatings such as Sigmacoat (R): this was used on the cover glasses.

Microscopic examination inevitably involved an increase in temperature and fall in humidity since it required removal of the cover glass and exposure to laboratory temperatures of 15 - 20°C, and when returned to lower temperatures, condensation occurred within the cells. Fluctuations in temperature and humidity also affected the behaviour of mites and, if involving physiological stress, could have affected any experiments adversely. Such problems were minimised by making microscopic examination as brief as possible and using indirect lighting.

Provided that adequate food was available, mites showed no tendency to hide beneath or actually burrow into the filter paper substrate used in the perspex block technique. Evans et al. (1961) recorded this problem as being acute in some cases.

DETERMINATION OF SUITABLE FOODS FOR CULTURING.

After a number of trials using mosses, moss protonema and yeast, the fungal component of the pleurococcus association was found to provide attractive feeding for T. floricolus.

Although pleurococcus taken directly from trees provided little attraction to the mites, after "incubation" in the culture cells for about one week at 10 - 15°C the fungal component of the association, previously very much subordinate, became dominant and a dense "down" of hyphae developed over the algal cluster. The breakdown of such associations under laboratory conditions is a

common phenomenon, for example with lichens.

It seems likely that more than one fungus was associated in pleurococcus, but apart from classifying them as belonging to the "imperfect fungi" no further identification was made. The same fungal group is widespread in soil, but no attempt was made to isolate and identify the actual foods utilized by T. floricolus in the field study area. While all forms of hyphal development from pleurococcus were eaten by the mites, fungus developing from bark fragments proved unpalatable and was removed.

Following seven days' incubation of the food, almost all T. floricolus introduced into the culture cells began feeding on the hyphae within two hours. Once established, they rarely moved away from the food source, provided that the quantity of mycelium was adequate. However, provision of large quantities of pleurococcus created so much hyphal growth that, although it did not appear to hamper the activities of the mites, it made counting them difficult.

For the size of culture cells employed and with the temperature and humidity conditions chosen (10°C and approximately 100%) it was found that 2 - 3 fragments of pleurococcus, each 3 - 4 mm. in diameter, generated sufficient hyphal growth for 6 - 8 mites, and that a good balance between growth and grazing was achieved quickly. This small quantity of pleurococcus did not impede counting, an important feature in view of the need to minimise disturbance of the micro-environment of the culture cells, as noted earlier in this section.

Some preference was shown by mites for feeding on the shorter, more recent, growths of hyphae. Also, growth from some clumps of pleurococcus appeared preferable to others, but these aspects were not investigated further.

When collected, T. floricolus had a distinctive green and gold colouration. This was retained during culturing but some intensification or darkening of the green colour occurred. This may have been the result of ingestion of some algal food but this was not observed. Alternatively, the hyphae were perhaps utilizing and breaking down the pleurococcus algae and might, therefore, take up some

chlorophyll.

The balance between hyphal growth and grazing by T. floricolus could be maintained with only slight changes in the quantity of food material, for more than one month, and even at the end of this test period showed no sign of breaking down. While it must be assumed that the pleurococcus algae were undergoing some breakdown to provide the fungal growth, this was not evident and the algae appeared to remain healthy. However, as a precautionary measure, fragments of pleurococcus were usually removed after about three weeks. During this period the fungi of the pleurococcus showed no tendency to invade the filter paper substrate.

Initially, suitable food sources were also sought for both Scutacarus (Variatipes) montanus and the Pygmephorus sp. but the search was discontinued when a suitable food was found for T. floricolus. Neither of these other two Prostigmatid species fed on the algal or fungal components of pleurococcus (each similar to those occurring in soils), although these foods are suggested by Wallwork (in Burges and Raw, 1967).

However, both Tectocephus velatus and the Oppia sp. found in the sampling area fed satisfactorily, again for periods of over one month, on the pleurococcus algae. Combined culturing of both these species with T. floricolus proved quite feasible, although requiring more food material and, therefore, more time to complete counting, thereby exaggerating disturbances of the micro-environment.

THE CHOICE OF CULTURING METHODS - OVERALL APPRAISAL.

Each of the culturing systems I tested had a number of disadvantages, largely from inadequacies in design which could have been overcome by refinement of the techniques; but time did not allow this.

Below, the principal drawbacks for the culturing of T. floricolus (and other small Prostigmata) are itemised.

Method (a), Using a plaster of Paris/soil substrate:

- (i) This system, designed primarily for larger mites such as the *Cryptostigmata*, proved cumbersome for microscopic examination. Manipulation within individual cells was also difficult because of the depth of the cell. A minimum depth was fixed by the need to use a stopper to each cell rather than a glass cover. The stopper itself also had to be searched for mites.
- (ii) Having a solid base and being rather large, the culture unit proved difficult to illuminate adequately.
- (iii) All unit systems for culturing suffer from the fault that, while one cell is being examined, all others are subjected to environmental disturbance. This problem was exaggerated with using this system since, for reasons noted above, examination was prolonged.

Method (b), Micro-immersion filter technique:

This system was generally preferable for detailed study, since individual cells could be examined easily without the need to remove the whole unit from constant conditions. Furthermore, the individual cell was more convenient for microscopic examination than either of the unit systems.

However, the technique had the following problems:

- (i) The system was essentially unstable. For example, the cover glass was held in position simply by friction: there was no means of attaching it more firmly. It proved very easy for the cover glass to shift even as the incubator cooling unit stopped or started, but particularly when exclusive use of constant temperature facilities was not possible.
- (ii) While the cells themselves are small, the whole framework of the unit occupies a considerable space, again a problem where facilities are limited and when a large number of replicates are required in an experiment.
- (iii) The system required more frequent irrigation than for the other systems tested and, therefore, created somewhat more physical disturbance of the

cultures.

Method (c), Perspex block technique:

This method combined a number of good features. It was easily illuminated, compact for storage and both the individual cells and the unit as a whole were easy to manipulate under the microscope.

Minor problems included:

- (i) The tendency of the plasticine anchoring the cover glass to harden at 10°C so that it was difficult to re-use.
- (ii) Condensation, which occurred on the perspex block when it was removed from low temperatures, prevented good adhesion of the plasticine when replacing the cover glass. When condensation occurred rapidly, the cover glass adhered firmly to the perspex.
- (iii) The need to open each culture cell to add water to the filter paper substrate. Normally, however, this was necessary only once weekly and was carried out after routine examination.

On the basis of these investigations, I concluded that methods (b) and (c) were the more useful for this study, the former more appropriate for frequent examination (perhaps the study of behavioural changes), the latter more suitable for provision of large numbers of replicates, requiring less frequent attention, where counting the numbers of mites is the principal objective.

Proposals for employing these culturing techniques in laboratory tests to establish more precisely the means by which mites are affected by triphenyl-tins are outlined in Appendix 3. Unfortunately, sufficient time was not available to undertake this work.

OBSERVATIONS ON THE POPULATION CHANGES
AND ABUNDANCE OF MITES WITHIN THE STUDY
AREA AT DURHAM.

Whilst the period of my study, somewhat less than two years, must be considered inadequate to demonstrate any long term regularity in seasonal changes in the density of soil mite populations, the monthly frequency of sampling does enable some details of the short term changes to be established.

The results presented in this section are based largely on the densities of mites recorded in the control plots of each experimental series. Small numbers of additional samples were taken during the intervals between the beginning and end of different trials and for a period of seven months after the final trial series was terminated.

Since soil cores were taken to a depth of only 3 cm., the results I obtained do not necessarily represent absolute population levels. They do, however, show the pattern of seasonal change. The validity of this pattern assumes that similar changes in population density (although not necessarily of equal magnitude) occur in soil levels below 3 cm. throughout the year. While this was not tested in my study, more rigorous examination of vertical movements of mites, for example by Curry (1971), support this assumption for all major groups except the known deep-living Acari, such as the Rhodacaridae (Evans, 1961). Notwithstanding the fact that my records do not give an exact measure

of the density of mite populations, it is possible to provide some interesting comparisons with other studies in terms of the abundance of mites in the upper layers of the soil.

THE PATTERN OF SEASONAL CHANGES IN MITE POPULATIONS AT DURHAM.

The seasonal variations in populations of the numerically important groups of Acari and of three single species of Prostigmata are given in Figs. 15 - 20. Each individual point in these figures represents the median density per square metre based on 16 or more samples. For each observation the median and mean values and the standard error of the mean are tabulated in Appendix 4.

Two major groups of mites, the Cryptostigmata and Astigmata, have been included only in the total counts of mites (Fig. 15), since each of these orders occurred in very small numbers in my study area. Although the variety of species of Cryptostigmata increased during the study period, no statistically significant increase in density was found of the group as a whole. Of the Astigmata only a single Schwiebia sp. was recorded regularly in samples, often only as occasional individuals.

Fig. 15 shows the seasonal variation in density of all mite species during my study, and indicates maxima in November 1972, May 1973 and June 1974. The irregularity of changes in density of total counts of Acari is common to most studies of mites and stems from the composite nature of this total, whereby peaks in numbers are frequently due to a single extremely abundant species rather than to an increase in all species or even a single order. For example, Macfadyen (1952) found that seasonal variation in total Acarina in a fen soil was principally due to the fluctuation in a number of species of Cryptostigmata. Although hitherto considered unusual, early summer peaks were also observed by Curry (1971) and Dhillon and Gibson (1962), and by Edwards et al. (1967), and in each study were due principally to changes in the abundance of a small number

FIGURE 15: THE SEASONAL VARIATION IN THE TOTAL NUMBERS OF SOIL MITES.

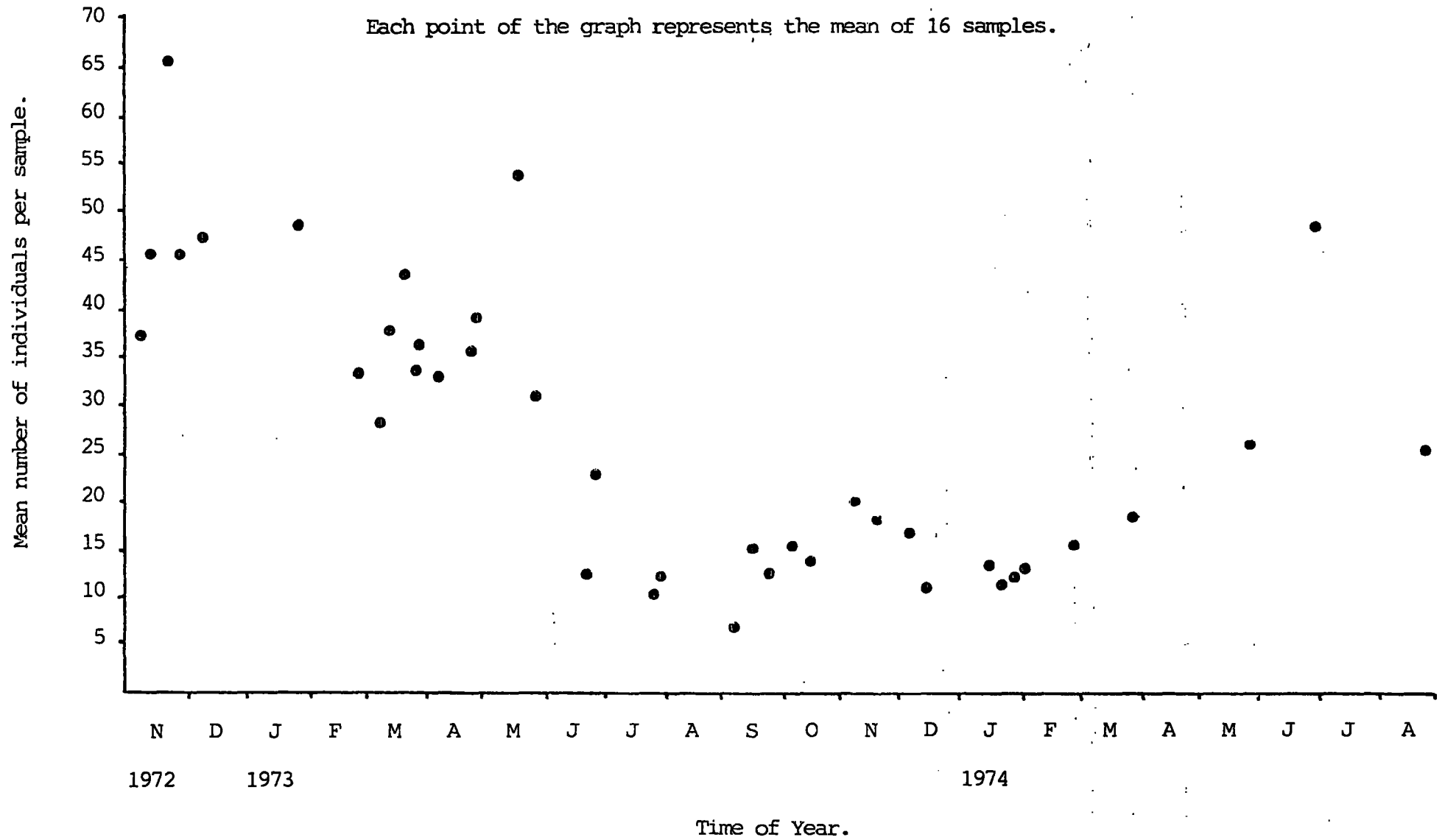


FIGURE 16 : THE SEASONAL VARIATION IN THE NUMBERS OF MESOSTIGMATA.

Each point of the graph represents the mean of 16 samples.

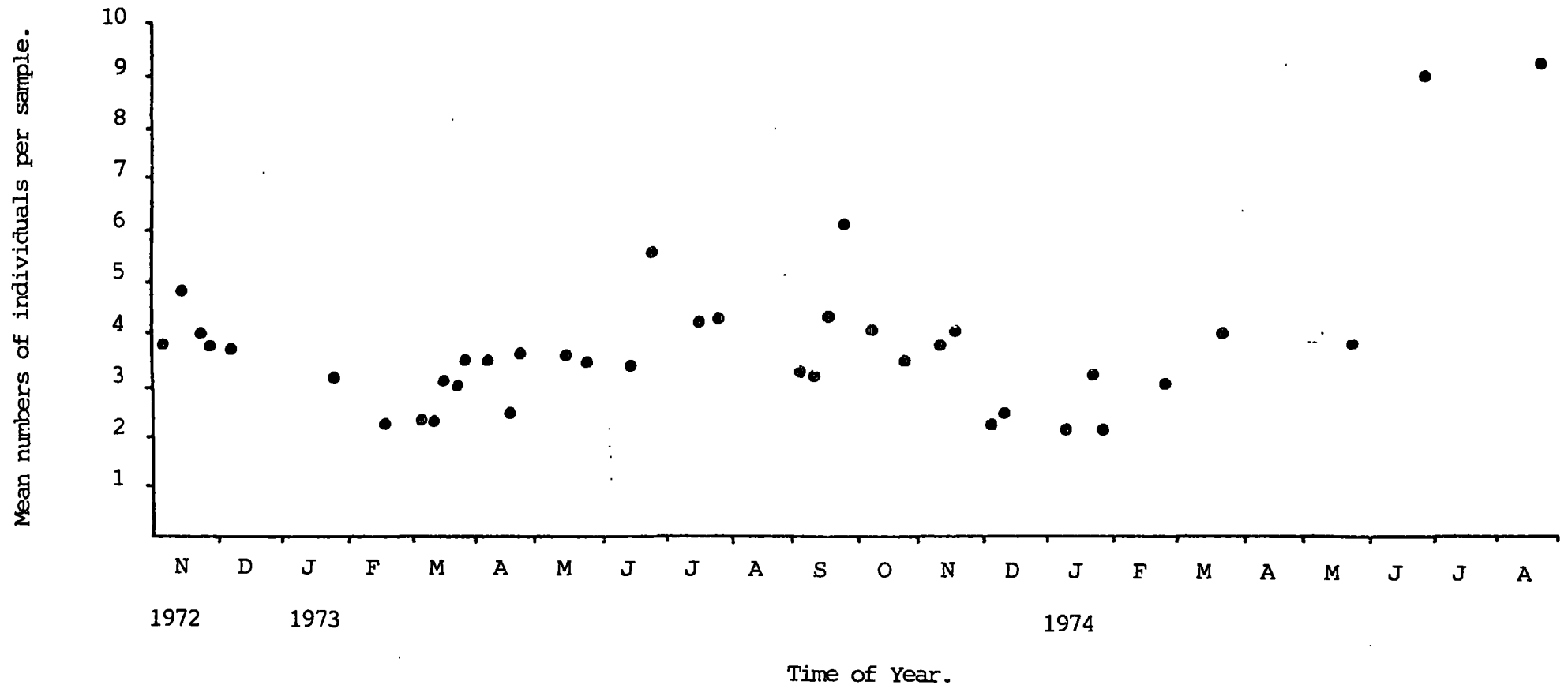
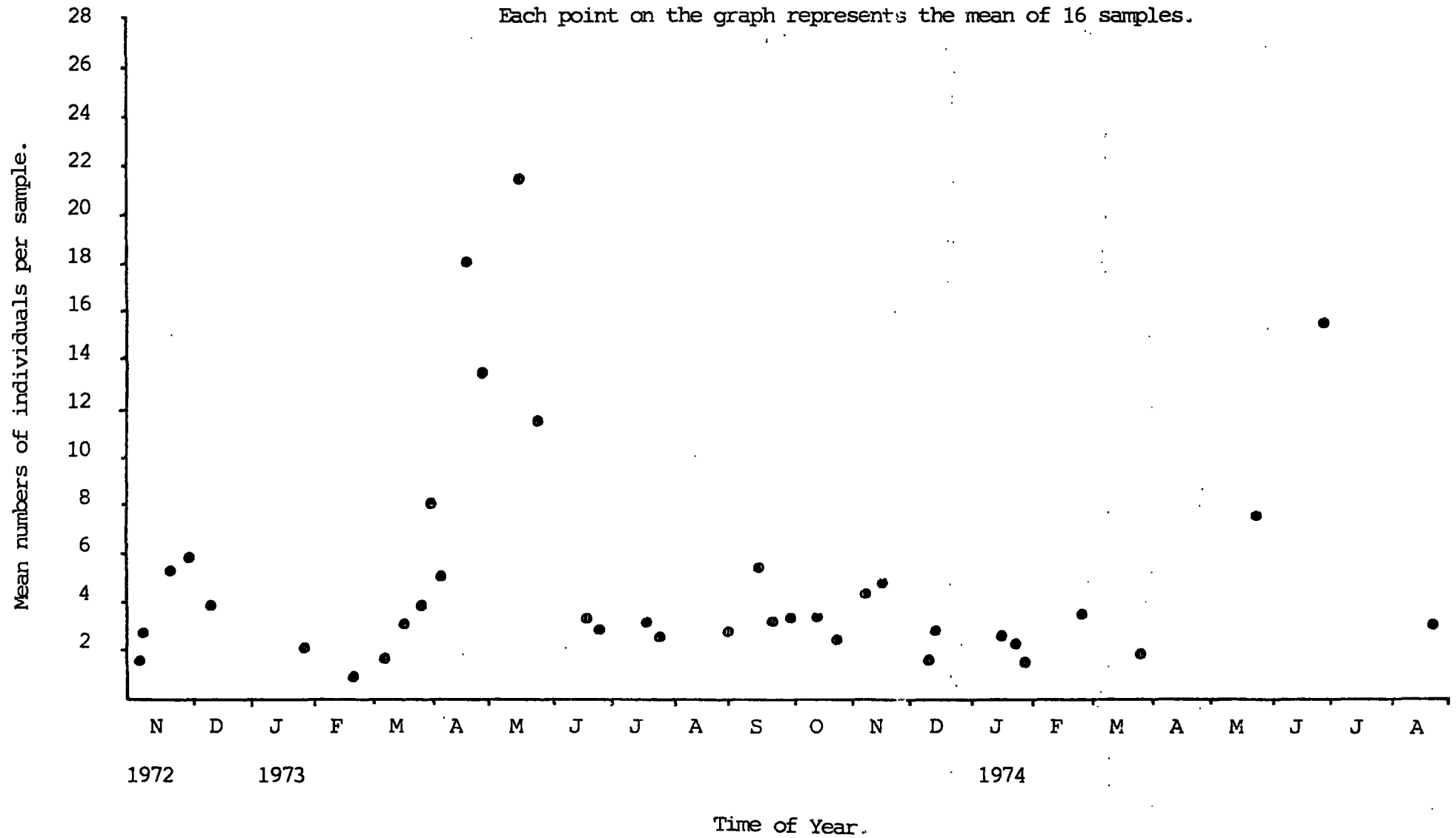


FIGURE 17 : THE SEASONAL VARIATION IN 'OTHER' PROSTIGMATA.



of dominant Prostigmata.

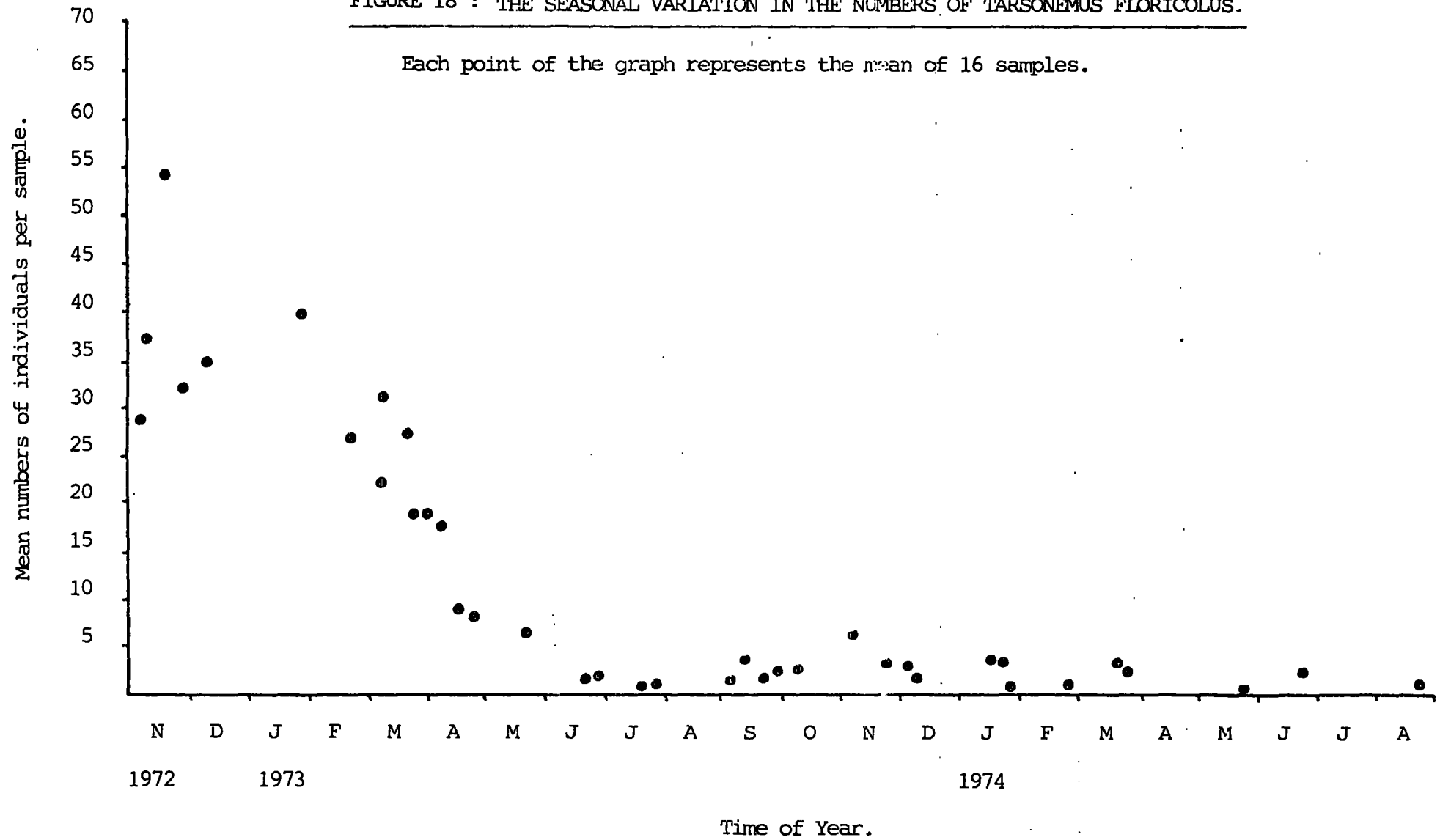
With the exception of the last two months of my study, the density of Mesostigmata (Fig. 16) showed very little fluctuation. However, in both 1973 and 1974 the lowest median densities were recorded in late winter and higher values in autumn and summer. Similarly, only slight variation in the density of Mesostigmata was found by Sheals (1957) in uncultivated mineral soil and by Evans (1955) in a soil of a Sitka spruce plantation. The phenomenon appears to be widespread in Britain (Wallwork, 1967) and may result from the similarity of Mesostigmatid communities, with common, widely distributed species having a wide tolerance of physical conditions (Evans, 1961). However, this relative stability of densities may be true of only the upper soil layers. Curry (1971), for example, found little variation in abundance of Mesostigmata in the top 3 cm. of old pasture, but greater seasonal variation at deeper soil levels. A similar pattern was found by Dhillon and Gibson (1962) who took samples to a depth of 9 ins.

The numbers of Prostigmata, Fig. 17 (excluding the species shown separately in Figs. 19 - 20) show very abrupt maxima in May 1973 and June 1974, with relatively steady population levels throughout the other months of the year. The magnitude and rapidity of development of the maxima, and the existence of only a single annual peak, probably indicates that only a few species, perhaps only one species, were involved, with most species remaining at steady levels throughout the year as found by Evans (1955). Dhillon and Gibson (1962) and Curry (1971) both found maxima in May/June but also recorded a mid-winter peak. In both of their studies, the Prostigmata were dominated by the genus Eupodes and this was the most important group of my category of 'Other' Prostigmata.

It is possible that the peak population density I measured arose from closely synchronised maturation to adult size and behaviour, the new year class thereby becoming available for extraction by the techniques I used. This occurs, for example, in grasshoppers (Richards and Waloff, 1954). The equally

FIGURE 18 : THE SEASONAL VARIATION IN THE NUMBERS OF TARSONEMUS FLORICOLUS.

Each point of the graph represents the mean of 16 samples.



rapid falls in numbers following the maxima may be interpreted in terms of predation as, for example, shown in the predator-prey oscillations of mites in laboratory culture (Huffaker, 1958). Climatic changes are capable of providing "crashes" in population (Andrewartha and Birch, 1954) but this would be an unusual event and it would be unlikely to produce a similar decline in successive years. An alternative or additional explanation of this decline (or perhaps of both the increase and decline) is that individuals of the specie(s) concerned were moving from, and possibly into, the 0 - 3 cm. soil level which I sampled. Thus, the maxima I recorded might represent the movement of adults into the 0 - 3 cm. level either from the surface vegetation or deeper soil levels to copulate or lay eggs, the adults returning to their more usual habitat after this function was completed. Equally, if the situation initially proposed occurred, that is a synchronised maturation, there may have been emigration of newly developed adults to a different habitat. Certainly Riha (1951: cited by Sheals, 1957) found immature Cryptostigmata inhabiting different habitats from the adults and considered that seasonal minima were occasioned by migration of adults to other habitats for reproduction. Sheals considered this a reasonable explanation for the absence of immature individuals of some species of Cryptostigmata and Mesostigmata in his samples.

For Tarsonemus floricolus (Fig. 18) the very high densities recorded in the 1972/73 winter did not recur in the subsequent winter. The reason for such year to year variation, a frequent feature of species populations of Acari, is not explicable in terms of gross climatic variation, since both years of my study had broadly similar patterns of temperature and rainfall (Fig. 1.) The absence of any other species of Prostigmata with a discernible winter peak in population density allows no similarities or contrasts to be drawn. Furthermore, although it seems that only a single annual peak occurs in numbers of T. floricolus, the life cycle is insufficiently well-known to correlate its timing with climatic conditions.

As mentioned earlier, the vegetation of my study site was established by re-seeding only 18 months before the study began. It seems likely, therefore, that the micro-arthropod fauna was undergoing transition to that more typical of mature pasture. This process may have been accelerated somewhat by the absence of regular mowing after my study began, and subsequently only a single pre-treatment cut was made for each experimental series. The taller vegetation that developed would shade the soil surface and this might have greatly modified the soil micro-climate, especially the moisture conditions, within the study area. It is possible, therefore, that the absence of a resurgence in the numbers of T. floricolus in the 1973/74 winter may represent a permanent reduction of this species as part of this transition process. Although Edwards et al. (1967) found small numbers of Tarsonemids in arable soil, the only published record of the genus Tarsonemus occurring in soil in high numbers comes from a study by Davis (1963) where it occurred in pasture of 12 years standing, whereas in truly permanent pasture the family seems rare. Furthermore, Davis found Tarsonemids during sampling in mid-November which coincides with the highest levels of population at the Durham site. Previously, T. floricolus has been more usually found in association with stored cereals (Hughes, 1959) rather than in soils.

Two other findings of my study support the idea of a faunal transition occurring: firstly, the increased density and diversity of Cryptostigmata, a group more characteristic of permanent pasture (Loots and Ryke, 1967; Evans et al., 1961) and adversely affected by cultivation (Sheals, 1957), and secondly, the progressive increase in density of a previously uncommon species of Prostigmata, Scutacarus (Variatipes) montanus (Fig. 19). Davis (1963) found this genus to be abundant in mature pasture but uncommon in adjacent disturbed soils. The genus was also abundant in the established pasture studied by Curry (1971).

The genus Pygmephorus (Fig. 20) showed maxima in May and June in both 1973

FIGURE 19 : THE SEASONAL VARIATION IN THE NUMBERS OF SCUTACARUS (VARIATIPES) MONTANUS.

Each point of the graph represents the mean of 16 samples.

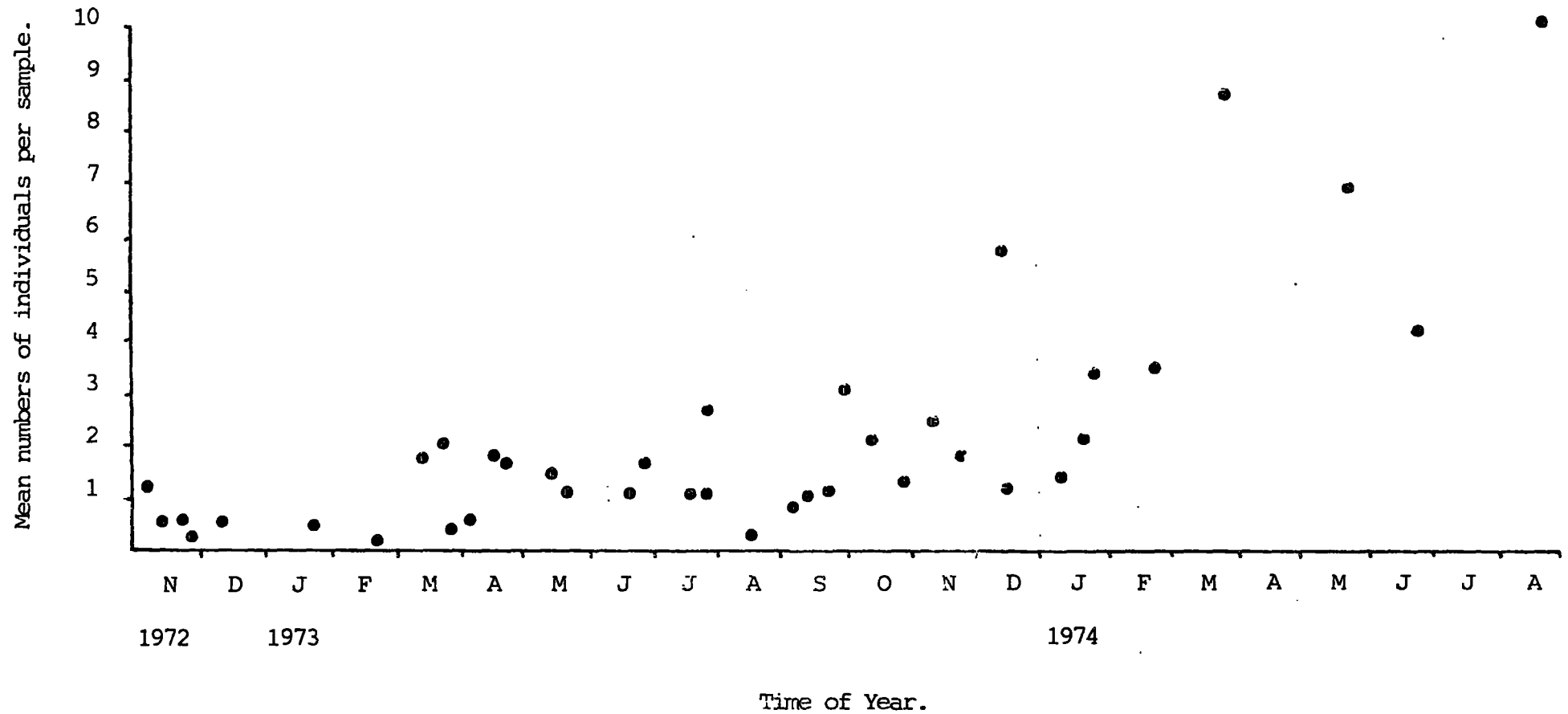
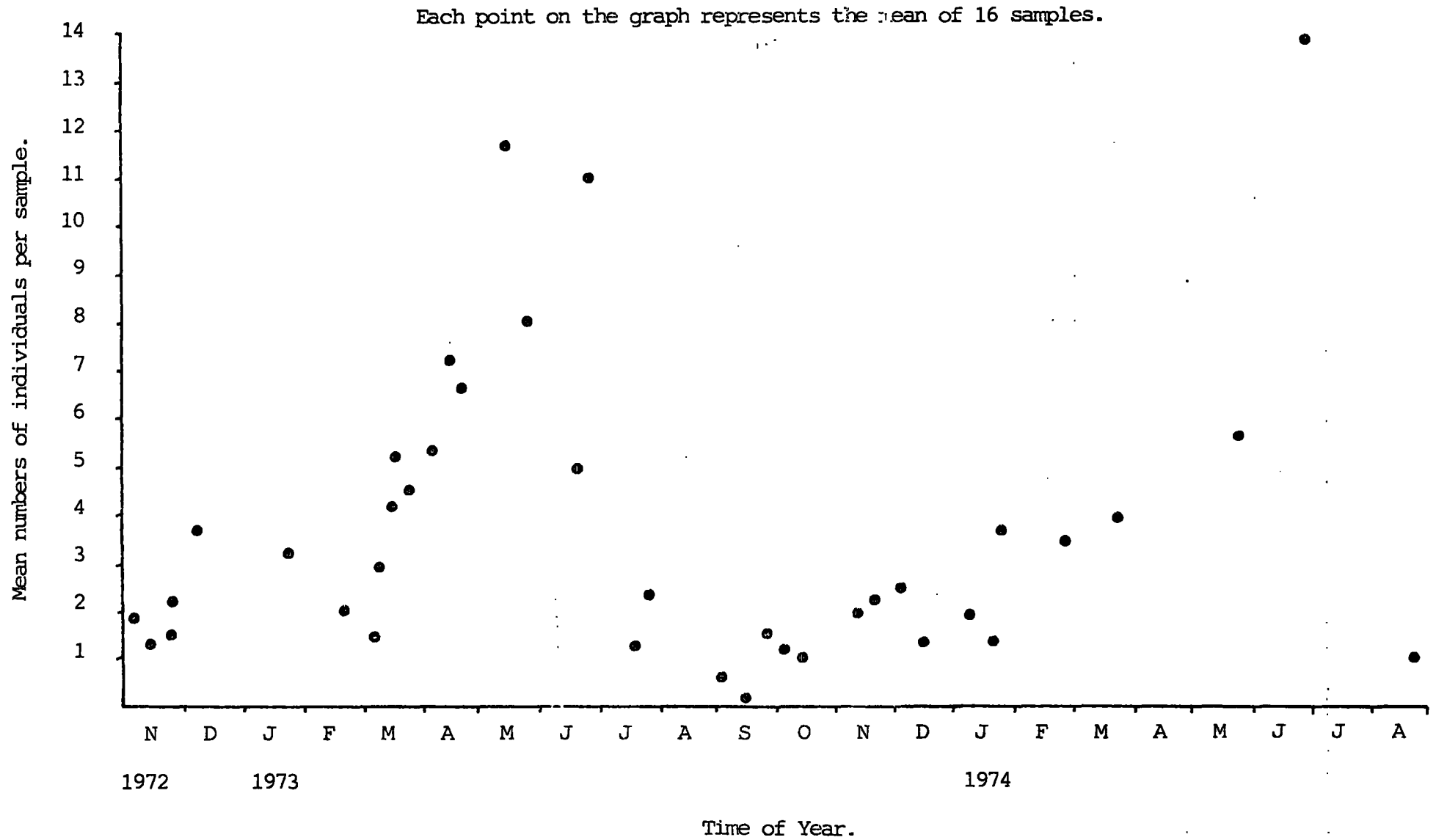


FIGURE 20 : THE SEASONAL VARIATION IN THE NUMBERS OF THE GENUS PYGMEPHORUS.



and 1974, at about the same times, therefore, as the unseparated groups of Prostigmata (Fig. 17). The regularity of this peak contrasts with the irregular fluctuations of this genus recorded by Dhillon and Gibson (1962) who recorded peaks in September, December and March as well as in May. The single annual peak recorded in my study suggests the presence of only a single generation per year in the specie(s) present. If this is a common feature of the genus, it would seem likely that the study area chosen by Dhillon and Gibson contained a number of species each of which reached peak abundance at different seasons. Similarly, Currey (1971) found a May/June peak for this genus in two successive years, but an autumn peak also. Unfortunately, in both these studies and in my own, the species of the genus *Ergasiphon* were not separated but since each study was made in a similar habitat - grassland developed on a clay soil - it is possible the May/June peak densities recorded in each study were of the same species.

Since no detailed study was made of seasonal variation in soil factors (soil moisture, pH, soil temperature, etc.) within the sampling area no attempt has been made to find correlations between population changes and gross climatic changes recorded at the Durham Meteorological Observatory. Although these environmental variables are likely to be important, the relationships are probably complex, and even a thorough investigation of soil factors by Dhillon and Gibson produced few significant correlations. Similarly, Sheals (1957) found no correlation between seasonal changes in population of Cryptostigmatid species and gross climatic variation.

THE ABUNDANCE OF MITES IN THE STUDY AREA AT DURHAM.

The median and the ranges of mean density exhibited by the major groups of mites and by three species of Prostigmata throughout the period of study are tabulated in Table 20 (densities being expressed as the numbers of mites/

TABLE 20:

THE MEDIAN AND THE RANGES OF MEAN DENSITY EXHIBITED BY THE MAJOR GROUPS OF
MITES AND BY THREE SELECTED SPECIES OF PROSTIGMATA DURING THIS STUDY.

<u>Groups separated.</u>	<u>Median mean density</u> <u>per square metre</u>	<u>Maximum mean</u> <u>density</u>	<u>Minimum mean</u> <u>density</u>
Total Acarina	23346	58150	6843
All Prostigmata	15805	54622	4627
Mesostigmata	3055	8953	1651
Cryptostigmata	159	618	0
Astigmata	75	2384	0
Tarsonemus floricolus	3858	47733	274
Scutacarus montanus	1183	8918	53
Pygmephorus spp.	2207	13554	53
'Other' Prostigmata	2701	19037	1042

TABLE 21: THE ABUNDANCE OF SOIL MITES IN DIFFERENT HABITATS.

In each case the density of mites are expressed as the mean numbers/m². For my study, the value given is the mean of all samples taken over a 1½ year period. For other studies, the period of sampling varies and is frequently less than one year.

<u>Author(s)</u>	<u>Habitat</u>	<u>Total Acarina</u>	<u>Prostigmata</u>	<u>Mesostigmata</u>	<u>Astigmata</u>	<u>Cryptostigmata</u>
Evans (1961)*	Oak Woodland	405,000	87,000	28,000	6,000	284,000
Evans (1955)*	Sitka Spruce Plantation	99,000	35,000	5,000	2,000	57,000
Macfadyen (1952)	Fen Soil	77,600	2,000	6,000	600	69,000
Sheals (1957)*	Permanent Pasture	33,300	300	9,000	5,000	19,000
Curry (1971)**	Permanent Pasture	77,100	15,600	21,600	2,300	36,600
Dhillon and Gibson (1962)**	Permanent Pasture	24,900	15,900	8,200	500	300
Sheals (1956)*	Recent Pasture	12,200	200	4,000	3,000	5,000
Davis (1963)	Unreclaimed Quarry	7,742	1,498	3,970	497	1,777
Davis (1966)	Arable	15,374	1,995	4,890	334	8,155
This study	Recent Pasture	23,937	20,152	3,554	157	74

N.B. * These records are also shown in Evans et al. (1961).

** These values are calculated from histograms since no tabulated data are published.

square metre).

These figures have been extracted from the complete tabulated records in Appendix 4. In addition to the category of 'Other' Prostigmata, this having been used exclusively in previous sections of this thesis, Table 20 gives the densities of 'all' Prostigmata.

Comparison with the results of other studies is frequently difficult since the data on population densities are usually incomplete in published accounts and the brief consideration here did not warrant review of unpublished material. In Table 21 the mean densities of the major orders of mites determined in a number of other studies is shown. These cover a variety of habitats and include most published British studies concerning soils in agricultural use. Since the frequency of sampling, depth of samples, extraction techniques and the season of sampling, etc. vary considerably amongst these studies and my own, comparison must only be superficial and inevitably all similarities and differences require qualification. Notwithstanding these difficulties, some interesting comparisons may be made.

Since decaying organic matter directly or indirectly (e.g. by supporting algae or fungi) provides food for the majority of soil mites, it is not unexpected that densities of mites are highest in soils where the organic content is high, for example, in woodlands where there is a well developed litter (Evans et al., 1961). At the opposite end of the scale from woodland is the unreclaimed quarry studied by Davis (1963). Differences in soil pore size, moisture content and other components of micro-climate which also influence mite densities, tend to be positively correlated with the organic content of soils and for purposes of simple comparison no distinction is warranted. Thus, between the two extremes referred to above, lie soils subject to agricultural use. They generally contain lower levels of organic material and are increasingly subject to periodic cultivation (a process which disrupts the development of a surface litter), and perhaps to drainage and artificial fertilization. The various

effects of agricultural practice on micro-arthropods are reviewed by Edwards and Loftly (1968). Where cultivation is infrequent and pasture may be retained on a semi-permanent basis, the vegetation sward becomes matt-like, the diversity of plants increases and a distinct humus layer develops. In these situations the densities of mites may approach those in monoculture woodlands, such as Sitka spruce plantation (Evans, 1955); for example, within the permanent pasture studied by Currey (1971). Sheals (1957) and Dhillon and Gibson (1962), also studying old pastures, found substantially lower densities of mites than recorded by Curry. In the former, the difference was probably due to an under-estimation of Prostigmata arising from the use of a floatation extraction technique, while in the latter the very low numbers of Cryptostigmata found were attributed to the low moisture content of the soil in their study area.

The densities of mites in recently established grassland, such as that sampled by Sheals (1956) and my own at Durham, are lower than for permanent pastures and thus fit the general pattern of association between the numbers of mites and the development of a soil profile with a definite humus layer. Sheals' records in this instance seem again to be deficient in the numbers of Prostigmata and this is true also of the arable soil and unreclaimed quarry soil studied by Davis (1966 and 1963). This is an important contrast with my study and probably hinges on the fact that in each of these three studies a floatation extraction method was used. Although the recovery of Prostigmata by floatation methods was no lower than by dynamic techniques in a comparative study of extraction methods by Edwards and Fletcher (1971), Evans (1951) did find this to be the case, the recovery of the smaller more delicately built Prostigmata being particularly poor. This is important since it is these smaller species which probably predominate in compact cultivated soils. It is of interest that in my study the densities of Prostigmata approach most closely those recorded in permanent pasture by Curry (1971) and Dhillon and Gibson (1962). This suggests that the Prostigmata had recovered rapidly in numbers,

if not in diversity, following previous arable use. In both their studies, high gradient extraction methods, similar to mine, were employed.

Had it not been for the high numbers of Cryptostigmata recorded by Curry (1971), the paucity of this group identified from the sites studied by Dhillon and Gibson (1962), and more particularly at Durham, might have been attributed to the use of a high gradient extraction method in the same way that I have interpreted the scarcity of Prostigmata in other studies. However, other studies of agricultural soils support the likelihood of very low densities of Cryptostigmata. For example, Edwards et al. (1967) found high numbers of Prostigmata associated with a complete absence of Cryptostigmata in an arable field situation. Unfortunately, their published results are not presented in a way that enables calculation of the absolute densities of mites: therefore direct comparison is not possible. But at least this shows that my results with respect to the Cryptostigmata are not necessarily atypical.

Clearly a variety of factors operating in agricultural soils, in addition to the presence of low levels of organic matter, conspire against the development of high densities of Cryptostigmata. Butcher et al. (1971), for example, consider that this order of mites in particular might be greatly influenced by the water content of soils and the pore size and living space available in upper soil layers. Since the site I sampled at Durham, having been seeded with grass 18 months before my study began, had been mown very frequently (somewhat similar to a playing field), it seems possible that this activity on a quite heavy clay soil would have caused considerable compaction. This might have reduced its suitability for any Cryptostigmata which had existed during arable cultivation or which might have attempted recolonization when the grass sward was established. I have noted previously that towards the end of my study there appeared a tendency for the density and diversity of Cryptostigmata to increase. This coincided with changes in the abundance of certain Prostigmata, namely Tarsonemus floricolus and Scutacarus (Variatipes) montanus, the former

decreasing while the latter increased over the study period (Figs. 18 and 19). I tentatively attributed these contrasting changes to a natural transition in the micro-environment of the soil in the study area, a possible reason being the absence of mowing and, therefore, the absence of compaction of the upper soil layers. My findings follow the relatively simple prediction that these changes would provide a more suitable habitat for the Cryptostigmata. Since Sheals (1956) found that only one species of Cryptostigmata recolonized soils within a year after cultivation and insecticidal treatments, and since very slow recovery was found in the study of irradiated soils (Coleman, 1966), the gradual increase in the numbers of Cryptostigmata at Durham is perhaps characteristic of this group.

Of any order of Acarina, the densities of Mesostigmata which I recorded at Durham showed closest similarity to the densities in similarly disturbed habitats which had been studied elsewhere. In the previous sub-section, the similarity in the pattern of seasonal population change of this order in most British studies of soil-mites was cited as being related to the finding that many species of this group are widely distributed and appear tolerant of a wide variety of environments (Wallwork, 1967). It is perhaps for this reason also that this group achieves similar densities under similar soil conditions. Several widely occurring and abundant species of this group appear not to be confined to the upper soil layers, having a poor association with the total amount and localization of organic material in the soil profile. Furthermore, the ability, even preference, of some species of Mesostigmata to inhabit lower levels of the soil would make them less susceptible to problems of soil pore size, the feature which I have suggested might have contributed to the paucity of Cryptostigmata at Durham.

The few published details concerning the biology of soil-inhabiting Astigmata provide no clues as to why this group should be so poorly represented in terms of diversity ^{and} abundance at Durham. Certainly relatively low

densities are recorded in other studies of disturbed soils but the densities which I recorded lie far below these. While there may be some link with the very low levels of Cryptostigmata, no available literature really gives any support to the possibility of an association. Curry (1969), also using a high gradient extractor, obtained a low recovery of Astigmata and perhaps it is the use of this extraction technique in my study which results in such low densities being recorded. Curry attributed the higher densities of Astigmata in the studies of Davis (1963) and Sheals (1957) to the more efficient recovery by floatation methods, but this contrasts with the findings of Edwards and Fletcher (1971).

B I B L I O G R A P H Y .

- Abo-Elghar, M.R. and Radwan, H. (1971). Toxicological, chemosterilant and histopathological effects of triphenyltin hydroxide on Spodoptera littoralis. *Acta Phytopathologica Academiae Scientiarum Hungaricae*, 6(1-4), 261-280.
- Allison, W.E.; Doty, A.E.; Hardy, J.L.; Kenega, E.E.; and Whitney, W.K. (1968). Laboratory evaluation of Plictran miticide against two-spotted spider mite. *Journal of Economic Entomology* 61(6), 1254-1257.
- Aldridge, W.M. and Rose, M.S. (1969). The mechanism of oxidative phosphorylation. A hypothesis derived from studies of trimethyltin and triethyltin compounds. *FEBS. letters*, 4(2), 61-68.
- Aldridge, W.M. and Street, B.W. (1971). Oxidative phosphorylation. *Biochemical Journal*, 124, 221-234.
- Andrewartha, H.G. and Birch, L.C. (1954). "The distribution and abundance of animals". University of Chicago Press, Chicago.
- Asher, K.R.S. and Rones, G. (1964). Fungicide has residual effect on larval feeding. *International Pest Control*, 6(4), 4-6.
- Asher, K.R.S. and Nissim, S. (1964). Organotin compounds and their potential use in insect control. *World Review of Pest Control*, 3, 188-211.
- Asher, K.R.S. and Nissim, S. (1965). Quantitative aspects of antifeeding. *International Pest Control*, 7(2), 21-24.
- Baker, E.W. and Wharton, G.W. (1952). "Introduction to Acarology". Macmillan Company, London.
- Barnes, R.D.; Bull, A.T.; and Poller, R.C. (1971). Behaviour of triphenyltin acetate in soil. *Chemistry and Industry*, February 13th, 204.
- Barnes, R.D. (1973). Studies on the persistence of the organotin fungicide fenitrothion acetate in the soil and on surfaces exposed to light. *Pesticide Science*, 4, 305-314.

- Barth, K.; Bruggeman, J.; Gotte, M.; Herok, J.; Klimmer, O.; and Niesar, K. (1964). Nutritional physiology, analytical and toxicological investigations on the fungicide triphenyltin acetate. *Zentralblatt fuer venterinaermedizin*, 11, 1-48.
- Beer, R.E. (1954). A revision of the Tarsonemidae of the western hemisphere (Order Acarina). *University of Kansas Scientific Bulletin*, 36(2), 1091-1387.
- Ben-Dyke, R.; Sanderson, D.M.; and Noakes, D.M. (1970). Acute toxicity data for pesticides (1970). *World Review of Pest Control*, 9(3), 119-127.
- Block, W.C. (1965). "Studies on the Acaria of moorland areas". Unpublished Ph.D. thesis, University of Durham.
- Block, W.C. (1966). Some characteristics of the Macfadyen high gradient extractor for soil micro-arthropods. *Oikos*, 17, 1-9.
- Bollen, W.E. and Tu, C.M. (1972). Effects of an organotin on microbial activities in soil. *Tin and its Uses*, 94, 13-15.
- Bullock, R.C. and Johnston, R.B. (1968). Performance and phytotoxicity of three fentins in citrus rust mite control in Florida. *Florida Entomologist*, 51(4), 223-227.
- Butcher, J.W.; Snider, R.; and Snider, R.J. (1971). Bioecology of edaphic Collembola and Acarina. *Annual Review of Entomology*, 16, 249-288.
- Byington, K.H. (1971). Effects of triphenyltin compounds on the ATPase activity of beef heart sub-mitochondrial particles. *Biochemical and Biophysical Research Communications*, 42, 16-22.
- Byington, K.H.; Yeh, R.Y.; and Forte, L.R. (1974). The haemolytic activity of some trialkyltin and triphenyltin compounds. *Toxicology and Applied Pharmacology*, 27(2), 230-240.
- Coleman, D.C. (1966). The recolonization of gamma irradiated soil by small arthropods. A preliminary survey. *Oikos*, 17, 62-70.
- Cremer, J.E. (1968). Some influences of triethyltin on brain glucose metabolism in vivo and in vitro. *Biochemical Journal*, 106, 8-9 (Proceedings of the Biochemical Society).
- Curry, J.P. (1969). The qualitative and quantitative composition of an old grassland site at Celbridge, Co. Kildare. *Soil Biology and Biochemistry*, 1, 219-227.
- Curry, J.P. (1972). Seasonal and vertical distribution of arthropod fauna of an old grassland soil. *Proceedings Royal Dublin Society (B)*, 3, 49-71.
- Davis, B.N.K. (1963). A study of micro-arthropod communities in mineral soil near Corby, Northants. *Journal of Animal Ecology*, 32(1), 49-71.
- Davis, B.N.K. (1965). The immediate and long term effects of the herbicide M.C.P.A. on soil arthropods. *Bulletin of Entomological Research*, 56(2), 357-366.

- Deschiens, R. and Floch, H. (1962). Bulletin de la Societe de Pathologie Exotique 55(5), 816-825 (cited by Evans, C.J., 1971).
- Dhillon, B.S. and Gibson, N.H. (1962). A study of Acarina and Collembola of agricultural soils. Pedobiologia, 1, 189-209.
- Dittrich, V. (1962). A comparative study of toxicological test methods on a population of two-spotted spider mite (Tetranychus telarius). Journal of Economic Entomology, 55, 644-648.
- Downing, R.S. and Moilliet, T.K. (1970). Plictran as an orchard acaricide in British Columbia. Canadian Entomologist, 102, 1604-1607.
- Edwards, C.A. (1969). Soil pollutants and soil animals. Scientific American, 220 (4), 88-99.
- Edwards, C.A.; Dennis, E.B.; and Empson, D.W. (1967). Pesticides and the soil fauna: effects of Aldrin and D.D.T. in an arable field. Annals of Applied Biology, 60(1), 11-22.
- Edwards, C.A. and Lofty, J.R. (1968). The influence of agricultural practice on soil micro-arthropod populations. In: "The Soil Ecosystem", Symposium of the Systematics Association, pp. 237-247.
- Edwards, C.A. and Fletcher, K.E. (1971). A comparison of extraction methods for terrestrial arthropods. In: "Methods of study in quantitative soil ecology", IBP Handbook No. 18 (Ed. Phillipson, J.), Ch. 10, pp. 150-185. Blackwell, London.
- El-Sebae, A.H. and Ahmed, Y.M. (1963). Factors affecting the efficiency of some organotin compounds against cotton leaf and bollworms. Zeitschrift fuer Angewandte Entomologie, 72(4), 367-376.
- Evans, C.J. (1971). Organotins against bilharzia. Tin and its Uses, 88, 7-10.
- Evans, G.O. (1955). The identification of terrestrial mites. In: "Soil Zoology", (Ed. Kevan, D.K. Mc.E.), pp. 55-61. Butterworths, London.
- Evans, G.O.; Sheals, J.G.; and Macfarlane, D. (1961). "The terrestrial Acari of the British Isles - an introduction to their morphology, biology and classification". Vol. 1. British Museum, London.
- Farbenind, I.G. (1930). Chemisches Zentralblatt. (Cited by Asher et al., 1964).
- Findlay, J.B. (1970). The use of antifeedants for the control of bollworm on cotton and diamond-back moth larvae on cabbage. Phytophylactica, 2(1), 57-58.
- Frankland, E. (1853). Ann. 85, 329. (Cited by Asher et al., 1964).
- Frankland, E. (1854). Journal of the Chemical Society, 6, 57. (Cited by Asher et al., 1964).
- Frick, L.P. and Jimenez, W. (1964). Molluscicidal qualities of three organotin compounds revealed by 6 hour and 24 hour exposures against representative stages and sizes of Australorbis glabratus. Bulletin of the World Health Organisation, 31, 429-432.

- Gardiner, B.G. and Poller, R.C. (1964). Insecticidal activity and structure of some organotin compounds. *Bulletin of Entomological Research*, 55, 17-21.
- Ghilarov, M.S. (1965). Some practical problems of soil zoology. *Pedobiologia*, 5, 189-204.
- Grahame-Bryce, I.J. and Briggs, G.G. (1970). Pollution of Soils. *R.I.C. Reviews*, 3(2), 87-104.
- Graves, J.B.; Bradley, J.R.; and Bagent, J.L. (1965). Laboratory evaluation of several organotin compounds against Heliothis sp. *Journal of Economic Entomology*, 58(3), 583-584.
- Harris, C.R. and Sans, W.W. (1972). Behaviour of heptachlor epoxide in soil. *Journal of Economic Entomology*, 65(2), 336-341.
- Hardon, H.J.; Bessemer, A.; and Brunick, H. (1962). Field trials with triphenyltin. *Deutsche Lebensmittel-Rundschau*, 58, 349-353.
- Hartel, K. (1958). Organic tin compounds as a crop fungicide. *Tin and its Uses*, 43, 9-14.
- Hays, S.B. (1968). Reproductive inhibition in house flies with triphenyltin acetate and triphenyltin chloride alone and in combination with other compounds. *Journal of Economic Entomology*, 61(5), 1154-1157.
- Herok, J. and Gotte, H. (1962). The radiometrical estimation of the distribution and excretion of triphenyltin acetate in ruminants. In: "The use of radioisotopes in animal biology and medical science", pp. 177-188. Academic Press, London.
- Herok, J. and Gotte, H. (1963). Radiometric investigations on the behaviour of TPTA in plants and animals. *International Journal of Applied Radiation and Isotopes*, 14, 461-479.
- Heugens, A. (1968). The influence of DBCP on the soil fauna in azalea culture. *Pedobiologia*, 8, 281-287.
- Hof, T. and Luijten, J.G. (1959). Organotin compounds as wood preservatives. *Timber Technology*, 67, 83-84.
- Hopf, H.S. and Muller, R.L. (1962). *Bulletin of the World Health Organisation*, 27, 783-789. (Cited by Evans, C.J., 1971).
- Huffaker, C.A. (1958). Experimental studies on predation: dispersion and predator-prey oscillations. *Hilgardia*, 27, 343-383.
- Hughes, T.E. (1959). "Mites or the Acari". University of London, Athlone Press, London.
- Hull, J.E. (1916). Terrestrial Acari of the Tyne Province. *Transactions of the Natural History Society of Northumberland*, 4, 381-409.

- Kaas-Sijpesteijn, A. (1959). Organotin compounds as potential agricultural fungicides. Mededelingen van de Landbouwhogeschool en de Opzoekingsstations van der Staat te Gent, 24, 850-856.
- Kaas-Sijpesteijn, A.; Luijten, J.G.; and Van der Kerk, G.J. (1971). Organometallic fungicides. In: "Fungicides", Vol. 2, (Ed. Torgeson, D.C.), Ch. 7, pp. 337-366. Academic Press, London.
- Karg, W. (1963). Die edaphischen Acarina in ihren Beziehungen zur Mikroflora und ihre Eignung als Anzeiger für Prozesse der Bodenbildung. In: "Soil Organisms", (Ed. Doekson, J. and Van der Drift, J.), pp. 305-315. North Holland Publishing Co., Amsterdam.
- Karg, W. (1964). Untersuchungen über die Wirkung von Dinitroorthokresol (DNOC) auf die Mikroarthropoden des Bodens unter Berücksichtigung der Beziehungen zwischen Mikroflora und Mesofauna. Pedobiologia, 4, 138-157.
- Karl, E. (1965). Untersuchungen zur Morphologie und Ökologie von Tarsonemiden gärtnerischer Kulturpflanzen, 2. Biologischer Zentralblatt. 84, 331-357.
- Kenega, E.E. (1965). Triphenyltin compounds as insect reproductive inhibitors. Journal of Economic Entomology, 58(1), 4-8.
- Kerk, Van der, G.J. (1970). Present trends and perspectives in organotin chemistry. Chemistry and Industry, May, 644-647.
- Kerk, Van der, G.J. and Luijten, J.G. (1954). Investigations on organotin compounds III. The biocidal properties of organotin compounds. Journal of Applied Chemistry, 4, 314-319.
- Kevan, D.K. McE. (Ed.) (1955). "Soil Zoology". Butterworths Scientific Publications, London.
- Kassim, J.B. and Hays, S.B. (1966). Mortality and fertility responses of Musca domestica adults to certain known mutagenic and anti-tumour agents. Journal of Economic Entomology, 59(3), 748-749.
- Kotchkin, D.A.; Vashkov, V.I.; and Dremova, V.P. (1964). Journal of General Chemistry, Moscow, 34, 325-328. (Cited by Asher et al., 1964).
- Ladd, T.L. (1968). Some effects of three triphenyltin compounds on the fertility of Japanese beetles. Journal of Economic Entomology, 61(2), 577-578.
- Lloyd, G.A.; Otaci, C.; and Last, F.T. (1962). Triphenyltin acetate residues on potato leaves in blight spraying trials. Journal of the Science of Food and Agriculture, 13(7), 353-358.
- Loots, G.C. and Ryke, P.A.J. (1967). The ratio Oribatidae : Trombidiformes with reference to the organic matter content in soils. Pedobiologia, 7, 121-124.

- Lowig, A. (1852). Ann. 84, 308. (Cited by Asher et al., 1964).
- Macfadyen, A. (1952). Soil arthropod sampling. In: "Advances in Ecological Research", (Ed. Cragg, J.B.), pp. 1-31. Academic Press, London.
- Macfadyen, A. (1952). The small arthropods of *Molinia fen* at Cothill. Journal of Animal Ecology, 21, 87-117.
- Madge, D.S. (1964). The humidity reactions of Oribatid mites. Acarologia, 6(3), 566-591.
- Mahunka, S. (1965). Identification key for the species and family Scutacaridae (Acari : Tarsonemini). Acta Zoologica Academiae Scientiarum Hungaricae, 11, 353-401.
- Mahunka, S. (1970). Consideration of the systematics of the Tarsonemidae and the description of them. Acta Zoologica Academiae Scientiarum Hungaricae, 16, 137-174.
- McCollister, D.D. and Schober, A.E. (1975). Assessing toxicological properties of organotin compounds. In: "Environmental quality and safety", Vol. 4, (Ed. Coulson, F. and Korte, F.), pp. 80-95. Academic Press, New York and London.
- Michael, A.D. (1883). "British Oribatidae". Ray Society, London.
- Ministry of Agriculture, Fisheries and Food (1973). Agricultural Chemicals Approval Scheme - approved products for farmers and growers.
- Murphy, P.W. (1962). Extraction methods for soil animals.
1. Dynamic methods with particular reference to funnel processes. In: "Progress in Soil Zoology", (Ed. Murphy, P.W.), pp. 75-114. Butterworths, London.
- Murphy, P.W. and Doncaster, C.C. (1957). A culture method for soil meiofauna and its application to the study of nematode predators. Nematologia, 2, 202-214.
- Newton, D.W. and Hays, R.L. (1968). Histological studies of ovaries in rats treated with hydroxyurea, TPTA and TPICL. Journal of Economic Entomology, 61, 1668-1669.
- Pieters, A.J. (1962). Triphenyltin hydroxide, a fungicide for the control of Phytophthora infestans on potatoes and some other fungus diseases. Proceedings of the British Insecticide and Fungicide Conference, 2, 461-470. Held November 1961. Association of British Manufacturers of Agricultural Chemicals, London.
- Poller, T.C. (1970). Biological effects and consequent applications. In: "The Chemistry of Organotin Compounds", pp. 271-285. Academic Press, London.
- Rack, G. (1965). Scutacaridae von Hamburg II. (Acari : Trombidiformes). Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins und Hamburg, 10, 97-112).



- Richards, O. W. and Waloff, N. (1954). Studies on the biology and population dynamics of British Grasshoppers. Bulletin 17, Anti Locust Research Centre, London. (Cited by Solomon, M.E., (1969) "Population Dynamics", Edward Arnold Ltd., London).
- Richle, D.E. (1977). The role of soil invertebrates in nutrient cycling. In: "Soil organisms as components of ecosystems", Ecological Bulletins, 25, pp. 145-156, (Ed. Lohm, U. and Persson, T.). Swedish Science Research Council, Stockholm.
- Riha, G. (1951). Zurokologie der oribatiden in Kalksteinboden. Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tieve., 80, 407-450. (Cited by Sheals, J.G., 1957).
- Rohde, C.J. (1956). A modification of the plaster charcoal method for the rearing of mites and other small arthropods. Ecology, 37, 843-844.
- Saba, F. (1971). A simple method for evaluating response to toxicants in mite populations. Journal of Economic Entomology, 64, 321.
- Salama, H.S. and Rasmy, A.H. (1970). Artificial feeding of mites and its use in screening acaricides. Zeitschrift fuer Angewandte Entomologie, 67, 31-33.
- Schaarschmidt, L. (1963). Tarsonemiden - Studien I. Zoologische Anzeiger, 170, 265-269.
- Scholz, T. (1965). Letter to the Editor: Chronic Toxicity Testing, Nature (London), 207, 870.
- Selwyn, M.J.; Stockdale, M.; and Dawson, A.P. (1970). Multiple effect of trialkyltin compounds on mitochondria. Biochemical Journal, 116, 15p - 16p. (Proceedings of the Biochemical Society).
- Sharaf, V.M. (1972). Eine neue Methode der Direktapplikation van Wirkstoffen an Milben im Rahmen der Pestizidprufig. Zeitschrift fuer Angewandte Entomologie, 70, 342-344.
- Sheals, J.G. (1955). The effects of D.D.T. and B.H.C. on soil Collembola and Acarina. In: "Soil Zoology", (Ed. Kevan, D.K. McE.), pp. 241-252. Butterworths Scientific Press, London.
- Sheals, J.G. (1956). Notes on a collection of soil Acari. Entomologists' Monthly Magazine, 92, 99-103.
- Sheals, J.G. (1957). The Collembola and Acarina of uncultivated soil. Journal of Animal Ecology, 26, 125-134.
- Sheppard, H.A. (Ed.) (1958). "Methods of testing chemicals on insects". Vol. 1. Burgess Publishing Company, Minneapolis.
- Snedecor, G.W. and Cochran, W.G. (1967). "Statistical Methods" (6th Ed.). Iowa State University Press, Ames.

ADDENDUM

- Kotchkin, D.A., Vashkov, V.I. and Dremova, V.P.(1964). Journal of General Chemistry, Moscow. 34, 325-328. (Cited by Asher et al., 1964).
- Miller, R.C. and McBride, Q.C. (1931). Journal of Economic Entomology, 26. (Cited by Asher et al., 1964).
- Snedecor, G.W. and Cochran, W.G. (1967). "Statistical Methods" (6th Ed.). Iowa State University Press, Ames.
- Torgeson, D.C. (Ed.) (1967). "Fungicides": Vol. 2. Academic Press, London.
- Wolfenburger, D.A.; Guerra, A.A. and Lowry, W.L. (1968). Effects of organometallic compounds on Lepidoptera. Journal of Economic Entomology 61 (1): 78-81.

- Southwood, T.R.E. (1966). "Ecological methods". Chapman and Hall, London.
- Springett, J.A. (1965). "An ecological study of moorland Enchytraeidae".
Unpublished Ph.D. thesis, University of Durham.
- Stammer, H.J. (1959). Beitrage zur systematik und okologie Mitteleuropadcher
Acarina. Band 1, Teil 2. Leipzig.
- Sternlight, M. (1966). Trials in the control of the citrus rust mite
(Acaria sheldoni) in Israel.
Israel Journal of Agricultural Research, 16(3), 115-124.
- Stockdale, M.; Dawson, A.; and Selwyn, M. (1970). Effects of trialkyltin and
triphenyltin compounds on mitochondrial respiration. European
Journal of Biochemistry, 15, 342-351.
- Stoner, H.B. (1966). Toxicity of triphenyltin. British Journal of
Industrial Medicine, 23, 222-229.
- Stoner, H.B. and Heath, D.F. (1967). The cumulative action of triphenyltin.
Food and Cosmetics Toxicology, 5, 285-286.
- Thomas, B. and Tann, H.C. (1971). Pesticide residues in foodstuffs in
Great Britain: XV Triphenyltin residues in potatoes.
Pesticide Science, 2(1), 45-47.
- Walker, W.F.; Boswell, A.L.; and Smith, F.F. (1973). Resistance of spider
mites to acaricides: comparison of slide dip and leaf dip methods.
Journal of Economic Entomology, 60(2), 549-550.
- Wallwork, J.A. (1967). Acari. In: "Soil Biology", (Ed. Burges, A. and Raw, F.),
Ch. 11, pp. 363-393. Academic Press, London.
- White, T.O. (1881). Pathologist, 13, 53-59. (Cited by Asher et al., 1964).
- White, T.O. (1886). Pharmaceutical Journal, 17, 166. (Cited by Asher et al.,
1964).
- Verschuuren, H.G.; Koes, R.; Vink, H.; Von Esch, G.J. (1966). Short term
toxicity studies with triphenyltin compounds in rats and guinea
pigs. Food and Cosmetics Toxicology, 4, 35-45.
- Voss, G. (1961). Ein neues Akariid-Austestungsverfahren fur spinnmilben.
Anzeiger fuer Schaedingskunde, XXXIV Jahrg (5), 76-77.

APPENDIX: 1,

The commercially available formulations (in 1977) of organotin fungicides containing triphenyltin hydroxide and triphenyltin acetate as active ingredients are as follows:-

TPTH preparations:

<u>Registered trade name</u>	<u>Manufacturer</u>
Croptex Fentin 20	Croptex.
* Duter	Cuphar Midox
Erithane 50	Bayer
Farmatin	Farm Protection.
L & K Fentin	Lindsey and Kesteven
Profarma Tinspray	Boots
Tubotin	May and Baker
Vitospar	Vitox

TPTA preparations (with Maneb):

* Brestan 60	Boots
Brestan 60	Hoechst
Maneb-Brestan	Hoechst
Mantin 45	Ciba-Geigy
Trimastan	Bos

* These preparations were the subject of this study.

APPENDIX: 2.

THE DENSITIES OF SOIL ACARINA IN CONTROL AND TREATED PLOTS EXPRESSED AS A MEDIAN VALUE PER SQUARE METRE AND THE TOTAL RANGE OF DENSITY RECORDED AMONGST SAMPLES ON EACH OCCASION.

SERIES A.

(i) Total Acarina.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
07.11.72	28192	7048 - 75766	29073	13215 - 49336
12.11.72	36121	16739 - 116292	28632	11453 - 98672
17.11.72	53741	19382 - 153294	37883	17620 - 94267
23.11.72	37002	13215 - 76647	21144	10572 - 43169
08.12.72	42728	15858 - 86338	30394	14977 - 60789
27.01.73	38764	14096 - 96910	16739	8810 - 49336

(ii) 'Other' Prostigmata.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
07.11.72	881	0 - 7929	881	0 - 13215
12.11.72	1762	881 - 7048	881	0 - 6167
17.11.72	4405	0 - 13215	1762	0 - 7929
23.11.72	2643	881 - 30835	2202	0 - 4405
08.12.72	3083	881 - 7929	1762	0 - 16739
27.01.73	1321	0 - 4405	881	0 - 23787

(iii) Mesostigmata.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
07.11.72	3524	0 - 7929	2202	0 - 6167
12.11.72	3964	881 - 9691	1762	0 - 7929
17.11.72	3524	0 - 10572	1762	0 - 7929
23.11.72	2643	0 - 8810	2643	0 - 8810
08.12.72	2643	0 - 7929	5286	881 - 16739
27.01.73	3083	881 - 5286	2643	0 - 12334

(iv) Tarsonemus floricolus.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
07.11.72	21584	3524 - 66073	24227	8810 - 66075
12.11.72	24668	12334 - 103077	24227	7929 - 92505
17.11.72	44490	10572 - 146246	28632	12334 - 88981
23.11.72	26870	7929 - 66075	15417	2643 - 29954
08.12.72	28192	12334 - 78409	20703	6167 - 50217
27.01.73	28192	8810 - 81933	9691	5286 - 26430

(v) Pygmephorus spp.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
07.11.72	1762	0 - 4405	0	0 - 2643
12.11.72	881	0 - 2643	440	0 - 6167
17.11.72	881	0 - 4405	881	0 - 4405
23.11.72	1762	0 - 4405	881	0 - 6167
08.12.72	2643	0 - 11453	1762	0 - 6167
27.01.73	2202	0 - 7929	1762	0 - 4405

SERIES B.(i) Total Acarina.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
20.02.73	24668	8810 - 86338	28192	13215 - 65194
06.03.73	37002	7048 - 51979	25989	8810 - 80171
21.03.73	28192	16739 - 55503	31716	11453 - 49336
04.04.73	29954	21144 - 40526	33037	20263 - 49336
28.04.73	32597	16739 - 74885	33918	8810 - 89862
22.05.73	25108	14977 - 59905	33478	22025 - 59908
29.06.73	18941	7929 - 34359	29073	14977 - 49336
27.07.73	9691	3524 - 47574	13215	6167 - 28192

(ii) 'Other' Prostigmata.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
20.02.73	440	0 - 7048	440	0 - 6167
06.03.73	881	0 - 5286	1762	0 - 6167
21.03.73	3524	0 - 9691	3964	0 - 10572
04.04.73	4405	881 - 8810	4845	1762 - 9691
28.04.73	13655	6167 - 36121	18501	3524 - 45812
22.05.73	9691	4405 - 17620	13655	9691 - 26430
29.06.73	2643	881 - 5286	2643	0 - 9691
26.07.73	2202	0 - 4405	3524	1762 - 14977

(iii) Mesostigmata.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
20.02.73	1762	0 - 7048	1762	0 - 7048
06.03.73	2643	0 - 4405	881	0 - 6167
21.03.73	2643	0 - 5286	3964	881 - 7929
04.04.73	2643	881 - 6167	2643	0 - 8810
28.04.73	3083	0 - 7048	2202	0 - 7048
22.05.73	3083	881 - 5286	2643	0 - 4405
29.06.73	4405	1762 - 8810	2643	881 - 10572
26.07.73	3524	1762 - 10572	3964	881 - 7048

(iv) Tarsonemus floricolus.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
20.02.73	17179	4405 - 79290	22906	7929 - 61670
06.03.73	31275	3524 - 46693	20263	5286 - 74004
21.03.73	17620	9691 - 29073	18941	8810 - 32597
04.04.73	16739	7929 - 29073	19822	7048 - 30835
28.04.73	6607	2643 - 29073	6607	1762 - 32597
22.05.73	6167	1762 - 10572	10131	4405 - 22906
29.06.73	1762	0 - 3524	1762	881 - 5286
26.07.73	0	0 - 881	0	0 - 1762

(v) Pygmaeophorus spp.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
20.02.73	1762	0 - 4405	881	0 - 6167
06.03.73	2202	0 - 7929	881	0 - 4405
21.03.73	3524	0 - 21144	1762	0 - 8810
04.04.73	4405	0 - 12334	3083	881 - 16739
28.04.73	4845	0 - 20263	4405	881 - 9691
22.05.73	4405	0 - 28192	4845	0 - 20263
29.06.73	8369	881 - 20263	19382	0 - 41407
26.07.73	1762	0 - 5286	3524	0 - 8810

SERIES C.(i) Total Acarina.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
03.03.73	26430	10572 - 59027	32597	14096 - 62551
17.03.73	30830	14096 - 111887	33918	15858 - 79290
31.03.73	30830	18501 - 59027	31275	18501 - 65194
25.04.73	29513	14977 - 59908	18941	14096 - 38764
17.05.73	36561	23787 - 135674	44931	30836 - 123340
25.06.73	11893	7048 - 21144	23787	10572 - 40526
23.07.73	9250	4405 - 18501	13215	4405 - 28192
21.08.73	7048	2643 - 13251	8810	3524 - 30835

(ii) 'Other' Prostigmata.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
03.03.73	1762	0 - 3524	1321	0 - 4405
17.03.73	1762	0 - 48455	3964	0 - 18501
31.03.73	7048	2643 - 13215	5726	3524 - 13215
25.04.73	11012	2643 - 22906	5286	1762 - 14096
17.05.73	14977	9691 - 59027	20263	11453 - 81933
25.06.73	2643	881 - 5286	7929	0 - 19382
23.07.73	2643	1762 - 3524	4405	881 - 18501
21.08.73	1762	0 - 8810	2643	0 - 7929

(iii) Mesostigmata.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
03.03.73	1762	0 - 7648	1762	0 - 7048
17.03.73	1762	0 - 11453	2643	0 - 7929
31.03.73	2643	0 - 7048	3524	1762 - 5286
25.04.73	2643	0 - 5286	2643	0 - 7048
17.05.73	3083	0 - 7929	2643	0 - 3524
25.06.73	2643	0 - 7048	1762	0 - 4405
23.07.73	3524	881 - 7048	2643	0 - 7048
21.08.73	2643	881 - 6167	2202	0 - 7929

(iv) Tarsonemus floricolus.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
03.03.73	18501	7929 - 40526	23787	9691 - 55503
17.03.73	19822	5286 - 64313	27311	7929 - 67837
31.03.73	15858	10572 - 33478	17179	7048 - 29954
25.04.73	7048	2643 - 22906	7929	4405 - 15858
17.05.73	14977	7048 - 23787	12334	4405 - 19382
25.06.73	881	0 - 3524	12334	2643 - 20263
23.07.73	0	0 - 1762	881	0 - 5286
21.08.73	0	0 - 1762	0	0 - 2643

(v) Pygmephorus spp.

Sampling Date	Control		Treated	
	Median	Range	Median	Range
03.03.73	1321	0 - 3524	1321	0 - 8810
17.03.73	2202	0 - 13215	1762	0 - 5286
31.03.73	2643	0 - 7929	3083	0 - 30835
25.04.73	2643	0 - 35240	2643	0 - 9691
17.05.73	4845	881 - 76647	8810	0 - 29954
25.06.73	3524	0 - 7929	5286	32524 - 20263
23.07.73	881	0 - 3524	1762	0 - 14096
21.08.73	881	0 - 3524	881	0 - 14977

SERIES D.(i) Total Acarina.

Sampling Date	Trial Designation	Median	Range
01.09.73	Control	7048	4405 - 10572
	D/1	7048	4405 - 21144
	D/2	11012	9691 - 16739
	D/3	8369	5286 - 12334
27.09.73	Control	13655	5286 - 22906
03.10.73	D/1	11453	5286 - 29073
	D/2	11453	5286 - 22906
	D/3	7929	3524 - 18501
06.11.73	Control	18060	5286 - 34359
	D/1	16739	6167 - 44050
	D/2	7048	1762 - 29073
	D/3	6167	2643 - 11453
05.12.73	Control	11893	3524 - 28192
08.12.73	D/1	14536	7048 - 37883
	D/2	6167	2643 - 18501
	D/3	4405	1762 - 12334
13.01.74	Control	12774	2643 - 21144
	D/1	7048	2643 - 58146
	D/2	6167	1762 - 25549
	D/3	6167	1762 - 13215

(ii) 'Other' Prostigmata.

Sampling Date	Trial Designation	Median	Range
01.09.73	Control	2202	881 - 6167
	D/1	1762	881 - 8810
	D/2	3524	881 - 7929
	D/3	3524	881 - 8810
27.09.73	Control	2643	881 - 6167
01.10.73	D/1	4845	1762 - 11453
	D/2	5286	881 - 7929
	D/3	3524	881 - 8810
06.11.73	Control	3524	881 - 11453
12.11.73	D/1	10131	3524 - 20263
	D/2	2643	0 - 12334
	D/3	2643	0 - 9691
05.12.73	Control	1762	0 - 3524
08.12.73	D/1	6607	1762 - 23787
	D/2	1762	881 - 6167
	D/3	1762	0 - 10572
13.01.74	Control	1762	0 - 8810
17.01.74	D/1	2202	0 - 7048
	D/2	1762	0 - 3524
	D/3	2202	0 - 7048

(iii) Mesostigmata.

Sampling Date	Trial Designation	Median	Range
01.09.73	Control	2202	881 - 2643
	D/1	3083	0 - 5286
	D/2	3083	881 - 7048
	D/3	2643	1762 - 4405
27.09.73	Control	3524	0 - 11453
03.10.73	D/1	2643	881 - 9691
	D/2	3524	881 - 10572
	D/3	2643	0 - 6167
06.11.73	Control	2643	0 - 8810
12.11.73	D/1	881	0 - 7048
	D/2	881	0 - 3524
	D/3	881	0 - 1702
05.12.73	Control	1762	0 - 4405
08.12.73	D/1	1321	0 - 4405
	D/2	881	0 - 3524
	D/3	0	0 - 1762
13.01.74	Control	1762	0 - 6167
	D/1	881	0 - 9691
	D/2	881	0 - 6167
	D/3	0	0 - 4405

(iv) Tarsonemus floricolus.

Sampling Date	Trial Designation	Median	Range
01.09.73	Control	881	0 - 2643
	D/1	881	0 - 7048
	D/2	881	0 - 3524
	D/3	1321	0 - 3524
27.09.73	Control	1762	0 - 7929
03.10.73	D/1	440	0 - 2643
	D/2	881	0 - 3524
	D/3	0	0 - 3524
06.11.73	Control	4845	881 - 16739
12.11.73	D/1	1321	0 - 12334
	D/2	0	0 - 1762
	D/3		0 - 881
05.12.73	Control	1762	0 - 7929
08.12.73	D/1	1321	0 - 6167
	D/2	0	0 - 881
	D/3	0	0 - 881
13.01.74	Control	2643	0 - 7929
17.01.74	D/1	881	0 - 3524
	D/2	0	0 - 4405
	D/3	0	0 - 1762

(v) Pygmephorus spp.

Sampling Date	Trial Designation	Medium	Range
01.09.73	Control	0	0 - 1762
	D/1	0	0 - 6167
	D/2	881	0 - 4405
	D/3	440	0 - 4405
27.09.73	Control	881	0 - 5286
03.10.73	D/1	881	0 - 15858
	D/2	0	0 - 3524
	D/3	440	0 - 3524
06.11.73	Control	440	0 - 21144
12.11.73	D/1	1762	0 - 8810
	D/2	881	0 - 10572
	D/3	440	0 - 5286
05.12.73	Control	881	0 - 9691
08.12.73	D/1	1762	0 - 4405
	D/2	881	0 - 11453
	D/3	881	0 - 881
13.01.74	Control	881	0 - 5286
17.01.74	D/1	1762	0 - 36121
	D/2	881	0 - 7929
	D/3	440	0 - 5286

(vi) Scutacarus (Variatipes) montanus.

Sampling Date	Trial Designation	Median	Range
01.09.73	Control	0	0 - 2643
	D/1	0	0 - 881
	D/2	0	0 - 5286
	D/3	0	0 - 2643
27.09.73	Control	881	0 - 10572
03.10.73	D/1	0	0 - 2643
	D/2	881	0 - 4405
	D/3	0	0 - 5286
06.11.73	Control	0	0 - 24668
12.11.73	D/1	881	0 - 18501
	D/2	0	0 - 9571
	D/3	0	0 - 5286
05.12.73	Control	1321	0 - 22906
08.12.73	D/1	881	0 - 23787
	D/2	0	0 - 5286
	D/3	0	0 - 4405
13.01.74	Control	0	0 - 7048
17.01.74	D/1	440	0 - 6167
	D/2	0	0 - 10572
	D/3	0	0 - 6167

SERIES E.(i) Total Acarina.

Sampling Date	Trial Designation	Median	Range
11.09.73	Control	13215	8810 - 19382
	E/1	12334	7929 - 23787
	E/2	14096	7929 - 18501
	E/3	8810	5286 - 25549
09.10.73	Control	10572	3524 - 34359
15.10.73	E/1	6607	2643 - 15858
	E/2	9691	3524 - 22906
	E/3	9250	4405 - 20263
16.11.73	Control	12774	5286 - 44931
19.11.73	E/1	11893	3524 - 29073
	E/2	8810	3524 - 17620
	E/3	12334	3524 - 33478
11.12.73	Control	8369	6167 - 20263
	E/1	6607	2643 - 20263
	E/2	2643	881 - 8810
	E/3	9191	1761 - 35240
21.01.74	Control	10572	5286 - 23787
24.01.74	E/1	8810	4405 - 51979
	E/2	5726	3524 - 21144
	E/3	8810	2643 - 27511

(ii) 'Other' Prostigmata.

Sampling Date	Trial Designation	Median	Range
11.09.73	Control	4405	881 - 11453
	E/1	4405	1762 - 6167
	E/2	3964	1762 - 5286
	E/3	881	0 - 6167
09.10.73	Control	3083	0 - 7929
15.10.73	E/1	1762	881 - 7929
	E/2	3524	1762 - 7048
	E/3	5286	1762 - 8810
16.11.73	Control	1762	0 - 22025
19.11.73	E/1	3964	881 - 17215
	E/2	2643	0 - 7048
	E/3	6167	1762 - 21144
11.12.73	Control	1762	0 - 10572
14.12.73	E/1	2643	0 - 7048
	E/2	440	0 - 1762
	E/3	2643	881 - 7048
21.01.74	Control	1762	0 - 5286
24.01.74	E/1	3524	881 - 10572
	E/2	2202	0 - 4405
	E/3	4845	881 - 14977

(iii) Mesostigmata,

Sampling Date	Trial Designation	Median	Range
11.09.73	Control	2643	881 - 5286
	E/1	3083	881 - 4405
	E/2	4405	2643 - 6167
	E/3	3524	881 - 8810
09.10.73	Control	3083	0 - 11453
15.10.73	E/1	1762	0 - 6167
	E/2	2643	0 - 8810
	E/3	1762	881 - 10572
16.11.73	Control	3083	881 - 7929
19.11.73	E/1	440	0 - 3524
	E/2	881	0 - 6167
	E/3	1762	0 - 4405
11.12.73	Control	1762	0 - 7929
14.12.73	E/1	881	0 - 3524
	E/2	881	0 - 3524
	E/3	881	0 - 4405
21.01.74	Control	2202	881 - 7929
24.01.74	E/1	881	0 - 4405
	E/2	881	0 - 4405
	E/3	881	0 - 2643

(iv) Tarsonemus floricolus.

Sampling Date	Trial Designation	Median	Range
11.09.73	Control	3524	881 - 7929
	E/1	3083	1762 - 7048
	E/2	3524	1762 - 7048
	E/3	2202	0 - 4405
09.10.73	Control	1321	0 - 10572
15.10.73	E/1	0	0 - 1762
	E/2	881	0 - 4405
	E/3	881	0 - 6067
16.11.73	Control	2643	0 - 8810
19.11.73	E/1	0	0 - 881
	E/2	0	0 - 881
	E/3	881	0 - 9691
11.12.73	Control	1762	
14.12.73	E/1	0	
	E/2	0	
	E/3	440	
21.01.74	Control	2643	0 - 5286
24.01.74	E/1	0	0 - 1762
	E/2	0	0 - 881
	E/3	881	0 - 7929

(v) Pygmephorus spp.

Sampling Date	Trial Designation	Median	Range
11.09.73	Control	0	0 - 881
	E/1	0	0 - 10572
	E/2	440	0 - 5286
	E/3	0	0 - 5286
09.10.73	Control	440	0 - 3524
15.10.73	E/1	881	0 - 6167
	E/2	0	0 - 7048
	E/3	881	0 - 1762
16.11.73	Control	0	0 - 23787
19.11.73	E/1	881	0 - 5286
	E/2	1762	0 - 9691
	E/3	881	0 - 5286
11.12.73	Control	881	0 - 3524
14.12.73	E/1	881	0 - 4405
	E/2	881	0 - 1762
	E/3	881	0 - 6167
21.01.74	Control	881	0 - 7929
24.01.74	E/1	881	0 - 11543
	E/2	881	0 - 1762
	E/3	881	0 - 3524

(vi) Scutacarus (Variatipes) montanus.

Sampling Date	Trial Designation	Median	Range
11.09.73	Control	440	0 - 3524
	E/1	440	0 - 881
	E/2	0	0 - 1762
	E/3	440	0 - 2643
09.10.73	Control	440	0 - 19382
15.10.73	E/1	440	0 - 2643
	E/2	881	0 - 2643
	E/3	881	0 - 2643
16.11.73	Control	881	0 - 9691
19.11.73	E/1	0	0 - 7929
	E/2	881	0 - 7929
	E/3	440	0 - 7929
11.12.73	Control	881	0 - 3524
14.12.73	E/1	440	0 - 12334
	E/2	440	0 - 5286
	E/3	881	0 - 26430
21.01.74	Control	1762	0 - 8810
24.01.74	E/1	1762	0 - 41407
	E/2	881	0 - 14096
	E/3	1321	0 - 12334

APPENDIX : 3.

TOXICOLOGICAL TESTING USING MITES IN CULTURE - AN ASSESSMENT OF SUITABLE METHODS.

Although an acceptable standard of culturing was achieved, the time available was insufficient for meaningful toxicological experiments to be undertaken. This situation was aggravated by the developing shortage of T. floricolus within the sampling areas towards the end of my study. Below, a brief outline of the proposed experimental programme is given, along with the reason for its choice and some attendant problems.

The economic importance of insects and also of mites as agricultural pests has generated a vast number of toxicological screening tests. Since a review of toxicological test methods by Sheppard (1958), there have been a number of refinements, some quite elaborate, but basic techniques have remained the same.

With respect to mites, the slide dip method, first described by Voss (1961), is the most widely used method, although some modifications have been developed: the alternative cage spray and loaf dip methods provide roughly comparable results (Dritsch, 1962, and Walker et al., 1973). These techniques were developed to evaluate the effectiveness of potential acaricides for use primarily against phytoparasitic and phytophagous species, and aim to reproduce their field use conditions in the laboratory. They are not directly applicable for determining toxicity to soil mites. Two deficiencies common to these methods are:

(i) They make no distinction between toxicity caused by ingestion and by contact with the active ingredient. Generally, there is no need to distinguish these two sources of mortality for external plant mites; it is sufficient to establish that mortality does occur. However, in the present case, the importance of contact toxicity in the field situation is probably small in that TPT's are rapidly adsorbed on to soil particles (Barnes, 1971), and also it is suspected that saturation of high concentrations is required (Bullock and Johnston, 1968). The important feature is the quantity ingested, as suggested by antifeedant

studies on insects, for example El Sebae (1973). Only with the larger species of free living mites, and more particularly with insects, are suitable micro-application techniques available whereby a precise quantity of toxicant may be administered orally or at least to the mouthparts (Sharaf, 1972).

(ii) TPT's have a low solubility in water and are sprayed as suspensions. With dipping or spray methods it seems likely that no meaningful relationship would be obtained with the quantity in suspension. Solvents such as acetone are widely used in standard screening tests to overcome similar problems, but for TPT's effective solvents, such as dimethylformamide, are excessively toxic of themselves and cannot be used.

It must be concluded that at present no method exists by which individual mites of this size can be given directly, and solely by ingestion, a known quantity of TPT. No meaningful LD50 value can, therefore, be produced by standard methods.

In the present situation, therefore, the aim should be to determine the extent of mortality, if occurring at all, when mites are forced to feed on food contaminated with TPT's at levels which are assumed to be similar to those occurring in soil. Unfortunately, the inability to adequately remove TPT adsorbed to soil particles necessitates a very approximate assumption of equivalents in this respect.

The principal problems of the technique relate to the means by which the food is contaminated. While the use of a reasonably natural, fungal food makes the laboratory test more similar to the field situation, the food will itself be affected adversely by the fungicide, thereby tending to induce the effect of "indirect" toxicity. To exclude this, it would be necessary to maintain the quality of food available. This would not be a problem if an artificial food medium were found, and substitute food materials are now used frequently for the evaluation of acaricides against Tetranychus sp. (O. Prostigmata) as outlined by Salama et al. (1970).

Assuming the pleurococcus food is used, it would be necessary to replenish the cultures with freshly contaminated food, a process which would remove any feature of progressive degradation of the active fungicide as occurs in the field situation. A reduction in the level of TPT treatment, appropriate to the degradation of fungicide might be made to successive replacement pleurococcus fragments in a further attempt to recreate the field situation more exactly.

The contamination of incubated pleurococcus fragments, that is where the hyphal growth is well established, might be achieved either by dipping in a suspension of the fungicide or by spraying with a quantity equivalent to that received by the surface soil layer in the field situation. The latter appears preferable, not only in being more nearly equivalent to administration in the field, but in that it would also reduce matting and collapse of the hyphae (which might further reduce its attractiveness for feeding to T. floricolus).

The following experimental programme would, therefore, be adopted to determine the presence or absence of a direct toxicity of TPT's to T. floricolus. (It must be assumed that the levels of fungicide on the food in culture are similar to levels on the food within the treated plots of the field trials).

- (i) Contamination of the incubated pleurococcus by a microspray dispenser using a range of treatment levels spanning, but not necessarily identical to, the range used in field trials.
- (ii) Preliminary testing of the treated food alone, in a micro-immersion filter system, to determine the rate of breakdown of the fungal mycelia and, therefore, the rate at which replacement is necessary at various levels of treatment so as to maintain the quality of food.
- (iii) Setting up perhaps two treatment series using 16 or more replicate cells. Each cell would contain 6 - 8 T. floricolus plus the appropriate quantity of food material as determined by preliminary culturing. All mites would be obtained from established cultures rather than directly from samples;

they may, therefore, be presumed healthy and acclimatised to the food and environments of the culture system. For this purpose, the perspex block system would be appropriate. The number of mites alive and their general condition and behaviour would be checked at least once weekly.

- (iv) For each series of replicates using the perspex block system, additional replicates would be made in the micro-immersion system for the purpose of more detailed daily observation of behaviour, for example, any developing tendency to leave an apparently adequate food supply. This would provide an additional check on any rapid deterioration in the food quality.
- (v) Each series would be maintained until appreciable mortality was evident or, if no mortality occurred, until the period at which, in field trials, the maximum fall in numbers was observed.

The above programme merely outlines the approach which was anticipated initially. No doubt a number of modifications would have been developed and certain aspects of the investigations extended. For example, where a clear behavioural change was seen, perhaps a refusal to eat the treated food, indicating the possibility of "indirect toxicity" by way of emigration from treated areas in the field rather than actual mortality, a series of preference tests might be employed to assess discrimination between treated and untreated food material, as used by Madge (1964) to determine the humidity reactions of Oribatid mites.

APPENDIX : 4.

CHANGES IN THE POPULATION LEVELS OF SOIL MITES IN THE STUDY AREA AT DURHAM.

On the following pages are tabulated the mean numbers of soil Acarina/
sample ⁺ one standard error, obtained from collections within control plots of
successive trial series and from the small number of additional collections
made after the completion of field trials.

The date of sampling and the trial series are indicated for each set of
records; the additional records are marked thus: a

The number of samples contributing to each mean is 16.

Sampling Date	Series	Total Prostigmata	Other Prostigmata	Mesostigmata	Tarsonemus floricolus	Scutacarus (V) montanus	Pygmephorus spp.	Total Acarina
07.11.72	A	33.11 [±] 5.36	2.59 [±] 0.38	3.75 [±] 0.59	29.30 [±] 5.14	-	1.81 [±] 0.43	37.43 [±] 5.47
12.11.72	A	41.74 [±] 6.79	2.94 [±] 0.48	4.81 [±] 0.74	37.68 [±] 6.69	-	1.13 [±] 0.25	46.93 [±] 7.10
17.11.72	A	61.86 [±] 9.72	6.37 [±] 1.01	4.00 [±] 0.79	54.12 [±] 9.33	-	1.37 [±] 0.31	65.93 [±] 9.60
23.11.72	A	41.13 [±] 5.35	6.09 [±] 2.12	3.69 [±] 0.76	32.61 [±] 4.5	-	2.37 [±] 0.46	45.00 [±] 5.69
08.12.72	A	44.00 [±] 5.62	4.43 [±] 0.82	3.75 [±] 0.61	35.75 [±] 5.22	-	3.81 [±] 1.00	48.31 [±] 5.65
27.01.73	A	46.06 [±] 6.18	2.37 [±] 0.43	3.18 [±] 0.43	40.31 [±] 5.7	-	3.37 [±] 0.72	49.5 [±] 6.46
20.02.73	B	30.61 [±] 5.88	1.24 [±] 0.52	2.51 [±] 0.63	27.45 [±] 5.65	-	2.00 [±] 0.35	33.18 [±] 5.63
03.03.73	C	32.22 [±] 3.40	3.03 [±] 0.32	2.56 [±] 0.63	27.82 [±] 3.0	-	1.37 [±] 0.33	28.81 [±] 2.7
06.03.73	B	35.99 [±] 3.58	1.62 [±] 0.36	2.63 [±] 0.38	31.25 [±] 3.72	-	3.12 [±] 0.63	38.81 [±] 3.76
17.03.73	C	37.19 [±] 6.51	4.68 [±] 0.58	3.19 [±] 0.86	28.20 [±] 5.10	-	4.31 [±] 1.12	43.68 [±] 7.26
21.03.73	B	31.04 [±] 3.08	6.16 [±] 0.70	3.12 [±] 0.42	19.70 [±] 1.54	-	5.18 [±] 1.44	34.31 [±] 3.23
31.03.73	C	32.99 [±] 2.66	8.79 [±] 0.99	3.46 [±] 0.66	19.66 [±] 1.89	-	4.50 [±] 0.68	36.33 [±] 2.93
04.04.73	B	29.69 [±] 1.79	6.23 [±] 0.66	3.53 [±] 0.48	18.13 [±] 1.59	-	5.33 [±] 0.93	33.40 [±] 1.65
25.04.73	C	32.16 [±] 3.86	15.35 [±] 1.66	2.68 [±] 0.42	9.50 [±] 1.46	-	7.31 [±] 2.99	35.56 [±] 4.06
28.04.73	B	36.21 [±] 4.29	19.81 [±] 2.5	3.50 [±] 0.7	9.37 [±] 1.95	-	7.00 [±] 1.36	39.87 [±] 4.12
17.05.73	C	50.8 [±] 8.03	23.12 [±] 1.78	3.68 [±] 0.56	16.00 [±] 1.53	-	11.68 [±] 5.33	54.69 [±] 8.18
22.05.73	B	27.31 [±] 3.61	12.44 [±] 1.14	3.51 [±] 0.37	6.93 [±] 0.80	-	7.94 [±] 2.43	30.87 [±] 3.72
25.06.73	C	10.21 [±] 0.93	4.45 [±] 0.38	3.37 [±] 0.57	1.68 [±] 0.27	-	4.06 [±] 0.54	13.56 [±] 1.03
29.06.73	B	17.9 [±] 2.10	4.75 [±] 0.38	5.25 [±] 0.50	1.87 [±] 0.27	-	11.25 [±] 1.66	23.25 [±] 2.28

Sampling Date	Series	Total Prostigmata	Other Prostigmata	Mesostigmata	Tarsonemus floricolus	Scutacarus (V) montanus	Pygmephorus spp.	Total Acarina
23.07.73	C	5.92 ⁺ 0.88	4.12 ⁺ 0.23	4.25 ⁺ 0.48	0.37 ⁺ 0.15	-	1.43 ⁺ 0.32	10.56 ⁺ 0.95
26.07.73	B	8.36 ⁺ 2.33	5.74 ⁺ 0.62	4.37 ⁺ 0.61	0.31 ⁺ 0.12	-	2.31 ⁺ 0.49	12.8 ⁺ 1.12
21.08.73	C	4.13 ⁺ 0.68	2.88 ⁺ 0.28	3.30 ⁺ 0.34	0.38 ⁺ 0.12	-	0.87 ⁺ 0.25	8.06 ⁺ 0.89
01.09.73	D	5.24 ⁺ 0.82	2.87 ⁺ 0.64	1.87 ⁺ 0.23	1.12 ⁺ 0.39	0.63 ⁺ 0.37	0.62 ⁺ 0.26	7.75 ⁺ 0.77
11.09.73	E	11.25 ⁺ 1.29	5.62 ⁺ 1.38	3.25 ⁺ 0.59	4.37 ⁺ 0.98	1.00 ⁺ 0.50	0.26 ⁺ 0.06	15.13 ⁺ 1.47
27.09.73	D	10.24 ⁺ 1.43	3.56 ⁺ 0.42	5.06 ⁺ 0.87	2.50 ⁺ 0.56	3.12 ⁺ 1.05	1.06 ⁺ 0.39	15.60 ⁺ 1.53
09.10.73	E	9.34 ⁺ 1.76	3.44 ⁺ 0.71	4.06 ⁺ 0.77	2.68 ⁺ 0.74	2.18 ⁺ 1.35	1.06 ⁺ 0.34	14.15 ⁺ 2.27
06.11.73	D	15.17 ⁺ 2.00	4.37 ⁺ 0.83	3.62 ⁺ 0.64	6.06 ⁺ 1.15	2.68 ⁺ 1.73	2.06 ⁺ 1.47	20.07 ⁺ 2.28
16.11.73	E	12.86 ⁺ 2.86	4.62 ⁺ 1.57	4.12 ⁺ 0.51	3.93 ⁺ 0.87	1.81 ⁺ 0.76	2.50 ⁺ 1.66	17.94 ⁺ 2.80
05.12.73	D	13.61 ⁺ 2.29	1.68 ⁺ 0.29	2.31 ⁺ 0.38	2.87 ⁺ 0.58	6.31 ⁺ 2.21	2.75 ⁺ 1.01	16.56 ⁺ 2.34
11.12.73	E	7.61 ⁺ 1.10	2.81 ⁺ 0.75	2.62 ⁺ 0.46	2.31 ⁺ 0.48	1.12 ⁺ 0.30	1.37 ⁺ 0.31	11.37 ⁺ 1.09
13.01.74	D	10.42 ⁺ 1.42	2.62 ⁺ 0.64	2.62 ⁺ 0.57	4.06 ⁺ 0.78	1.56 ⁺ 0.63	2.18 ⁺ 0.62	14.25 ⁺ 1.33
21.01.74	E	9.52 ⁺ 1.47	2.40 ⁺ 0.48	3.4 ⁺ 0.68	3.06 ⁺ 0.47	2.53 ⁺ 0.86	1.53 ⁺ 0.57	13.66 ⁺ 1.77
a 28.01.74	X	10.24 ⁺ 1.75	1.92 ⁺ 0.34	2.42 ⁺ 0.37	0.91 ⁺ 0.31	3.66 ⁺ 1.19	3.75 ⁺ 1.43	13.75 ⁺ 3.01
a 28.02.74	X	11.15 ⁺ 2.42	3.9 ⁺ 0.62	3.15 ⁺ 0.46	0.40 ⁺ 0.13	3.30 ⁺ 0.67	3.55 ⁺ 1.34	15.65 ⁺ 1.65
a 25.03.74	X	15.86 ⁺ 1.83	2.0 ⁺ 0.39	4.00 ⁺ 0.64	1.18 ⁺ 0.27	8.62 ⁺ 2.75	4.06 ⁺ 1.39	19.04 ⁺ 2.14
a 25.05.74	X	21.88 ⁺ 2.81	7.67 ⁺ 1.29	3.87 ⁺ 0.62	1.25 ⁺ 0.49	7.12 ⁺ 1.21	5.75 ⁺ 2.62	26.94 ⁺ 2.83
a 28.06.74	X	37.48 ⁺ 4.07	15.42 ⁺ 2.05	9.00 ⁺ 1.17	2.21 ⁺ 0.39	4.50 ⁺ 1.36	15.35 ⁺ 2.87	49.60 ⁺ 3.88
a 20.08.74	X	14.40 ⁺ 1.43	2.93 ⁺ 0.57	10.14 ⁺ 1.07	0.43 ⁺ 0.17	10.10 ⁺ 2.65	0.93 ⁺ 0.26	25.93 ⁺ 2.95

PART 2.

THE EFFECTS OF RECLAMATION OF INTERTIDAL
LAND ON OVERWINTERING WADERS AND SHELDUCKS
AT SEAL SANDS, TEESMOUTH.

INTRODUCTION

In 1970 the Tees and Hartlepool Port Authority embarked on a three stage reclamation programme which, when completed, would have eliminated almost all the remaining areas of intertidal mudflats on the north side of the mouth of the River Tees, Co. Cleveland ($54^{\circ}37'N$, $1^{\circ}12'W$), along with associated areas of sand dunes and fresh water marsh.

Concern over the possible loss of Teesmouth as an important feeding site for overwintering waterfowl led to a research programme to monitor the effects on the fauna of 'Stage I' of this reclamation and to determine the carrying capacity for birds of the remaining portion of Seal Sands (Fig. 1). This study, the first of its kind in Britain, was based at Durham University under the supervision of Dr. P. R. Evans. The first phase was carried out between 1970 and 1973; a second phase is still in progress. From 1971 onwards, additional surveys of the invertebrate fauna of the estuary in relation to pollution of the River Tees have been made from time to time by the Leeds Wellcome Marine Research Laboratory (Gray, 1976, and pers. comm.).

The conclusions of the first phase of the Durham study, including prediction as to the value to shorebirds of the remaining mudflats, if not engulfed by Stages II and III of the reclamation programme (Evans, 1973) led to an

expansion of the study, with the aid of funds from the Natural Environment Research Council, Coastal Ecology Research Station (C.E.R.S.), during the winter of 1972/73 (Pienkowski, 1973). My study, conducted between October 1973 and December 1974 and funded partly by the C.E.R.S. and also by the Royal Society for the Protection of Birds (R.S.P.B.), continued and enlarged upon Pienkowski's work. Since adequate monitoring of invertebrate densities was undertaken by other workers during this period, my studies concentrated on the changes in numbers and behaviour of estuarine birds in relation to the reclamation.

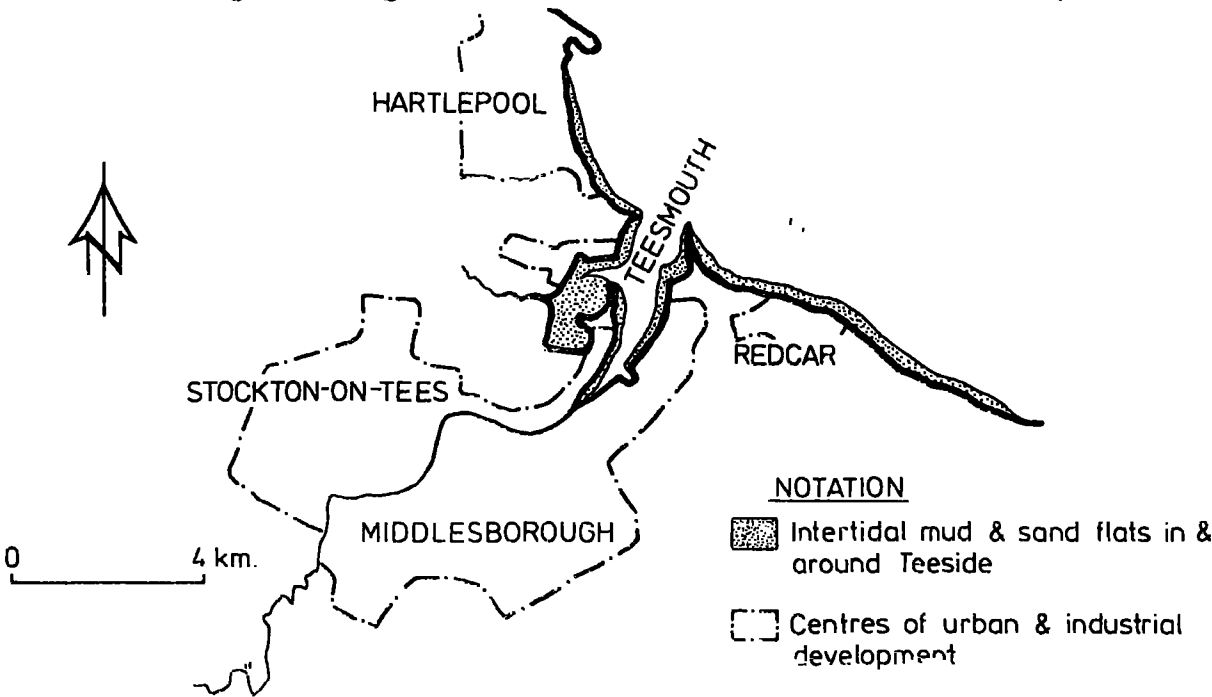
The aim of my work was to test the predictions of changes in 'carrying capacity' made by Evans (1970) and to identify any ways in which the birds' original feeding strategies (outlined by Pienkowski, 1973) changed after completion of Stage I of the reclamation, thereby testing other predictions made by Goss-Custard (1972). My work at Teesmouth was summarized in two unpublished reports to the C.E.R.S. in 1974 and 1975, and part in a report to the R.S.P.B. (Evans, 1975).

At the present time, reclamation of the remaining areas of mudflats is in abeyance, being examined with a view to their retention, along with associated areas, under the Teeside Structure Plan (Newell, 1974; Nature Conservancy Council, 1972). With the aim of contributing further support for this possibility by monitoring further changes in the numbers and behaviour of shorebirds a number of studies continue at Durham University.

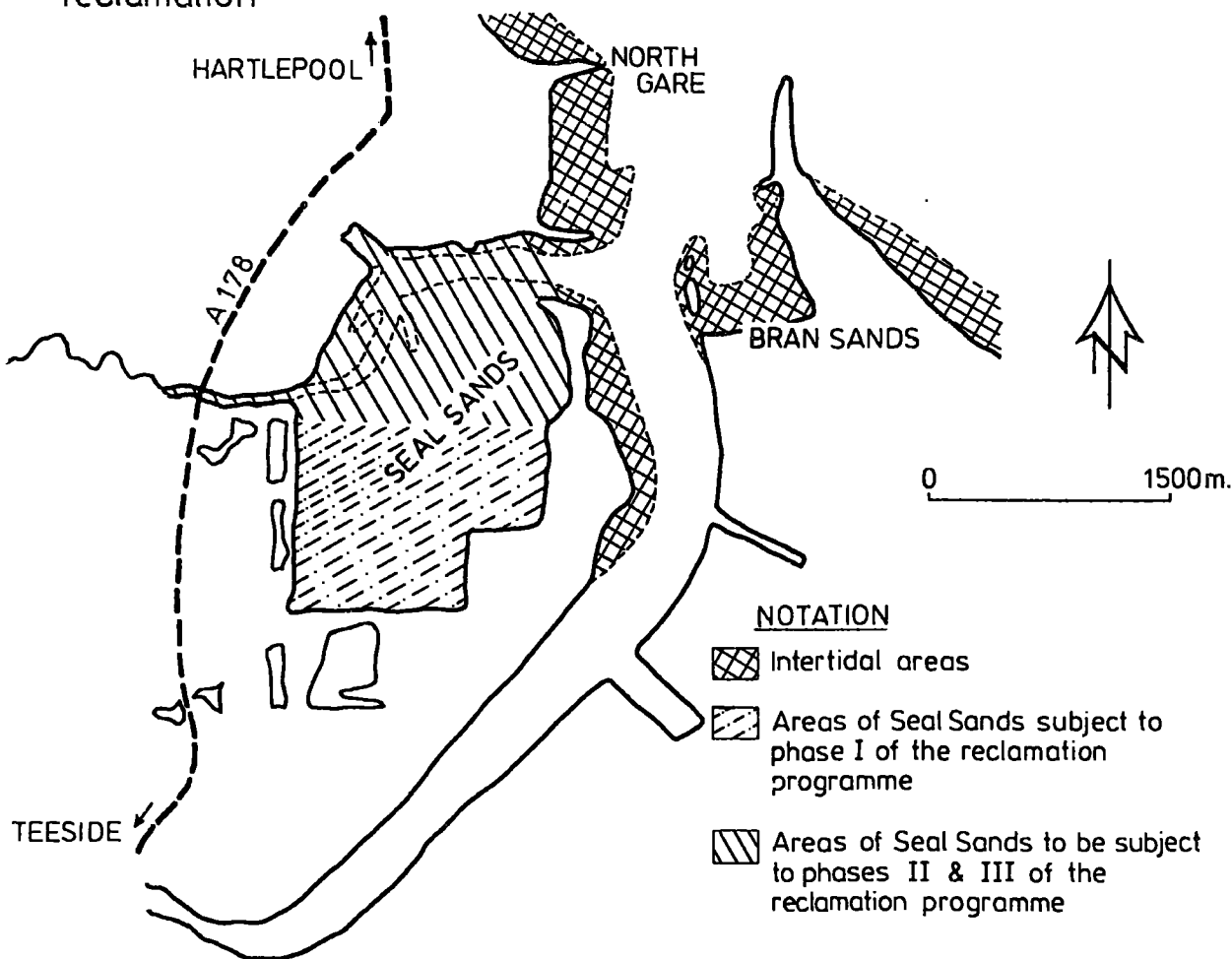
The reclamation programme for Seal Sands was examined by the Department of the Environment in June 1975 as part of the Co. Cleveland Structure Plan.

Figure 1

A. The location of intertidal sand & mudflats at Teesmouth in relation to the neighbouring centres of urban & industrial development in '73



B. The areas of Seal Sands which have been or are scheduled for reclamation



THE RECLAMATION OF THE TEES ESTUARY

The past and present reclamation of the Tees estuary illustrates well the fate of many estuarine environments around the coast of Britain. In 1840 the Tees estuary contained some 6,000 acres (2,430 ha.) of intertidal sand, mudflats and saltmarsh. Subsequent reclamation reduced intertidal areas on the north side of the estuary to around 650 acres (263 ha.) at the beginning of my study in October 1973. Despite this, Teesmouth remains of international importance as an overwintering ground for Shelduck (*Tadorna tadorna*), since it holds more than 1% of the European population (Ramsar Convention, 1975). In terms of total numbers of waders and wildfowl, it ranked fifteenth amongst British estuaries in 1971 (Prater, 1972).

THE HISTORY OF RECLAMATION AT TEESMOUTH.

The extent and pattern of reclamation at Teesmouth is illustrated by a short series of maps (Figs. 2 - 4). Fig. 2(A) is a simplification of the Ordnance Survey (1st edition) series of 1840. At this time industrial development was centred on Middlesborough and Stockton, more than four miles upstream from Teesmouth.

Before this date and primarily in the late 18th Century, reclamation for agriculture had occurred by the enclosure of the higher areas of saltmarsh with earth banks. Cowpen Marsh to the north of the estuary and Coatham Marsh to the south represent relics of this type of reclamation, which typically created areas of rough grazing divided by fresh water dykes, fleets and occasional pools. Cowpen Marsh, particularly, retains this original form, although some better-drained areas have been improved and ploughed, and some areas used for industrial waste disposal. The A178 road between Port Clarence and Seaton Carew and the Middlesborough - Redcar railway closely follow the northern and southern late 18th Century boundaries of the estuary at this time.

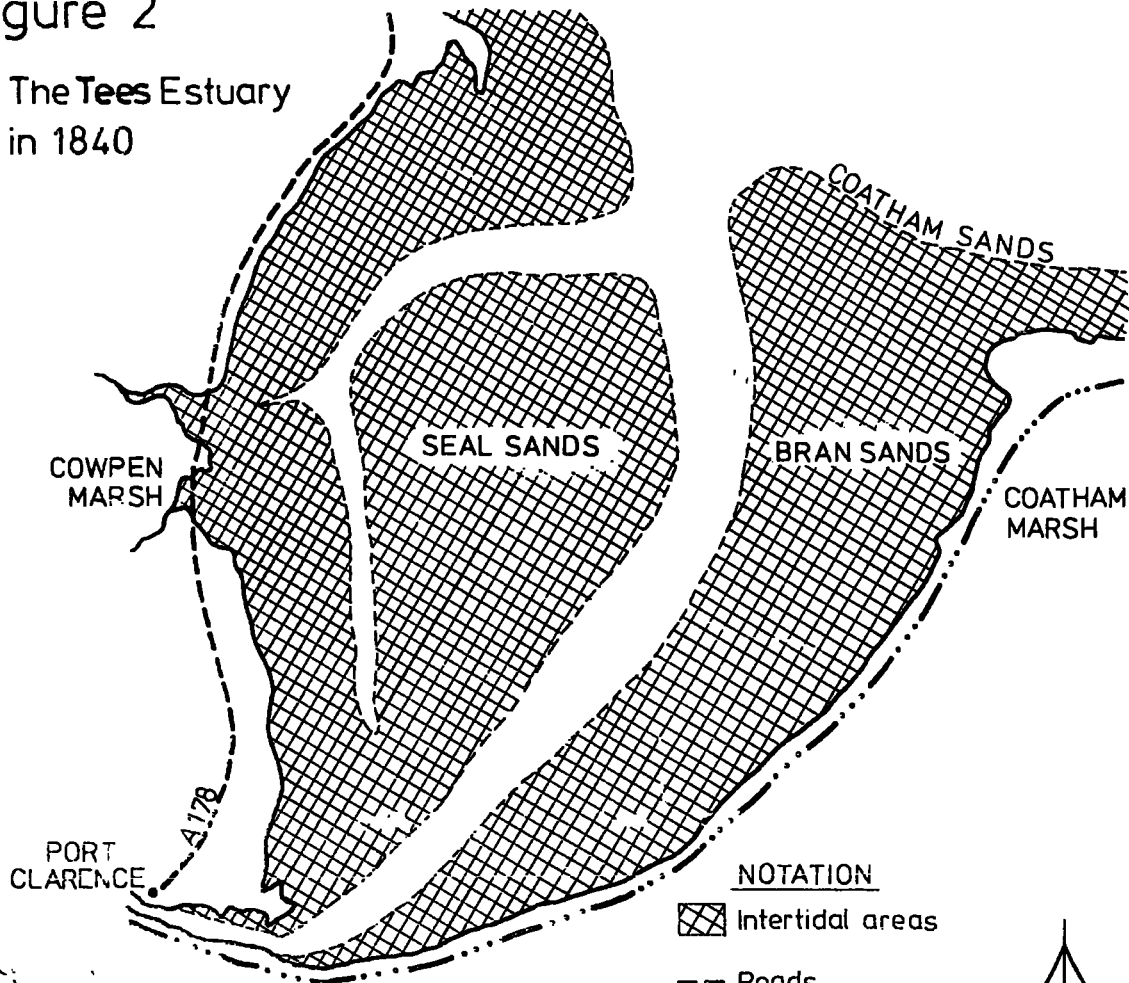
In the mid 19th Century the estuary was approximately pear shaped with only narrow intertidal areas upstream of Port Clarence. The main channel of the river separated two large intertidal areas: Seal Sands to the north and west, and Bran Sands to the south and east. A subsidiary channel flowed past the western edge of Seal Sands and separated it from a wide sandy beach, Seaton Sands, which extended northwards along the coast from the mouth of the estuary. Bran Sands was contiguous with a similar beach, Coatham Sands, extending southwards to Redcar.

(a) Reclamation 1840 - 1930. (Fig. 2(B)).

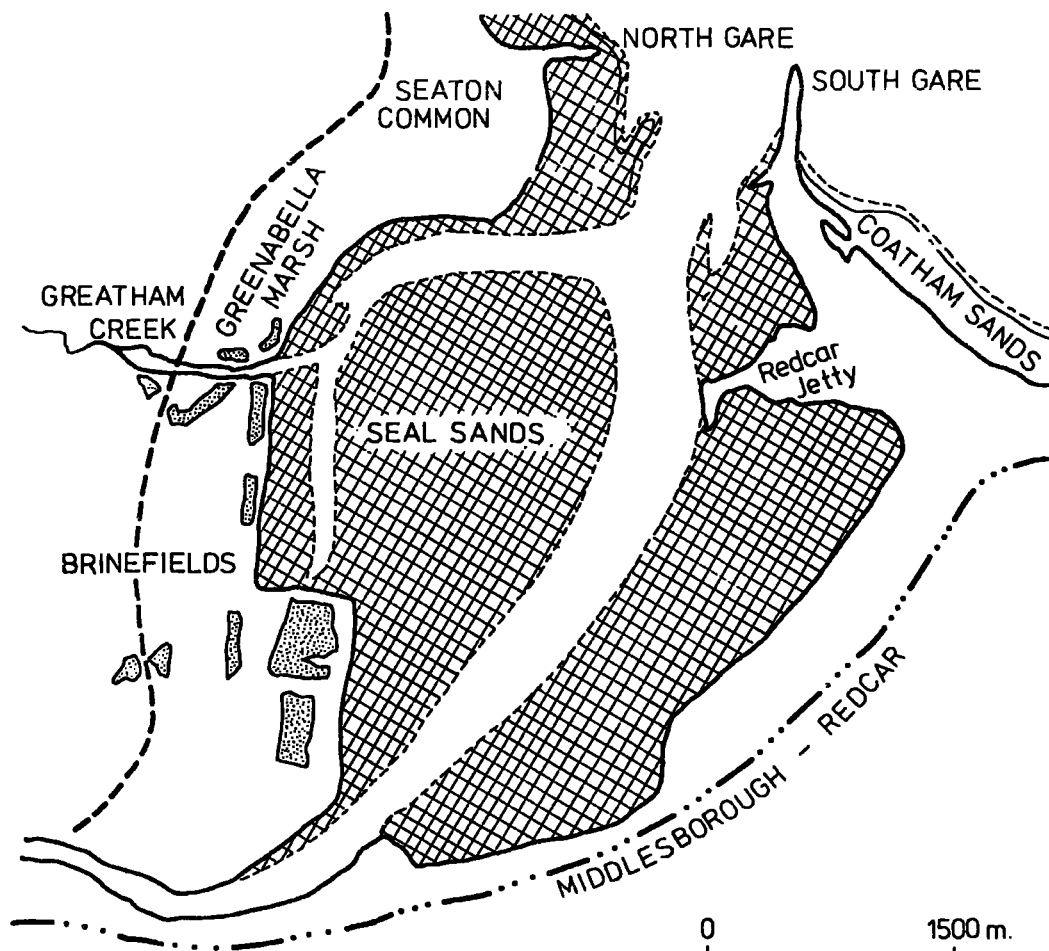
In the late 19th Century two breakwaters, the South Gare and North Gare, were constructed either side of the river mouth with slag, the by-product of the local steel industry. The South Gare, the more major development, was some two miles in length and split off a small portion of Bran Sands to its seaward side. This small area of intertidal sand flats became largely invaded by sand dunes, leaving a single inlet which is now flooded only on extreme

Figure 2

A. The Tees Estuary in 1840



B. The Tees Estuary around 1930



spring tides. It contains one of the two small areas of saltmarsh remaining at Teesmouth. Together with surrounding sand dunes, it was designated a Site of Special Scientific Interest (S.S.S.I.) in 1971.

A continuation of the South Gare called the 'German Charlies' runs parallel to the beach about $\frac{1}{2}$ km. offshore, being exposed only at low water, and is an important feeding area for some waders. On spring low water it extends southwards for about one mile.

Redcar Jetty was constructed, at about the same time as the two breakwaters, for the purpose of mineral export and this divided Bran Sands in two.

Sections of saltmarsh and higher parts of Seal Sands along the north-western edge of the estuary were enclosed by slag walls in the 1890's to form further areas of rough grazing land with fresh water and brackish dykes and pools. These remain as 'Greenabella Marsh' and the I.C.I. 'Brinefields'. During this reclamation the course of Greatham Creek was straightened and its waters confined by slag walls near its junction with the western channel of the Tees. Further inland, it remains less confined adjacent to Cowpen Marsh and here abuts the largest section of saltmarsh at Teesmouth. In 1965 this saltmarsh, together with parts of Cowpen Marsh (an R.P.S.B. reserve since 1969), were scheduled as an S.S.S.I. The former course of Greatham Creek, through the Brinefields, remains irregularly tidal.

In the early part of this century, further reclamation took place eastwards from the southern parts of the Brinefields, effectively blocking the subsidiary western channel of the Tees. This was generally a more solid reclamation, rather than enclosure, although one major pool, the 'Reclamation Pond', was created and separated from the remainder of Seal Sands only by a narrow wall of porous slag. This retarded movement of the tide through the wall but did not prevent it, thereby producing a delay in the tidal cycle inside the Reclamation Pond of over one hour. This phenomenon is a by-product peculiar to the use of blocks of waste material rather than fine debris in the initial

stages of enclosure. It occurred during all subsequent reclamations of the Tees estuary.

(b) Reclamation 1930 - 1960. (Fig. 3(A)).

During World War II the chemical industry of Teeside underwent considerable expansion, and has continued to grow steadily since then.

By 1960 the flats on both sides of the river between Port Clarence and Tees Dock were reclaimed, leaving a total of around 1,500 acres (607 ha.) on the north side of the river. In the late 1950's, Bran Sands suffered severe pollution which killed the intertidal invertebrates and left Seal Sands as the primary feeding area for waders and wildfowl (Stead, 1964).

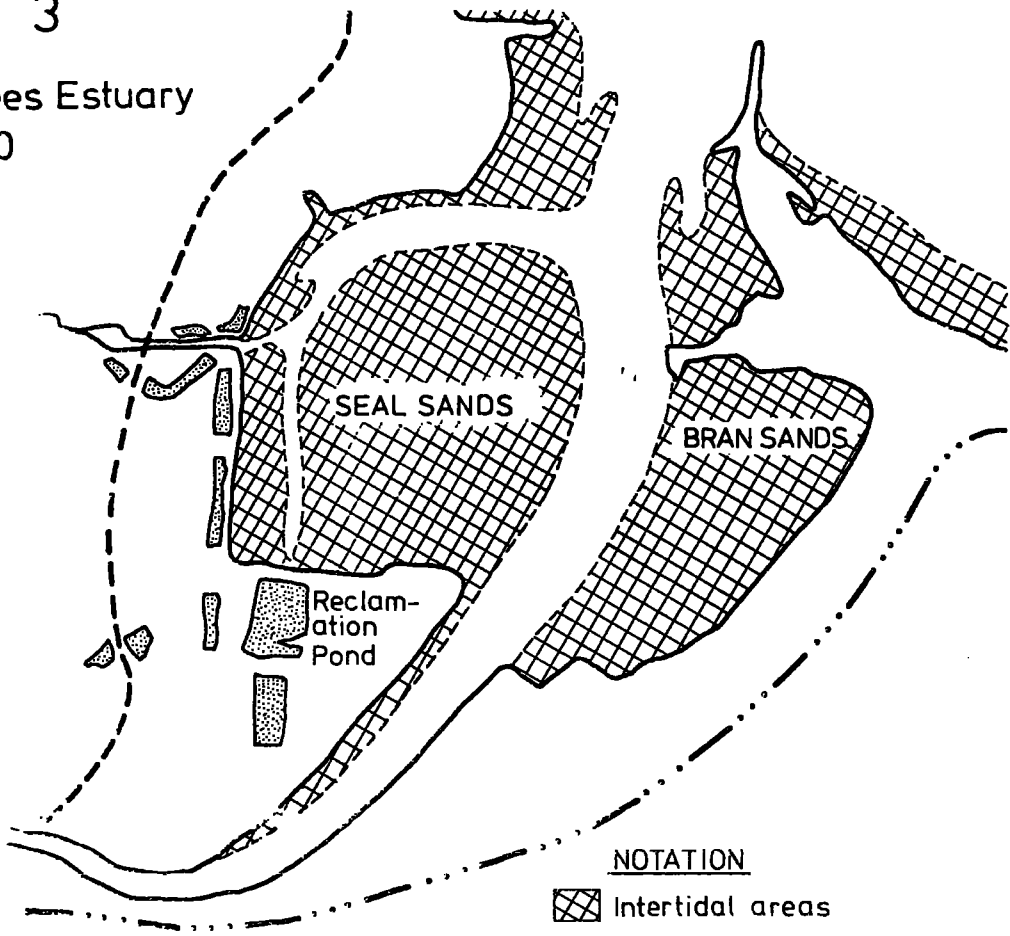
(c) Reclamation 1960 - 1970. (Fig. 3(B)).

During the early 1960's the major part of Bran Sands lying between Redcar Jetty and Tees Dock was totally reclaimed, leaving a small portion, around 100 acres (40 ha.), north of Redcar Jetty.

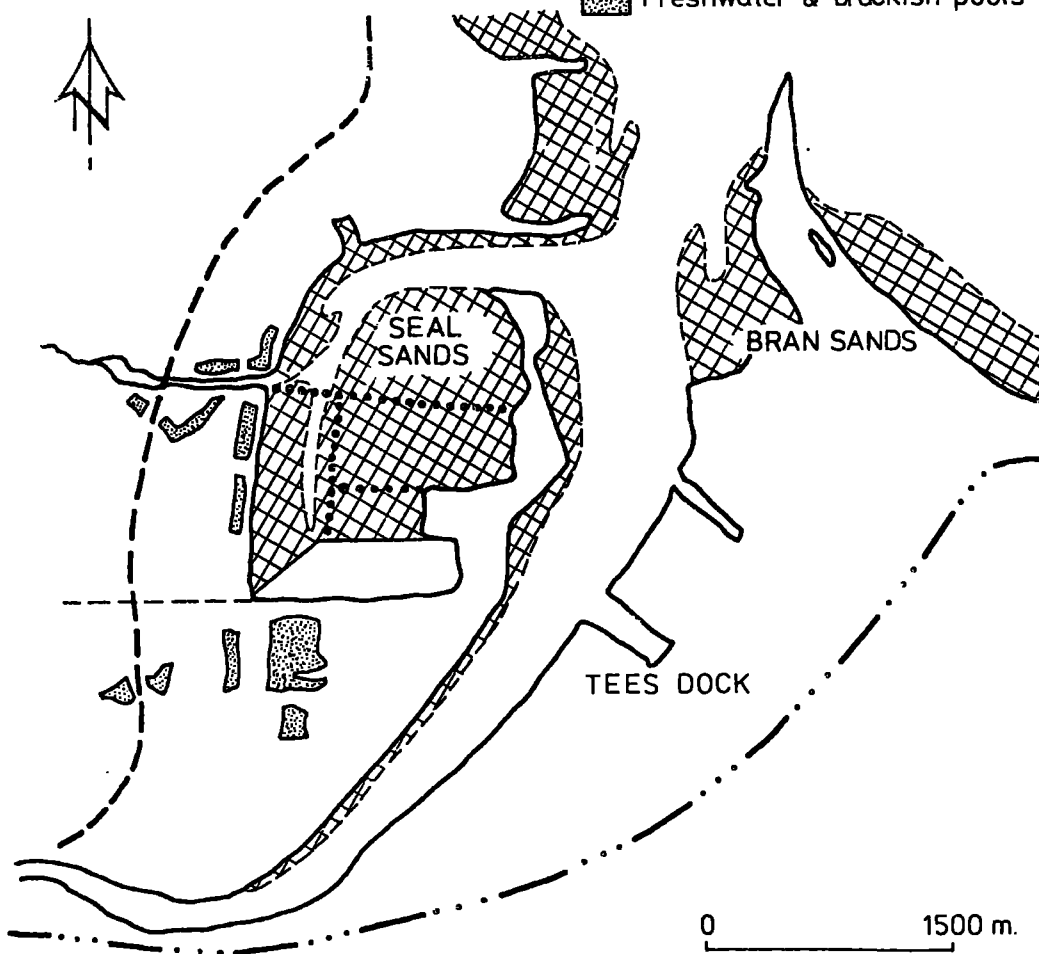
On the north-west side of the estuary two major developments occurred during this period. The first, between 1964-66, included the deepening of the main channel, the dredged material being pumped on to the eastern margin of Seal Sands. This created a raised bank of sand and clay, the 'Peninsula', which extended south to merge with the second important development, the enclosure in 1967 of 250 acres (101 ha.) of Seal Sands, later known as the 'Monsanto option'. This enclosure was progressively infilled by material dredged during maintenance of deep water in the river channel. Infilling continued irregularly until 1974. At an early stage this programme of infilling removed tidal influence from the 'Reclamation Pond'.

Figure 3

A. The Tees Estuary
in 1960



B. The Tees Estuary in 1970



NOTATION

-  Intertidal areas
-  Roads
-  Railways
-  Slag walls enclosing sections of Seal Sands
-  Freshwater & brackish pools

The Dutch technique of enclosure and infilling with 'liquid' dredged material (rather than solid waste dumped from lorries) was used almost exclusively during the further reclamation of Seal Sands.

In 1965 the northern and western portions of Seal Sands (some 640 acres (259 ha.) of the 1,000 acres (405 ha.) remaining after enclosure of the Monsanto option) were scheduled as a S.S.S.I.

(d) Reclamation after 1970 until the beginning of this study. (Fig. 4).

Industrial development on the southern part of the 'Peninsula' adjacent to the river Logan late in 1959 and continued throughout my study. A small enclosure of 100 acres (40 ha.) at the eastern corner of Seal Sands, north of the Monsanto option, was filled and built upon early in 1970.

In 1970 a major slag wall was completed which divided the remaining portion of Seal Sands into two parts. This wall, running approximately from east to west across the flats (and hereafter called the 'East/West wall'), separated a northern part, some 350 acres (140 ha.) of flats, (the 'North Area'), which remained open to direct tidal influence and a southern section, (the 'South Area'), of 550 acres (220 ha.) which was effectively enclosed and subject to tidal delay as water movement through the wall was retarded.

Reclamation of this 'South Area' was Stage I in the T.H.P.A.'s programme while Stages II and III would, if carried out, include complete removal of the 'North Area'.

Between 1972-73 the enclosed 'South Area' was further subdivided, giving the 'West', 'North-East' and 'South-East' enclosures. During the summer of 1973 the 'North-East' enclosure was almost completely infilled and therefore no longer of use as a feeding area for waterfowl by the beginning of my study in October 1973.

NOTATION

-  Intertidal areas
-  Recently reclaimed portions of South Area
-  Roads
-  Enclosing slag walls
-  Larger freshwater & brackish pools

ENCLOSURES OF SOUTH AREA

- 1 West
- 2 North East
- 3 South East
- 4 Monsanto Option

SITES INCLUDED IN THE STANDARD WALK

SEATON COMMON
 COWPEN MARSH
 GREENABELLA MARSH
 BRINEFIELDS
 SALTHOLM POOLS
 DORMANS POOL
 RECLAMATION POND

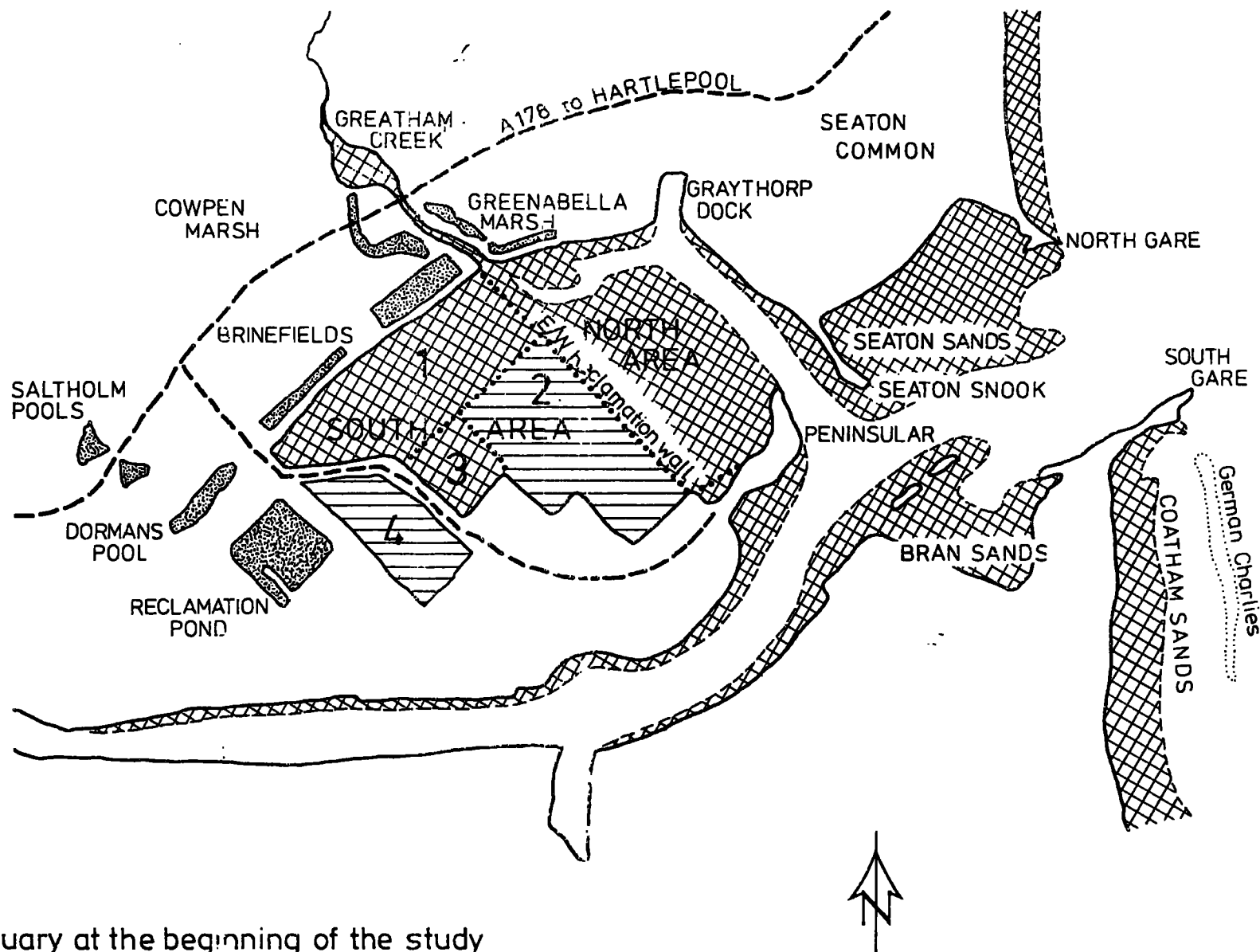


Figure 4 The Tees Estuary at the beginning of the study

The first phase of infilling of this 'North-East' enclosure was by dredged material pumped from Seaton Channel, which was deepened at this time to allow the removal of an oil drilling platform under construction for B.P. at Graythorp Dock. However, the majority of material for infilling this and the other two enclosures of the 'South Area' came from the creation, by dredging, of a deep water dock adjoining the south-east corner of the 'North Area'. This dock later assimilated a small portion of the 'North Area' enclosed by a short slag wall in 1973.

The construction of the porous E/W wall, which retarded the flow of water, caused a delay in the attainment of high water in the South Area of around two hours and reduced somewhat the tidal amplitude. This allowed birds to feed on the mud for 12 hours in each tidal cycle, an artificially favourable situation which was further improved by subdivision of the South Area, whereby tidal movement was further delayed and larger areas of flats were exposed, for longer periods. On neap tides considerable sections, particularly of the South-East Enclosure, remained available for feeding throughout the tidal cycle (Pienkowski, 1973).

THE EFFECTS OF RECLAMATION UP TO 1970.

In addition to the direct removal of intertidal feeding areas for waterfowl, reclamation of the Tees estuary appears to have caused radical changes of sediment type over the remaining flats. This in turn has changed the distribution and abundance of invertebrate prey species which may also have caused changes in abundance among overwintering waders and wildfowl.

While detailed records of such change have not been made until recently, the evidence which does exist is considered briefly below.

1) Changes in distribution and abundance of invertebrates and sediments.

During the 19th Century the majority of intertidal areas of the Tees estuary were probably sand, subject to vigorous tidal action, and only limited areas of mud existed. The presence of an extensive shell bed, well below the surface of the present substratum, comprised chiefly of cockles (Cardium edule L.), together with the designation of the flats as 'Sands', supports this argument. The small remaining portion of Bran Sands situated close to the river mouth still retains a mainly sandy substratum where, despite pollution, small numbers of cockles still exist and where some sand mason worms (Lanice conchilega) and lugworms (Arenicola marina L.) are found.

A survey of invertebrates at Teesmouth in 1930 (Alexander et al., 1935) revealed that cockles were present only in small numbers on Seal Sands and Macoma balthica (L), a bivalve species less susceptible to silting, was considered uncommon. Corophium volutator (Pallas) and Nereis diversicolor, O.F. Muller, were abundant but Hydrobia ulvae (Pennant) was not recorded at that date. The survey suggests that even by 1930 the estuary was becoming silted, a feature almost certainly caused by the restriction of the water flow and reduction in the scouring effect of the tide created by construction of the North and South Gare breakwaters.

The deposition of fine sediment on Seal Sands was greatly accelerated by the creation of the 'Peninsula' in the 1960's which separated it from the main Tees channel. From this date onwards Seal Sands received only slight through-flow of water from Greatham Creek. Rapid deposition of fine sediment continues to occur on Seal Sands, the supply of debris augmented recently by outwashed material from Stage I of the reclamation. Enrichment of these new

sediments occurs as the result of sewage effluent discharged into Greatham Creek. The net effect of these changes has been to provide an extremely productive feeding ground for waders. It may also be protected from the more severe effects of pollutants entering the main channel of the Tees from the steel and chemical industries.

By the 1970's the change to a more muddy substrate had produced several important changes in the distribution and abundance of invertebrates on Seal Sands. Hydrobia ulvae had colonized since 1930 and was present in very large numbers, whereas cockles were absent and Macoma declining. Nereis diversicolor had become the dominant large annelid although being itself displaced in areas of liquid mud by small oligochaetes (notably Paranais littoralis (Muller) and Manayunkia aestuarina (Bourne)), small polychaetes and nematodes (Gray, 1976), while Corophium had diminished in most sections of the flats.

2) Changes in the number of shorebirds at Teesmouth.

The extent of post World War II reduction in the available intertidal feeding areas at Teesmouth would have been expected to produce a marked decline in the numbers of overwintering shorebirds. However, although there are difficulties in comparing past records with more systematic counts of recent years (i.e. B.T.O. / R.S.P.B. Birds of Estuaries Enquiry), it would appear that the numbers of some species (those which prefer muddy substrates) have increased. This has been most evident for Shelducks which have increased in numbers from a few in the 1930's (Alexander et al., 1935) to a few hundred in 1950 (Temperley, 1951) and to around 1,000 in 1970. Similarly Dunlins (Calidris alpina (L.)) numbered around 2,000 - 3,000 before 1960 (Stead, 1964) while in 1970 they were in excess of 5,000.

Amongst the wader species for which adequate comparison can be made, only Curlews (Numenius arquata (L).) have shown a convincing fall in numbers from over 1,000 before 1950 (Stead, 1964) to between 200 - 300 in 1970, although this has been attributed to the pollution of Bran Sands. The numbers of Oystercatchers (Haematopus ostralegus L.) and Knots (Calidris canutus (L).), species more characteristic of sandy estuaries where Cardium and Macoma are most abundant, seem not to have changed since the 1940's. However, it is possible that their use of the estuary itself has diminished in favour of feeding on the adjacent coasts and offshore rocks and which counts of the estuary include. It would appear that while the total feeding area available to shorebirds was being reduced, a feature which would also intensify shooting pressure and other disturbance, various aspects of the reclamation programme were beneficial to a number of species, albeit perhaps only temporarily. The deposition of fine sediment, the changes in abundance of some invertebrate species and the overall enrichment and increased productivity of the flats by virtue of increased sewage effluent, seem to be important factors contributing to the maintenance of high numbers of some waders.

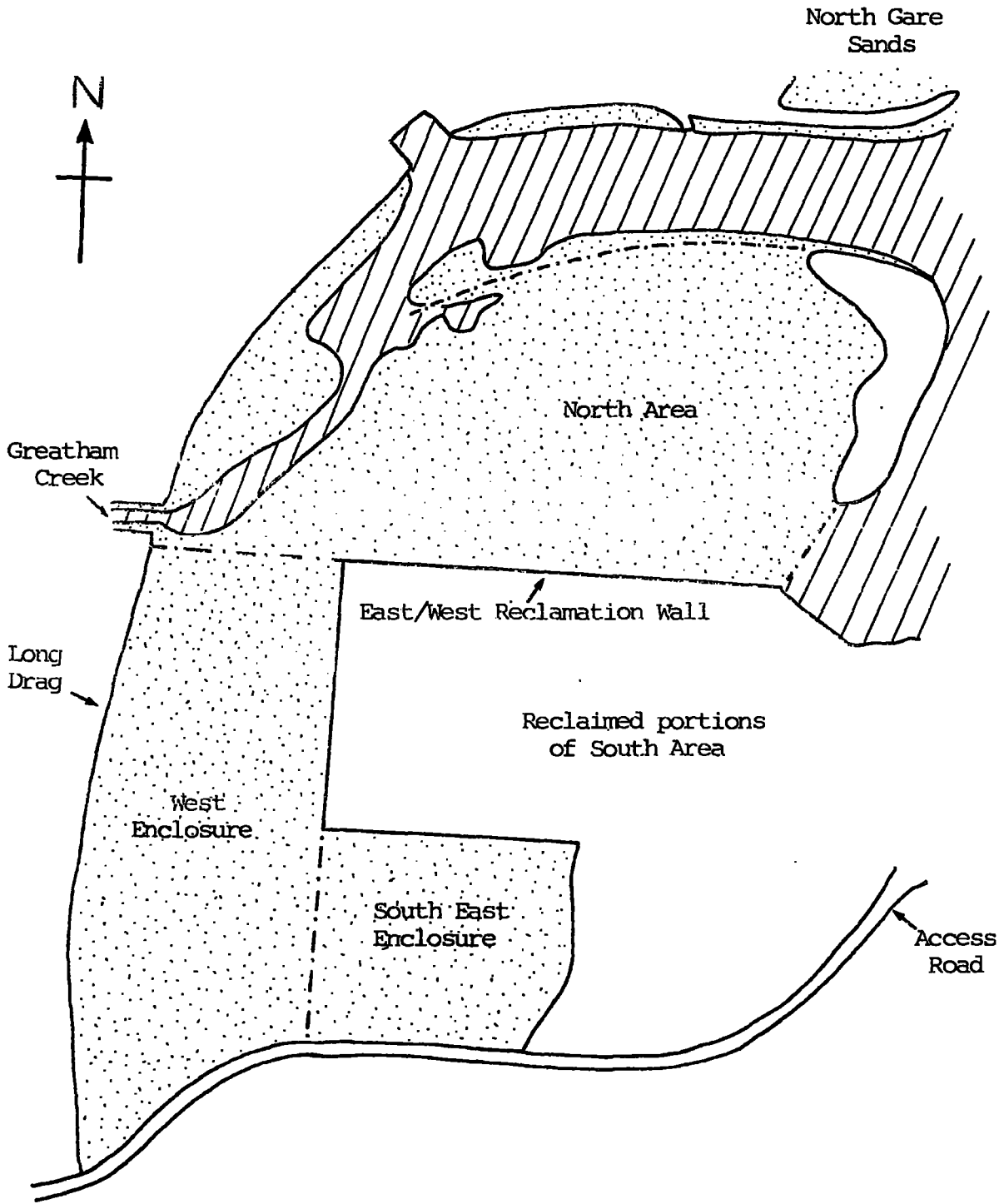
THE STUDY AREA.

Although many of the physical features of Seal Sands and its environs have been described whilst outlining the story of reclamation at Teesmouth, the sites which made up my study area deserve rather more specific description. Broadly, there are two divisions: firstly, the intertidal mudflats of Seal Sands (which by the middle of my study consisted of the North Area alone) and secondly, the fields and various pools, streams and dykes to the west of the estuary.

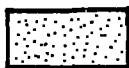
1. THE INTERTIDAL AREAS OF SEAL SANDS. (Fig. 5).

The construction of the East/West wall in 1970 created the primary division of intertidal areas during the present phases of reclamation, giving two areas of flats which have been designated as the North and South Areas. During the 1972/73 winter, subdivision and reclamation of the South Area began and continued during the course of the 1973/74 winter. Almost from the beginning of my study in autumn 1973, the two remaining unreclaimed subdivisions or enclosures of South Area existed only in a modified form. The reclamation of these two enclosures is recorded in some detail in this section since its timing and the methods by which it took place were probably important in determining the overwintering numbers of some wader species for which the enclosures remained important feeding areas.

FIGURE 5 : THE DIFFERENT INTERTIDAL AREAS OF SEAL SANDS
WHICH EXISTED IN OCTOBER 1973.



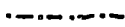
NOTATION



Intertidal Areas.



Water Area at Low Tide.



Slag walls through which the tide flowed.

Scale  300m.

(i) The North Area.

This comprises around 350 acres (140 ha.) of intertidal sediments separated from the main channel of the Tees by the small dune system of the 'Peninsula'. Parts of these dunes were removed during the period of my study in the course of developing a deepwater tanker dock. Disturbance during the course of its construction caused the temporary abandonment of a traditional high water roost of waders amidst the dunes.

The almost unbroken slag wall which forms the northern and western boundary of North Area gives the flats a cut-off appearance. The northern boundary wall extends eastwards forming Seaton Snook which separates North Area from North Gare Sands. There has been no development of saltmarsh along this perimeter, probably because the tidal amplitude is so great. The marshland and rough pasture which this wall once protected has mostly been given over to industrial development including a C.E.G.B. power station and a British Titan Products titanium dioxide factory, as well as docks and a variety of smaller factories. Only parts of Greenabella Marsh (to the west) and Seaton Common (to the north) lie undeveloped immediately adjacent to North Area.

Greatham Creek empties into the south-west corner of North Area and this quite small river, being highly charged with human sewage, is largely responsible for the enrichment of substrates within North Area.

To the west of the A178, the channel of Greatham Creek is quite diffuse, comprising some 40 acres of saltmarsh (now the only representative of this habitat on the western side of the estuary) and a small area of mudflats. For convenience and because of its position this portion, although estuarine, was not regarded as being part of North Area but rather as part of the field areas. Between the A178 and North Area the channel of Greatham Creek is closely confined by slag walls, but contains narrow marginal mudflats at low water, and, for purposes of counting birds that fed there, was regarded as part of North Area.

At low water the waters of Greatham Creek follow a deep channel through the flats of North Area close to its western boundary. This is joined by two north flowing channels which drained South Area before its enclosure and which continued to form (although not so prominently) the lines of drainage from the enclosures after the construction of the East/West wall which forms North Area's southern boundary. During the course of the reclamation of South Area these two channels deepened and other more minor channels developed through the flats of North Area close to the East/West wall. This appeared to be due to the continual flow of water from the enclosures which were infilled with dredged material. These gullies were extended laterally by wave erosion as the flats were exposed and covered by the tide. As the infilling of West Enclosure progressed, the fine silt fraction of dredged material was carried through the East/West wall and was deposited in these widened gullies and channels, and on adjacent areas of flats. Probably over 30 acres of flats were covered by this new sediment which in some places exceeded 20 cms. in depth. The influence of this factor on the feeding behaviour of some shorebirds is commented upon in the description of the West Enclosure (see subsequent sub-section). Temporary dredging activity near the outlet of Greatham Creek in the extreme south-west corner of North Area possibly created similar sedimentation (possibly over Greenabella Bank) as well as removing an acre or so of the original surface of the mudflats.

The union of the channel of Greatham Creek and those channels draining South Area creates Seaton Channel, which runs close to the northern boundary of North Area, separated by only a narrow strip of steeply sloping flats to its north. This major channel empties water from North Area into the main Tees channel close to the river mouth. The position of the mouth of Seaton Channel, close and almost pointed towards the sea, results in North Area being flooded by water derived primarily from the open sea; very little polluted water seems to enter North Area. It is probably for this reason that North Area has so far escaped some of the more serious effects of pollution to which Bran Sands, for example, has been

subject. The bed of Seaton Channel was deepened by dredging in 1974 to facilitate the removal of an oil drilling platform from Graythorp dock but whether this disturbed any low water feeding grounds for shorebirds is uncertain.

Along the southerly edge of Seaton Channel, but separated from it by a narrow strip of mudflats, is an old low ridge of slag now part-covered by mud which is exposed at around mid-tide. For this reason it is known as the mid-tide wall. This 'wall' begins close to the point where Seaton Channel arises from Greatham Creek and the other minor channels, and from here runs eastwards in a slight curve to join the Peninsula. It is to the south of this wall that the major flats of North Area lie.

The flats of North Area are for the most part gently undulating, having few deep drains through them. Much of the area becomes exposed between $HW+2\frac{1}{2}$ - $3\frac{1}{2}$. On the basis of the location of major creeks and features such as the surface configuration of the mud, its consistency and the existence of surface water, North Area was divided into a number of sections for the purposes of counting birds and recording their behaviour. These divisions are shown in Fig. 6 along with other prominent features which are referred to by name in the course of this thesis. Fig. 7 shows the approximate distribution of broad sediment types on North Area, this being a simplification of data collected by Evans and Herdson (pers. comm.). During the early part of my study the areas of liquid mud were extended considerably as described earlier, but probably these began to develop when the East/West wall was constructed. Gray (1976) noted that sediments over the whole area were noticeably finer in 1973 than in 1971. During autumn 1974 there was a contrasting but slight change in the sediments close to the East/West wall in that they became markedly more sandy. This occurred as the result of heavy deposition of wind-blown sand from the unconsolidated surface of the then fully-reclaimed parts of South Area, in particular from the former North-East Enclosure. Towards the end of my study the development of the tanker dock on the eastern edge of the Peninsula involved extensive removal of the sand

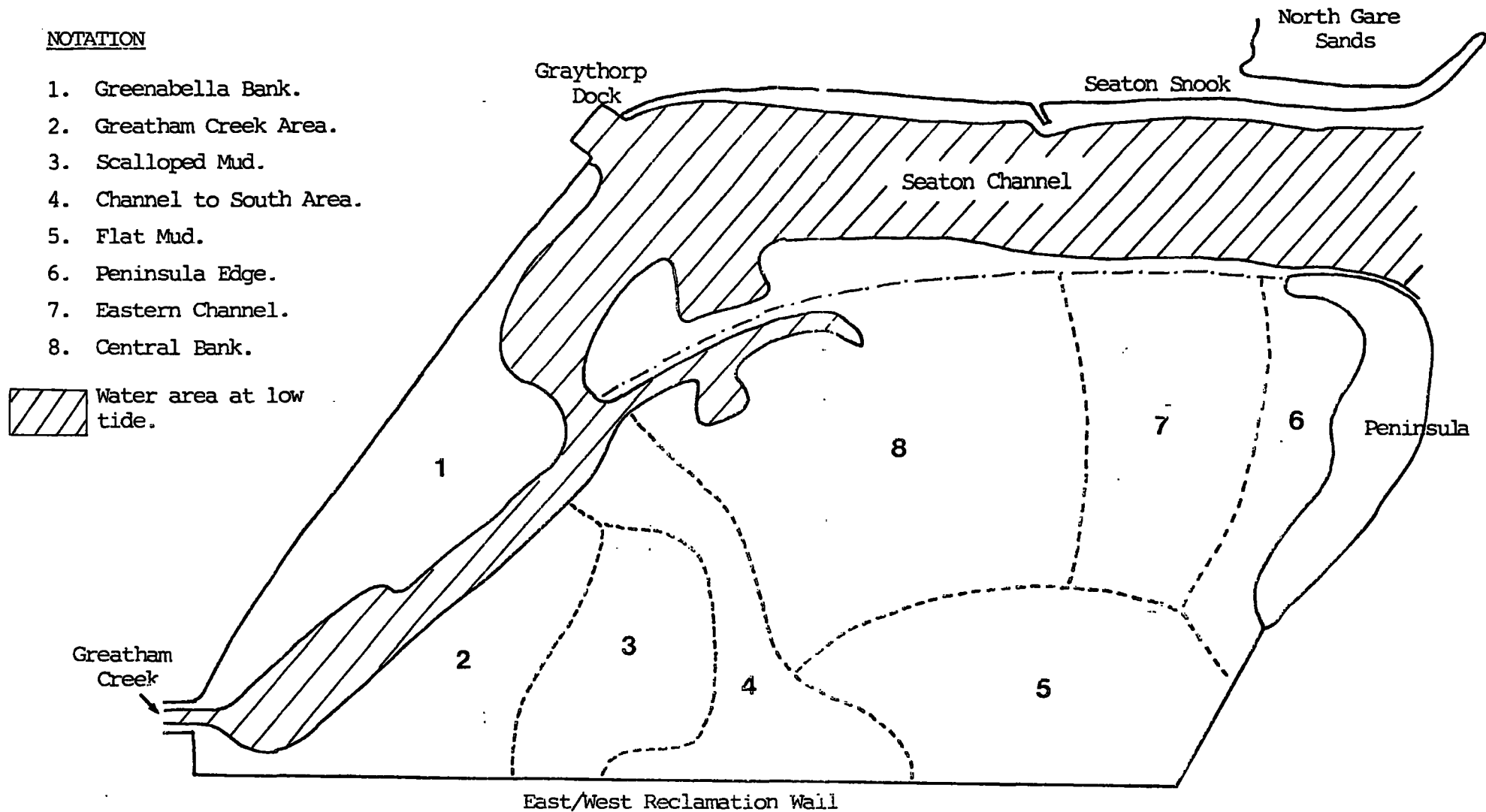


FIGURE 6 : THE SUBDIVISIONS OF NORTH AREA AS USED FOR RECORDING OBSERVATIONS.

SEDIMENT TYPES

- 3 : Fine sand
- 4 : Muddy sand
- 5 : Firm mud/sand
- 6 : Mud
- 7 : Soft mud
- 8 : Liquid mud

 Water area at low tide.

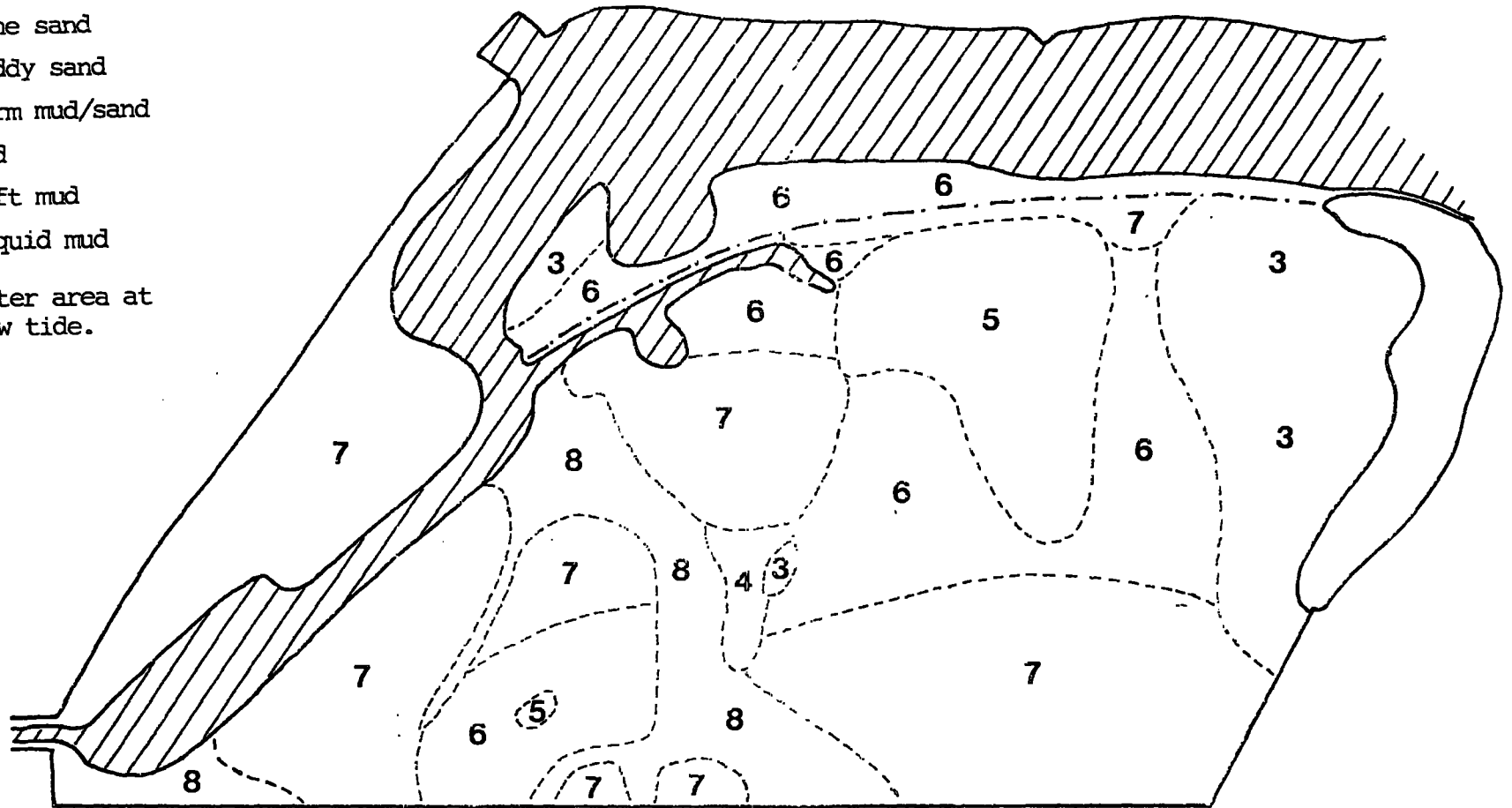


FIGURE 7 : THE DISTRIBUTION OF BROAD SEDIMENT TYPES WITHIN NORTH AREA.

(This map is based upon unpublished data of Evans et al., pers. comm.).

dunes there, and again the removal by wind of sand from the newly exposed surfaces onto the North Area may have been considerable. This extraction activity again created considerable disturbance of the roost on the Peninsula. It seems probable also that construction activity upon the North-East Enclosure which began in spring 1974 and continued beyond the end of my study also caused disturbance to the high tidal level feeding areas in the south-east corner of North Area.

Although my study did not include the collection of data on the abundance and distribution of invertebrates on North Area, work to this end was undertaken by other workers before and during my study, and these findings have been recorded in detail elsewhere (Evans et al., 1979; Gray, 1976). However, it is relevant here to record briefly the findings.

It appears that invertebrate macrofauna are not particularly diverse and only four species occur at levels of abundance which make them important items in the diet of shorebirds. The small spire shell Hydrobia ulvae is the most abundant of these and is widely distributed on firmer muddy substrates (substrate types 5/6) where it was recorded at densities in the order of about $12,000/m^2$ in autumn 1973 at the beginning of my study. Nereis diversicolor is the only abundant large annelid and is the single most important food of larger waders. It appears to reach its highest densities, up to $250/m^2$ (Gray, 1976), on firm muddy substrates (types 5/6), in similar locations, therefore, to those where Hydrobia are particularly abundant. Although Macoma balthica (probably a particularly abundant bivalve on Seal Sands before its increasing muddiness) remains widely distributed, it is usually found at densities lower than $200/m^2$, almost insignificant compared with maximum densities of over $4,000/m^2$ which occur at Morecambe Bay (Prater, 1970). Although the quadrat data of Evans et al. (1979) indicate that Macoma are most abundant within areas of muddy sand, observation showed this food was taken most frequently where the substrate was very sandy, for example, at higher tidal levels adjacent to the Peninsula. Shore crabs, Carcinus maenas, were widely distributed within the muddy substrates of North

Area in autumn but are recorded as occurring in frequencies of 1 or 2/m². They were seen to be taken by Curlews, Godwits and Redshanks in autumn of both years of my study. Usually crabs were taken by a small number of individual birds and not generally by the population nor over a large area. The high frequency with which they were taken by individuals suggested that relatively high densities occurred in patches.

Only the larger size classes of Nereis, Macoma and Carcinus were individually distinguishable when taken by feeding waders over the distances of observation required in this study. Smaller size classes of these species along with Hydrobia could only be distinguished and recorded when a definite feeding or swallowing movement was made. Included also in this group of prey (which I have labelled 'small items') were rarer macrofauna, such as Corophium volutator and a variety of small polychaetes, oligochaetes and nematodes which comprise a major part of the very abundant meiofauna of Seal Sands. Gray (1976) records the polychaete Manayunkia aestuarina (Bourne) and the oligochaete Paranais littoralis (Muller) as particularly abundant, the former occurring in stable substrates (for example, the muddy sand comprising most of the Central Bank) while the latter occurred on unstable substrates, such as the very soft muds. Another polychaete, the tube-dwelling Polydora ciliata (Johnston) forms extensive reefs at low tidal levels along Seaton Channel near its junction with the Greatham Creek channel. Small oligochaetes and polychaetes were recorded by Gray in densities of up to 206,000/m² and 30,000/m² respectively, and the meiofauna as a whole was estimated by Gray to have a biomass per unit area fifty times greater than the macrofauna on Seal Sands.

(ii) The South Area.

At the beginning of this study only two enclosures of South Area, namely the West Enclosure and the South-East Enclosure, remained available to waders and wildfowl for feeding. The progressive reclamation of these enclosures began in

early October 1973 and by February 1974 they ceased to be used for feeding at low water.

The following description of these two areas outlines their reclamation:

(a) The West Enclosure.

Formerly this was a gently sloping area of soft mud and firmer muddy sand comprising around 240 acres (95 ha.) and containing centrally a major channel which drained the southerly parts of South Area. When my study began a portion of saltmarsh existed at the extreme southern end of the enclosure bordering the main access road to the then embryonic Seal Sands industrial complex. This had developed since the access road was constructed in the mid 1960's. No information concerning the nature of the substrate nor the invertebrate densities of the original flats is available.

In early October infilling of the West Enclosure began by pumping in mud, sand and gravel, then being dredged from the tanker dock under construction adjacent to the south-east corner of the North Area. Initially infilling began at a point mid-way along the eastern edge of the enclosure, immediately adjoining the North-East Enclosure which had just been reclaimed. This, however, stopped shortly afterwards, and infilling, again with dredged material, recommenced at the southern end of the enclosure. This renewed infilling was carried out by two discharge pipes and quickly built a barrier of debris which removed tidal influence to the small South-East Enclosure.

The process of infilling with fluid dredgings created deltas of coarser material since the heavier boulders and gravels were deposited from the water body carrying them almost immediately they were discharged. Beyond this, finer sands were washed outwards to form an extending fan-shaped deposit while further away still, silt and mud were deposited as completely waterlogged 'liquid mud'. As the depth of coarser material built up around the discharge, the pipes were

raised and moved forward and thus the deltas pushed northwards along the enclosure. At any one time a considerable portion of the extending deltaic system was above the level of ordinary tides, enabling feeding to occur there throughout the tidal cycle. Beyond the distinct edge of the deltas, the finer material was deposited more generally over the original surface of the flats but appeared to accumulate particularly at the northerly end of the enclosure adjacent to the East/West wall. In fact, as has been noted in the previous sub-section, a considerable amount of fine sediment passed through the wall to be deposited on the flats of North Area, notably on the Greatham Creek Area.

By mid-December 1973, when active reclamation ceased, approximately half the West Enclosure was completely infilled with coarse material and two thirds of the remainder was rendered useless for feeding of most waders, simply by the great depth of liquid mud.

The method of infilling by using fluid, dredged material rather than by tipping, seemed to have the peculiar effect of making invertebrates, particularly Nereis, more available to waders. This feature of reclamation was possibly of considerable importance to the populations of some species at this time. It appeared that the deposition of new sediment, whether comprising coarse sands as along the margins of the deltas, or liquid mud on top of the original surface of the mudflats, drew the invertebrates from the deeper substrate. Once in the new substrate, these invertebrates were readily captured and Godwits, Grey Plovers and Redshanks in particular took immediate advantage of this food. Even Dunlins were seen to capture very large Nereis which they would be very unlikely to obtain in normal circumstances. While it might be expected that invertebrates would move upwards in a sediment as it increased in depth, possibly taking up stations at depths similar to those in the previous substrates, the reason for their unusual availability is not known. It might have been that invertebrates were forced almost to the surface of the new sediment and were thus much more readily detected. Alternatively, they might have become more active and again

more easily detected within the new sediment. While the deposition of sediment over a relatively small area might have resulted in exhaustion of the prey forced to the surface, the progressive feature of the reclamation meant that new areas of the original flats were being affected at a fairly steady rate as the deltas moved northwards, giving perhaps a reasonably constant yet much enhanced food supply. In fact, the continuity of infilling seemed vital to maintaining the food supply. When the active process of reclamation finished, the area abruptly ceased to be attractive.

The West Enclosure continued to be used as a roost at high water and there was a resurgence of feeding there, especially by Redshanks, but this was confined to the course of the overflow from the South-East Enclosure as this was infilled in February 1974. It is not known what prey were taken but it seems unlikely that they were derived from the original sediments of West Enclosure since these had been buried for about four months by eight feet of debris at this particular point. More likely, the food was obtained from the water body of the overflow which was more or less continuous and allowed feeding throughout the tidal cycle.

In summer 1974 infilling of the West Enclosure was resumed and by autumn it was almost completely reclaimed. Thereafter, it remained virtually undisturbed and the new surface came to hold a temporary pool which frequently attracted almost the entire North Area population of Grey Plovers as a roost over high water.

(b) The South-East Enclosure.

This 60 acre (25 ha.) enclosure was available for tidal feeding for only the first two weeks in October 1973, after which date infilling at the south end of West Enclosure removed all tidal influence. It soon came to hold a large and permanent body of water, mainly derived from burst and overflowing pipes carrying the dredged material to West Enclosure. In this condition it provided only

limited feeding opportunities for waders, with a few Redshanks and Dunlins feeding at high water in the sparse saltmarsh at its eastern end.

Infilling, again by dredged material, began in late January 1974 and continued through early February. Infilling occurred directly into the water body, so that many of the peculiar benefits in terms of improved food availability were lost. Feeding by waders was of necessity restricted to a narrow margin from several yards just above the water's edge (in the area coursed by the discharge) and extending as far as the birds could wade. Godwits in particular fed almost exclusively in the water in this situation.

As was observed in the case of the West Enclosure, feeding here ceased abruptly when active reclamation stopped.

2. THE FIELD AREAS NORTH OF THE ESTUARY.

For the purposes of estimating the extent of field feeding, a total of around 1675 acres (670 ha.) of fields and pools were included in regular counts of birds feeding or roosting there at high water. For the most part, these were areas of rough pasture dissected by freshwater and brackish dykes with small permanent pools, but more generally subject to temporary flooding in winter. In association with these are a number of major pools subject to a variable degree of flooding.

Below, the different and distinctive components of the field areas and each of the major pools are briefly described and each are identified in Fig. 4.

Seaton Common (162 ha.) This comprises a relatively small area of rough grassland with shallow dykes, some subject only temporarily to flooding, and with one rather diffuse and shallow pool. This whole portion was heavily grazed by horses throughout my study. The greater part of the common consists of a golf course fairway system and this was subject to regular and often heavy disturbance. On

the whole, the common was used only sparingly by waders either for feeding or roosting.

Greenabella Marsh (101 ha.) This comprises probably the roughest and most truly marsh-like of the field areas. Close to the boundaries with Greatham Creek and North Area exist a wide and elongated series of pools, fringed by rushes in some places, but mostly very open along their margins. This was an important roosting and feeding area for Curlews, being little disturbed during the day and being close to North Area. The marsh was regularly but never heavily used for grazing by horses.

During the course of my study, a road was constructed across this marsh from its north-west to south-east corner. The disturbance by construction seemed to have more effect than the existence of a completed road.

Brinefields (140 ha.) As a whole, the Brinefields were very heavily grazed both in summer and winter, the grass sward being typically short. The area is dissected by a system of small, permanent and temporary dykes, and portions of pasture were subject to winter flooding but such pools were never extensive. Brine is actively extracted from deposits below the area, and hence its name.

The principal area used by waders over the high water period was that immediately around the old, cut-off channel of Greatham Creek. This large creek is tidal and probably contained water of high salinity since the inflow of freshwater was generally slight. The fact that the channel is flooded only at the extreme top of the tide attracted many waders for feeding over high water, including Godwits. The majority of the channel is shallow and on ordinary tides is probably less than a foot deep over half its area. What prey were taken by birds feeding here is not known but may well have included Nereis.

In autumn 1974 a settlement lagoon close to the old Greatham Creek channel (and in fact once part of it) was filled in and associated with this a new

brine extraction head was set up nearby after a month or so of drilling. During periods of disturbance from this source, the channel was abandoned.

Cowpen Marsh (190 ha.) A moderate to heavily grazed rough pasture containing a mature system of drains, some of which are of large size and specially managed since the marsh became an RSPB reserve. At no time in my study was this an important roosting area for waders, although small groups of Curlews moved to the more inland parts of it and occasional Redshanks frequented the dykes.

Saltholme Pools (9 ha.) Two large freshwater pools separated by the A178, the western pool lying within improved pasture while the eastern pool was bounded in part by arable fields but with a dense area of rushes at its eastern end. Both pools have very little shallow marginal water and were generally not attractive to waders except when high water levels inundated the surrounding land.

Dormans Pool (11 ha.) A large predominantly shallow pool heavily fringed with rushes and very rough grassland which for the most part was ungrazed. At low water levels quite large areas of mud were exposed, providing attractive high water feeding for some waders, especially for Dunlins.

Reclamation Pond (22 ha.) This is the oldest enclosure of Seal Sands which remains unreclaimed. Until the infilling of the adjoining Monsanto option, from which it is separated by a slag wall, it remained subject to tidal flooding. The original surface of the mudflats remains and is usually flooded very shallowly by rainwater and by the overflow of water from Dormans Pool. Under dry conditions the area of flooding diminishes so that up to three quarters of its area is exposed but nevertheless the mud remains wet. The water is still brackish. Under almost all conditions of flooding it provided feeding at high

water for a variety of waders, especially Redshanks and Dunlins and also for Shelducks, although what prey were available here is not known.

Monsanto Option (38 ha.) Although this enclosure is almost completely infilled with dredged material and the new surface must be in the order of 3 metres above the original surface, substantial numbers of Dunlins and some Redshanks used this area for feeding and roosting at times when it was partly flooded by rainwater.

AIMS OF THE STUDY.

An observed reduction in the numbers of overwintering shorebirds could result from one or both of two processes:

- (1) By the settlement of smaller numbers of birds in autumn, that is some weeks before individuals are likely to be experiencing difficulty in collecting food at a sufficient rate. By some as yet unknown means, individuals of a species might be able to anticipate the approximate winter carrying capacity.
- (2) By death or emigration during winter, arising from the failure of individuals to satisfy their energy requirements.

The inability of a bird to collect sufficient food sufficiently quickly may arise either (a) because the stocks of invertebrate food either in terms of density or availability are inadequate, or (b) because the time for which the flats are exposed by the tide is simply too short to collect sufficient food.

At Teesmouth there was both a major reduction in feeding area and in potential feeding time during my study; the feeding area being reduced by

approximately $\frac{2}{3}$, from 900 acres (364 ha.) in the winter of 1972/73 to 350 acres (142 ha.) by the end of winter 1973/74, whilst feeding time was reduced from approximately 12 hours to 8 hours in each tidal cycle during this same period. It seemed likely, in view of the magnitude of the changes, that both factors would be involved in determining the overwintering populations of species for which no 'predicted' carrying capacity had been established in autumn. However, the relative importance of reduced feeding area and feeding time would be expected to vary between species.

The purpose of my study was two-fold:

- (1) To identify the means by which shorebirds adapted to the post reclamation situation, assuming in fact they needed to do so and were capable of doing so, and
- (2) To try to determine the relative importance of loss in feeding area and loss in feeding time in determining the overwintering populations of different shorebirds at Teesmouth after reclamation was completed.

These two problems are considered in respect of five species of waders: Curlew (Numenius arquata (L).), Bar-tailed Godwit (Limosa lapponica (L).), Grey Plover (Pluvialis squatarola (L).), Redshank (Tringa totanus (L).), and Dunlin (Calidris alpina (L).), and also a single species of duck, the Shelduck (Tadorna tadorna (L).). Substantial populations of each species overwintered at Teesmouth before Stage I of the reclamation programme began. A number of other wader species, although making regular use of Seal Sands at low water, sometimes in high numbers, have been excluded from my study, either because of the difficulty of observation in the time available (e.g. Ringed Plover) or because their dependance on Seal Sands for feeding was erratic (e.g. Oystercatchers, Turnstones, Knots).

Although a more complete insight into the effects of reclamation on shorebird populations requires consideration of the responses of invertebrate prey populations also, for example in terms of the standing crop available for shorebirds and its sequential reduction during winter, my study involved recording the responses of birds alone.

Invertebrate densities on Seal Sands were recorded by other workers in autumn, winter and spring between 1971 - 1974 and this information is given in the preceding description of the study area.

The aims and methodology of my work had a special relationship with the study of shorebirds at Teesmouth made by Pienkowski between February and May 1973. Pienkowski's study provided baseline data on the numbers of shorebirds using intertidal areas at Teesmouth and the extent of their dependance on different portions of the estuary. He also provided quantitative measures of feeding activity in the pre-reclamation situation. In my study these same measures of feeding activity were repeated, in accordance with rationale for Seal Sands research at Teesmouth prepared by Goss-Custard (1972), both during active reclamation (1973/74) and after reclamation was completed (October - December 1974).

Although the basic research methodology had been prescribed for me, I collected information additional to this, and all interpretations of the results are my own.

METHODS OF STUDY

(1) GENERAL PROVISIONS FOR THE RESEARCH PROGRAMME.

(a) Allocation of time for field observation.

Between October 1973 - March 1974 and October 1974 - December 1974 the study area at Teesmouth was visited on an average of three days each week. Between October - December 1973 emphasis was placed on obtaining observations of feeding behaviour during the day with only occasional visits at night. Throughout the remainder of my study there was a more equal spread of observation by day and night, including observation throughout each tidal cycle on any one day. For example, in a week when low water occurred around mid-day and midnight (spring tides) observations were made from approximately dawn to dusk on the first day and from dusk to dawn on the following day. In the following week, when low water occurred around dusk and dawn (neap tides), observations were made from mid-day to midnight on one day and vice versa the following day. This regime of study overcame the inevitable bias resulting from the desire to maximise observations of feeding behaviour towards days with the longest period of exposure of intertidal areas in daylight. The third day in each week was used for counting the numbers of birds present on the estuary or adjacent areas, as outlined below, and in making up deficiencies in the number of observations of feeding behaviour.

Between April - September 1974 the numbers of waders and Shelduck at Teesmouth were low and observations of feeding behaviour were difficult because heat haze reduced visibility. During this period, therefore, the programme of study outlined above ceased, apart from monthly counts which were continued so as to determine the pattern of reduction and build up of numbers through spring and early autumn migration, respectively.

(b) Methods of field observation.

All observations of feeding activities were made with a Swift 15 - 60 x telescope. Movements of birds, location of feeding and roosting flocks at high water were watched and counts at low water made with 20 x 50 binoculars.

The system of slag walls enclosing portions of Seal Sands, particularly the East/West reclamation wall, provided vehicular access to points from which all important feeding areas for waders and Shelducks could be observed. A long wheel base landrover was used as a mobile hide and this permitted close approach to feeding areas with minimal disturbance of birds. It also allowed movement to a number of different observation points throughout each day. Only by the use of this vehicle could the feeding activities of all species be monitored adequately: a series of static hides approached on foot would have restricted my study to one or two species only.

The slag walls, raised some 15 feet above the flats, provided an excellent range of vision which was important for the accurate determination of the proportion of birds feeding, since most feeding areas were between 150 - 350 m. distant.

(c) Recording field data.

All measurements of feeding activities and counts were recorded on

a battery powered cassette tape recorder, tapes being transcribed on return to Durham. Generally two tape cassettes, allowing 30 minutes recording on each, were adequate for each field visit.

The times used to describe observations and counts in this thesis are related to the time of high water preceding each observation; for example, HW+2 indicates two hours after the time of high water predicted for the mouth of the Tees estuary.

All timed observations of feeding activity were made using a stop watch accurate to $\frac{1}{10}$ second. This degree of accuracy was essential for measurements of searching rate of medium sized waders, such as Redshank, in which all values were separated by no more than one second. At night the interior light of the landrover or a head lamp was necessary to read a stop watch accurately but this caused no undue disturbance of feeding birds and did not prevent the use of the telescope.

When recording feeding behaviour a single tally counter was used to record less frequent feeding events.

(2) MONITORING OF SEASONAL AND TIDAL CHANGES IN NUMBERS OF BIRDS AND AREAS USED.

A single monthly count of the five wader species and Shelduck using the different areas of Seal Sands was made at low water towards the end of each month. All counts were made between one hour before and one hour after low water at which period movement between different portions of the estuary and within Seal Sands was negligible.

The typical programme of counting involved first walking along the mid-tide wall counting birds along either side of Seaton Channel and along the lower portions of Greatham Creek where it passes through the North Area.

The relatively minor disturbance this procedure caused was clearly visible and movement of birds were allowed for in totals. Birds using the remaining portions of the flats were counted from the enclosing slag walls. Various physical features of the flats, such as creeks and substrate boundaries, were used to subdivide the area for convenient counting. The same subdivisions were also used for recording the location of each series of observations of feeding activities.

Between December 1973 and December 1974 low water counts were also made each month on intertidal feeding areas south of the River Tees, comprising Bran Sands and the offshore rocks and sea beaches adjacent to Coatham and Redcar. These counts were made either the day before or day after those for Seal Sands and were again restricted to within one hour either side of low water.

Monthly counts of waders and duck at Teesmouth at high water were made by members of the Teesmouth Bird Club as part of the B.T.O. / R.S.P.B. Birds of Estuaries Enquiry. These counts, generally conducted around the middle of each month, provide useful comparison with my own records. However, because of the temporary nature of many high water roosts of waders, numbers of those were often underestimated when roosts were overlooked.

Regular counting of this type enabled the extent and pattern of seasonal change in the numbers of shorebirds to be identified with reasonable accuracy, though later experience suggests that counts at fortnightly or weekly intervals would have been preferable during the autumn when many birds moved through the estuary.

(3) QUANTIFICATION OF THE MEANS BY WHICH DIFFERENT SPECIES OF SHOREBIRDS ADAPTED THEIR PREVIOUS FEEDING STRATEGIES TO THE REDUCTION IN INTER-TIDAL FEEDING AREA AND FEEDING TIME.

(a) Estimation of the duration of feeding.

(i) Time spent feeding during daylight.

The proportion of feeding individuals of each species on the section of flats being observed (e.g. North Area, West Enclosure) was recorded once each hour, this value being termed the feeding intensity (FI). In the case of larger waders such as Curlew and Godwit it was possible to count the majority of all individual present, even on the North Area, particularly at and above mid-tidal levels when birds were restricted to the more level flats. These rather complete counts also gave support to the estimates of movements to and from Seal Sands (see below) and also provided a more accurate check on the timing of any rapid change in numbers from day to day as may occur, for example, in relation to changes in weather.

For other waders complete counts of feeding and non-feeding individuals were impossible, in the case of Dunlins because of their small size, in the case of Redshank, Grey Plover and also Shelduck because preferred feeding areas were frequently in gullies and troughs in the flats and were not visible from all observation points. For both Redshanks and Grey Plovers the general approach was to determine the activity of as many individuals as were visible. From some observation points and particularly at low water even this approach provided insufficient numbers of either species for an accurate measure of the proportion feeding. It became apparent during my study that resting birds of these two species tended to separate from feeding groups thereby introducing bias into recorded FI's. Grey Plovers, for example, tended to move out of sight into channels and creeks in the flats when not feeding, thereby resulting

in overestimation of the FI, whereas Redshanks tended to move to higher, firmer flats to rest and FI's were sometimes underestimated. For Shelducks and Dunlins, the most numerous species using Seal Sands during my study, the feeding activity of four or more samples, of perhaps 100 individuals each, was recorded in well-dispersed areas.

Generally the activity of individuals was quickly determined. Where there was any doubt as to whether a bird was actively feeding, for example, if it was standing or walking between pecking, the individual was watched until its activity was clear. This proved most time consuming with Grey Plovers since their characteristic feeding pattern involved infrequent pecking interspersed with periods of movement and long pauses.

(ii) Night feeding.

Not all feeding areas could be seen at night despite the quite high general level of illumination provided by nearby industrial lights. However, it was possible to obtain a qualitative assessment of feeding intensity. Under clear weather conditions there was little difficulty in identifying actively feeding birds at considerable distances, and for larger birds the range of visibility was the same as during daylight when seen against a wet substrate and in line with a bright light source. It was rather more difficult to find roosting individuals and small groups since most species chose drier substrates for roosting and these reflected less light.

Despite these problems, it was possible to make a reasonable estimate of the intensity of feeding of each species at night in the areas in which they preferred to feed during daylight, and to pick up any major changes in feeding distribution.

(iii) Field feeding.

Counts of the numbers of individuals of each species using

the fields and marshes north of the estuary for feeding at high water were made as frequently as possible. Effort was concentrated on days when high water on Seal Sands occurred around mid-day, i.e. when intertidal feeding areas were available for the shortest period during daylight. It was assumed that in this situation the FI in the fields would be maximal. At least three field counts were made at high water each month, following the procedure of a 'standard walk' established by Pienkowski (1973). This included all important field-feeding and roosting sites for individuals using Seal Sands at low water (see description of Study Area).

Although these counts were not intended to include all birds using the fields at high water, but rather to check a representative sample of high water sites, it seems likely that all individuals of some species might have been included, for example, of Godwits. For Redshanks and Curlews on the other hand it was evident that on occasions those birds feeding on Seal Sands at low water dispersed widely and used temporarily flooded pastures beyond areas included in the standard walk.

Although the principal purpose of the field counts was to establish the proportion of birds using these areas for feeding, that is to provide a FI equivalent to those prepared hourly for Seal Sands when this was exposed by the tide, only a single value was determined for each high water period. Counts were made between one hour before and one hour after high water.

High water counts were not possible on all the field areas along the standard walk at night, but occasional visits were made to larger semi-flooded feeding areas adjacent to industrial sites, for example, the Reclamation Pond.

(iv) Movements.

By determining the numbers of birds moving between Seal Sands and field areas during the tidal cycle, and combining this with the FI's

measured in the two habitats, it is possible to calculate the actual time spent feeding by the average individual of each species population (see section (v)).

Before infilling of the South Area of Seal Sands, movement of birds from and to North Area as it was covered and exposed by the tide took place almost exclusively to and from the enclosures of the South Area. This type of movement still predominated for most species in October 1973 when the West Enclosure was proving particularly attractive for feeding. From November onwards, however, and throughout 1974, birds tended to disperse from the North Area to a number of high water roosting and feeding sites on both sides of the River Tees.

Thus in the pre-reclamation situation and in the early part of my study, observation along the East/West reclamation wall enabled an effective count to be made of birds using Seal Sands. Subsequently, counts of moving birds generally included less than $\frac{1}{4}$ of the total number known to be feeding on North Area at low water, because of the distances involved and variable visibility. However, the counts are assumed to provide accurate information on the proportions of birds moving to the different sites.

Ideally, movements should have been monitored throughout a complete tidal cycle, for example, before and after low water counts conducted about mid-day. However, in mid-winter a complete tidal cycle could not be observed during the 8 hours of daylight and frequently poor visibility precluded observation of movement on chosen days. For these reasons, estimates of movements in each month were composite, with movements away from and on to North Area being counted on separate days within the same week. Since variation in the timing and size of movement on spring and neap tides was slight in the post-reclamation situation, movements for two complete tidal cycles were compiled near the beginning and end of each month on days which were convenient with respect to available daylight and visibility.

In the 1973/74 winter most birds moved between the North Area and fields to the north of the estuary, or to the remaining parts of the South Area. At this time both monthly counts monitored movement in this northerly direction. In autumn 1974, however, heavy movement, on occasions including most individuals of some species, for example Godwits and to a lesser extent Dunlins, took place to roosts south of the River Tees. This appeared to develop as the result of increasing disturbance in the immediate vicinity of traditional roosts adjacent to North Area. For this reason movements to the north and to the south of the Tees were recorded separately on one occasion each month between October and December 1974.

Together the records of movement to the south and north of the estuary provided a satisfactory assessment of dispersal from the North Area as it was covered by the tide. The hourly counts of Curlews and Godwits, made to determine feeding intensity, also served to confirm the timing and extent of movements in these species. The critical period for movements occurred as the water reached somewhat above mid-tide level (when preferred feeding areas were covered or exposed). At these times the numbers of other species, for example Grey Plovers, could also be counted sufficiently accurately to detect any unusual change in the pattern of movement, for example, in relation to cold spells or the use of new roost sites.

(v) Calculation of the actual time spent feeding in each tidal cycle.

The FI's recorded in field areas at high water and each hour at other stages of tide on Seal Sands relate only to that proportion of each species population present. By determining the pattern of movement between field and intertidal areas this proportion can be quantified for each hour,

thereby providing a weighting for respective feeding intensities. This may be illustrated by the following example.

At HW+2 the FI of a wader species measured on Seal Sands was 80% but only 40% of this species' population was present. If no other birds of this species were feeding elsewhere, the true FI of the population was only 32%. However, if the remaining 60% of the population were on field areas and maintained an FI of 20% (recorded at high water on the previous day), this is equivalent to an FI of 12% with respect to the whole population. The sum of these two corrected (i.e. weighted) FI's for the two feeding areas gives an overall FI of 44% for the whole population at HW+2.

For ease of presentation, the two corrected FI's for Seal Sands and the field areas, respectively, may be plotted as a box diagram in which the horizontal axis represents the 12½ hour tidal cycle and the vertical axis the complete species population (100%). When FI values for each hour of the tidal cycle are plotted (as illustrated in Fig. 8) it is possible by summation to determine the proportion of the 12½ hours for which the average individual of this species actually fed. In the box diagram the total available feeding time is equivalent to the area of the box, in this case 125 cm^2 , while the area which represents the proportion of feeding time used (left unshaded) has an area of 65 cm^2 , that is, 52% of the available time. This value is referred to as the Percentage Feeding Time (PFT).

The PFT index first developed by Murton et al. (1964) has several limitations both in its calculation and its application. It is based on a variable number of measures (which in my study were necessarily collected on different occasions) and no confidence limits can be attached. Additionally, the measures incorporated differ in their accuracy. For example, the record of FI at high water makes a significant contribution to the overall PFT and may be critical in species being limited by feeding time, yet this FI could be measured on only one occasion over high water but was assumed to apply through-

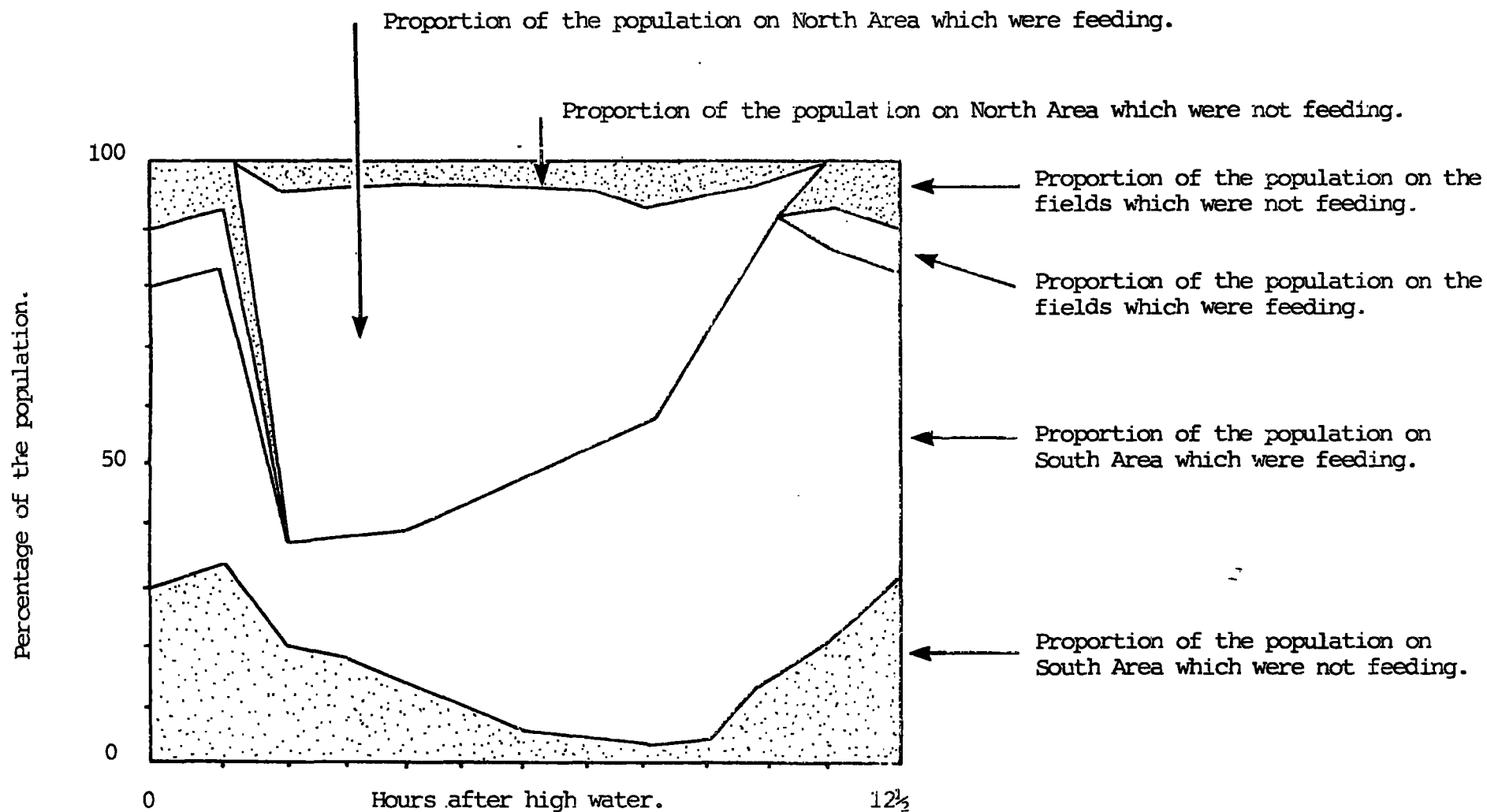


FIGURE 8 : AN EXAMPLE OF THE COMPOSITE DIAGRAMS OF FEEDING INTENSITY WHICH PROVIDED THE BASIS FOR THE CALCULATION OF PERCENTAGE FEEDING TIME (PFT).

out the four hours for which intertidal areas were unavailable. Additionally, and again, perhaps particularly relevant to those species experiencing difficulty in obtaining sufficient food, the PFT relates only to hours of daylight. It is possible that PFT may be maximal during daylight at all times of day but vary at night as necessary. PFT at night could not be calculated.

Each PFT for a species, which in this study has been calculated as an overall monthly value, relates to an average bird; it does not take into account the fact that the feeding time required by individuals will vary with age, sex, social status and general feeding ability.

Notwithstanding these reservations, PFT values do provide a useful means of comparison of pre- and post-reclamation feeding behaviour in daylight, enabling at least marked trends to be identified more clearly. However, it is possible that changes in the PFT at night may represent a more important behavioural adaptation to reclamation but, as noted above, this could not be calculated.

(b) The foraging behaviour and diet of shorebirds.

Since it was predicted before my study began (Goss-Custard, 1972; Evans, 1973) that shorebirds were likely to adapt to the reduction in feeding area and feeding time caused by the reclamation of the South Area by modifying their searching and feeding rates, I intended to make detailed and systematic measurements of these two aspects of foraging behaviour.

On each occasion which I allocated for studying foraging behaviour, I aimed to record the feeding rate and/or searching rate of at least twenty individuals of each species. In each month it was hoped to obtain a series of records for each hour between HW+2 and HW+10 (that is, during the period when preferred feeding areas were exposed). Over the study as a whole it was

hoped to collect data under a variety of climatic conditions, particularly during extremely cold weather when any influences of reclamation on foraging were expected to be more pronounced. In practical terms, however, this programme proved too ambitious and could not be achieved in the time which I had available for field work. These aims were approached most closely with respect to the larger shorebirds such as Shelducks and Curlews, but for some species data were obtainable very irregularly due, to a great extent, to the peculiarity of the birds' behaviour. This was particularly the case with Redshanks, a species whose numbers on Seal Sands varied so enormously during the winter, because of day to day variations in numbers using flooded fields, that a sample of twenty birds could not always be found. Even when their numbers were initially high on the ebb tide, many disappeared from view in creeks and channels within the flats at lower tidal levels, such that once again the sample of observable individuals was inadequate. Also, in Grey Plovers there was a tendency for all individuals to move to the central portion of Seal Sands at low water. At this range swallowing movements could not be seen, so that I was frequently unable to record their feeding rate between HW+5-7. For Coots and Curlews there were few difficulties of this sort since not only are they larger birds, but their preferred feeding areas, around the mid tidal level, were flat and relatively easy to observe.

The manner in which feeding rate and searching rate were measured are outlined below.

(i) The measurement of feeding rate.

This comprises two elements, the rate at which birds attempted to catch prey and the rate at which they actually caught prey. These were recorded simultaneously, individuals being observed for periods of one minute.

(a) Attempts made to capture prey.

In Godwits and Curlews occasional pecks at the mud surface were not considered as attempts to capture prey but as a means of detecting a prey item (although small prey were taken on rare occasions). Such movements were normally a preliminary to probing the bill into the substrate if prey was detected. Only probing was therefore recorded as the most realistic measure of the rate at which birds attempted to catch prey. The difference between surface pecking and probing by these two species was distinct, except where an individual fed in shallow water or in very liquid mud, for example, in the West Enclosure during the course of its reclamation. Since these feeding situations were not favoured by either species, individuals in such sites were not recorded. When probing for Nereis both Godwits and Curlews made several plunging movements of the head without necessarily removing the bill from the substratum. A separate probe was recorded only when the bill was removed from the substratum. Usually three or four probes of the bill were made to capture a worm.

For Grey Plovers and also for Redshanks when the latter were feeding on firm substrates, both pecks and probes were recorded as feeding movements by which prey were likely to be taken. In fact most prey were taken by pecks or shallow probes which were almost indistinguishable. Deep probing by Redshanks was rarely observed and was impossible for the short-billed Plovers.

Redshanks feeding in liquid mud generally used swishing, a feeding technique in which the bill, inserted to about half its length in the substrate, was moved from side to side as the bird walked forward, in the manner of a feeding Avocet. Usually prey seemed to be detected by contact rather than by visual cues. Thus the swishing motion of the bill was not a discrete feeding movement but rather a searching movement. Hence, of necessity, I had to obtain measures of the feeding behaviour of Redshanks by the observation of those small numbers of birds which fed by pecking and probing.

Similarly, the rate at which Shelducks and Dunlins attempted to capture prey could not be measured since discrete feeding movements were not distinguishable.

(b) The rate at which prey were captured.

The number of swallowing movements per minute and the identity of large prey were recorded for Godwits, Curlews, Grey Plovers and Redshanks (when pecking and probing). In addition I measured the size classes of those Nereis large enough to be recognised (generally those over 15 mm. in length), recording the lengths of the worms taken in terms of the birds' bill length, for example, $\frac{1}{4}$, $\frac{1}{3}$, $\frac{1}{2}$, in the case of Godwits; x 1, x $1\frac{1}{2}$, etc. for Grey Plovers. When recording this information in the field, allowance was made for worms which were unusually stretched or contracted and for worms broken into a number of separate pieces, the latter occurring frequently when Godwits took them.

(ii) The measurement of searching rate.

Searching rate was measured in two ways, the basis for each being pacing rate.

For Godwits, Curlews and Redshanks (when pecking and probing), birds employing discrete feeding movements interspersed with pacing, the method described by Goss-Custard and Rothery (1976) was used. This involved measuring with a stop watch the time taken for birds to make five paces and at the same time recording the number of exploratory surface pecks, if any, that were made. Records of individuals probing for a prey which was detected or actually capturing prey were excluded since the aim was to include only those movements associated with searching. When graphed, the relationship between the time taken for five paces and the number of pecks is approximately linear and the regression provides an intercept which represents the time for five paces in the absence of any time spent surface pecking, that is, a basic searching rate.

The foraging behaviour of Dunlins and Shelducks precluded the use of this method and for these species the number of paces taken in 30 seconds was counted. This value represents, in effect, a combined rate for feeding and searching.

For Grey Plovers no satisfactory method of measuring searching rate was devised.

CHANGES IN THE NUMBERS OF SHOREBIRDS
USING SEAL SANDS AND ADJACENT FIELDS
AND MARSHES NORTH OF THE TEES ESTUARY.

The monthly counts of the chosen shorebird species which fed at low water on Seal Sands are shown in Table 1. Counts for the North Area and South Area (the West and South-East Enclosures) are separated although the latter remained a viable feeding area at low water only between October 1973 and the end of January 1974. The counts of birds feeding on nearby fields at low water in the 1973/74 winter have been included in parenthesis in Table 1, while counts there at high water are given in Table 2.

For each species these monthly counts are displayed graphically, Figs. 9 - 11, the numbers using different portions of Seal Sands being distinguished in each case. The principal sections of North Area which each species used for feeding are shown in Figs. 12 - 14.

In the following sections the total use of Seal Sands, the numbers and pattern of use of the North and South Areas and the use of field areas are considered separately for each species in relation to the reclamation programme.

TABLE 1.

CHANGES IN THE NUMBERS OF SHOREBIRDS FEEDING ON INTERTIDAL FLATS AT TEESMOUTH.

L.W. field counts on north side of estuary between Oct 1973 - Feb 1974 and from Oct - Dec 1974 are given in parenthesis.

<u>SHELDUCK</u>	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
North Area	1240	750	921	716	448	420	100	6	250	96	250	450	830	1070	980
South Area	20	210	25	-	-	-	-	-	-	-	-	-	-	-	-
Total Seal Sands	1260	960	946	716	448	420	100	6	250	96	250	450	830	1070	980
	(6)			(15)	(22)	(41)		(87)					(12)	(2)	
<u>GREY PLOVER</u>															
North Area	63	49	98	35	88	84	50	16	3	10	32	96	50	72	73
South Area	190	90	5	58	-	-	-	-	-	-	-	-	-	-	-
Total Seal Sands	253	139	103	93	88	84	50	16	3	10	32	96	50	72	73
<u>CURLEW</u>															
North Area	250	120	101	76	146	102	120	10	100	180	95	130	50	150	92
South Area	18	71	10	6	-	-	-	-	-	-	-	-	-	-	-
Total Seal Sands	268	191	111	82	146	102	120	10	100	180	95	130	50	150	92
	(3)		(2)	(10)	(6)	(9)							(4)	(15)	(6)

TABLE 1. (continued).

<u>GODWIT</u>	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
North Area	65	52	175	52	118	105	50	2	4	31	83	70	55	78	65
South Area	310	160	48	145	-	-	-	-	-	-	-	-	-	-	-
Total Seal Sands	375	212	223	197	118	105	50	2	4	31	83	70	55	78	65

DUNLIN

North Area	6780	6270	7730	3870	2268	2220	3500	2000	320	2800	3500	6100	7200	6200	4000
South Area	2930	2060	335	520	21	80	-	-	-	-	-	-	-	-	-
Total Seal Sands	9710	8330	8065	4390	2289	2300	3500	2000	320	2800	3500	6100	7200	6200	4000

(150) (192)

(22)

REDSHANK

North Area	117	193	200	47	470	115	300	12	200	320	400	466	170	180	140
South Area	780	565	74	550	6	15	-	-	-	-	-	-	-	-	-
Total Seal Sands	897	758	274	597	476	130	300	12	200	320	400	466	170	180	140

(50) (20) (10) (20)

(28) (13) (17)

TABLE 2.

COUNTS OF WADERS AND SHELDUCKS USING THE FIELD AREAS NORTH OF THE TEES ESTUARY AT HIGH WATER.

	Date of counts.										
	18/10/73	24/10/73	7/11/73	20/11/73	22/11/73	[*] 2/12/73	4/12/73	15/1/74	19/1/74	2/2/74	17/2/74
Shelduck	0	0	1	0	0	30	19	96	35	17	47
Grey Plover	6	20	0	0	0	0	10	25	19	11	14
Curlew	180	65	14	50	30	30	X	106	70	70	60
Godwit	90	20	0	0	0	0	0	40	0	10	10
Redshank	291	250	215	240	125	70	119	250	75	109	100
Dunlin	780	1640	1950	1270	1950	440	2330	3250	1670	1900	690

N.B. X indicates the disturbance of usual roosting/feeding sites and where no count was made.

* On this occasion there was a very severe frost and freshwater and wet pasture were temporarily frozen.

All counts apply to areas covered by the 'standard walk'.

TABLE 2. (continued).

	Date of counts.										
	2/3/74	19/3/74	22/9/74	26/9/74	17/10/74	27/10/74	10/11/74	12/11/74	16/11/74	15/12/74	19/12/74
Shelduck	65	26	0	0	0	0	25	4	0	2	18
Grey Plover	2	1	14	11	8	4	4	2	3	2	2
Curlew	30	110	22	35	100	60	40	56	122	85	127
Godwit	0	0	12	0	0	0	0	16	14	45	34
Redshank	119	178	185	415	520	260	245	120	154	149	170
Dunlin	760	937	555	460	1390	1450	2160	1295	2800	1850	1510

FIGURE 9:

CHANGES IN THE NUMBERS OF SHELDUCKS AND GREY PLOVERS FEEDING ON THE
INTERTIDAL FLATS OF SEAL SANDS.

The stippled area represents that portion of the population feeding on the West Enclosure.

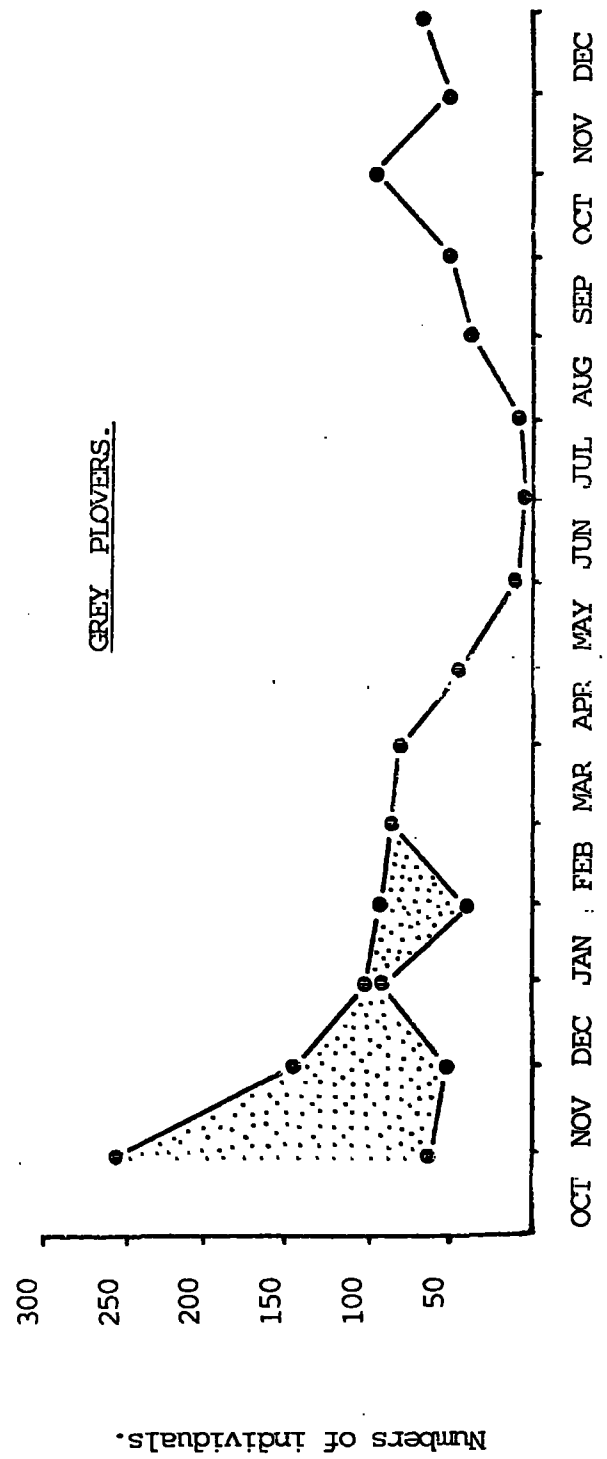
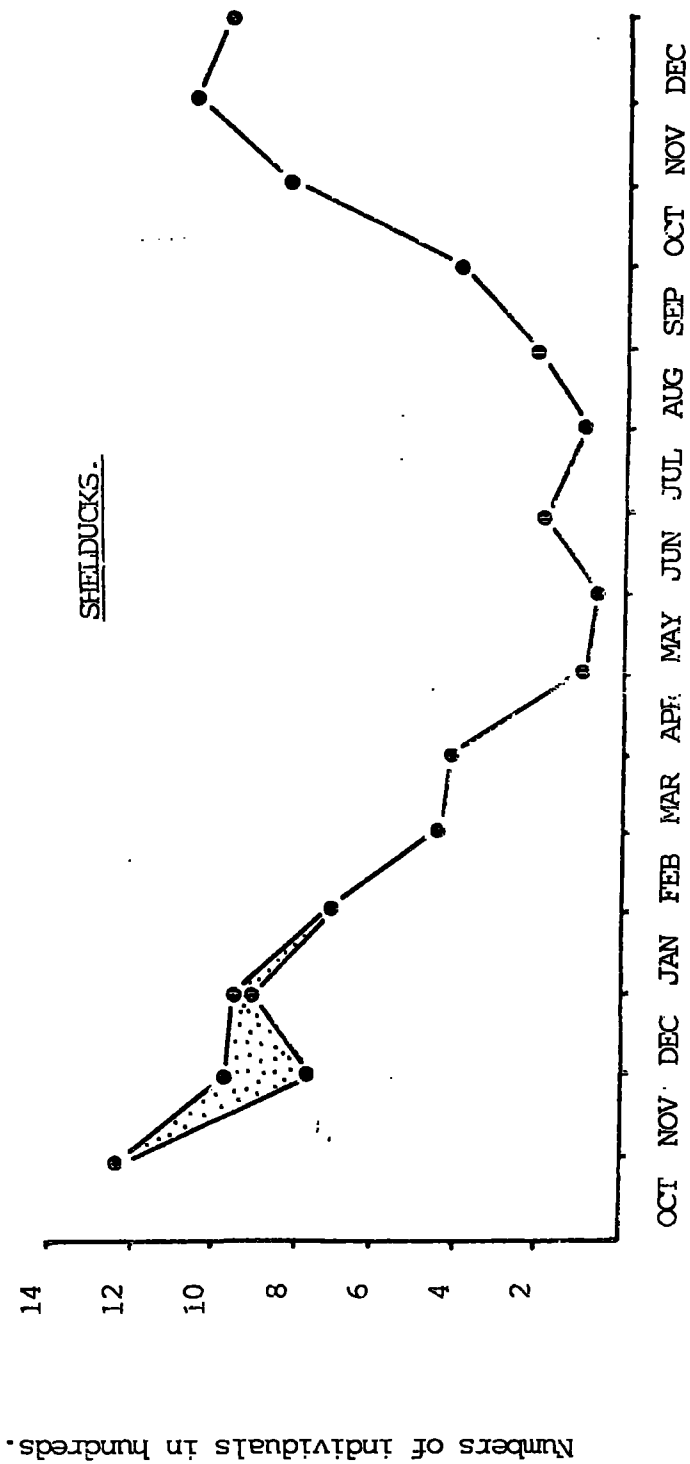


FIGURE 10:

CHANGES IN THE NUMBERS OF BAR-TAILED GODWITS AND CURLEWS FEEDING ON
THE INTERTIDAL FLATS OF SEAL SANDS.

The stippled area represents that portion of the population feeding on the West Enclosure.

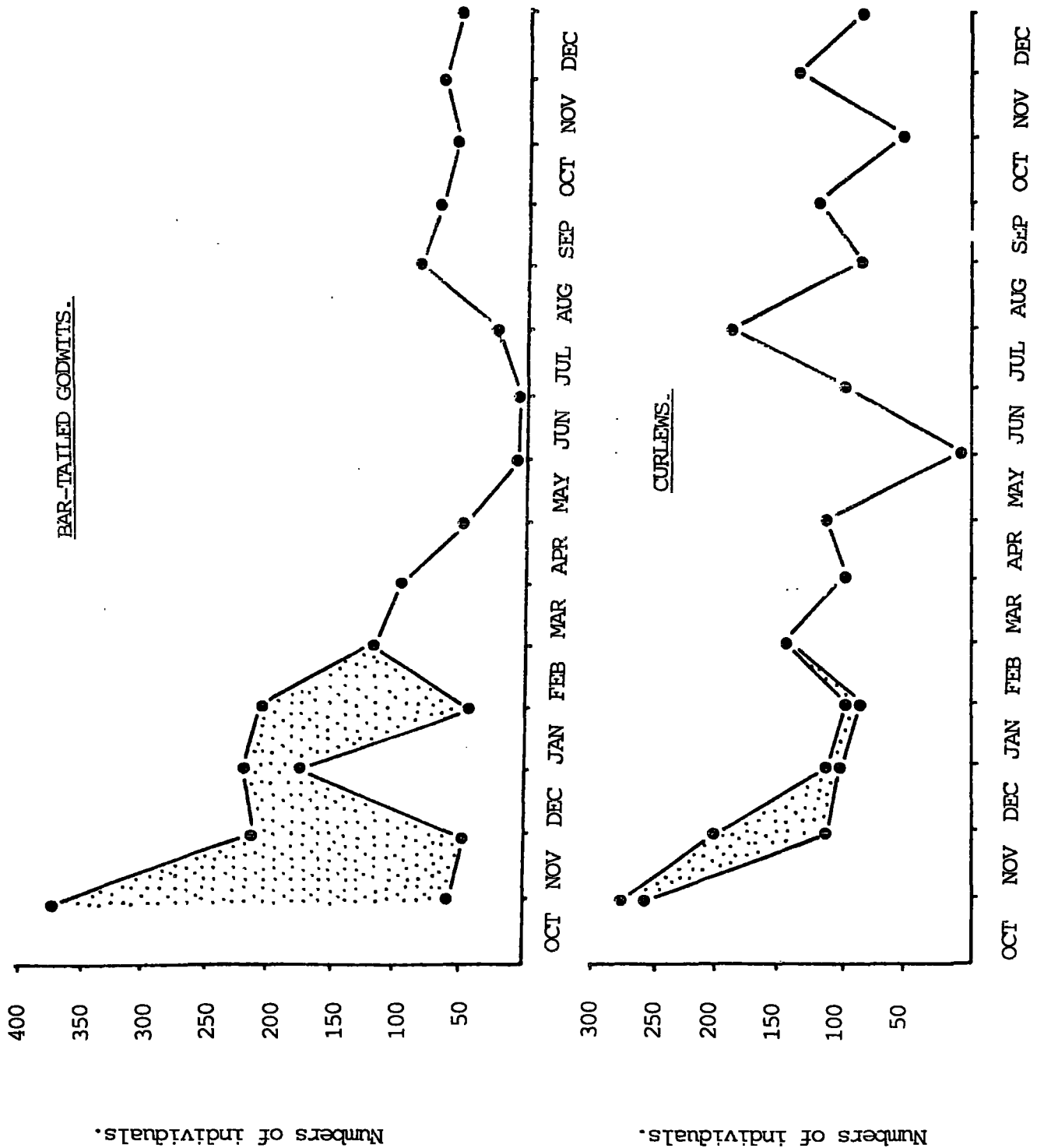


FIGURE 11:

CHANGES IN THE NUMBERS OF REDSHANKS AND DUNLINS FEEDING ON THE INTERTIDAL
FLATS OF SEAL SANDS.

The stippled area represents that portion of the population feeding on the West Enclosure.

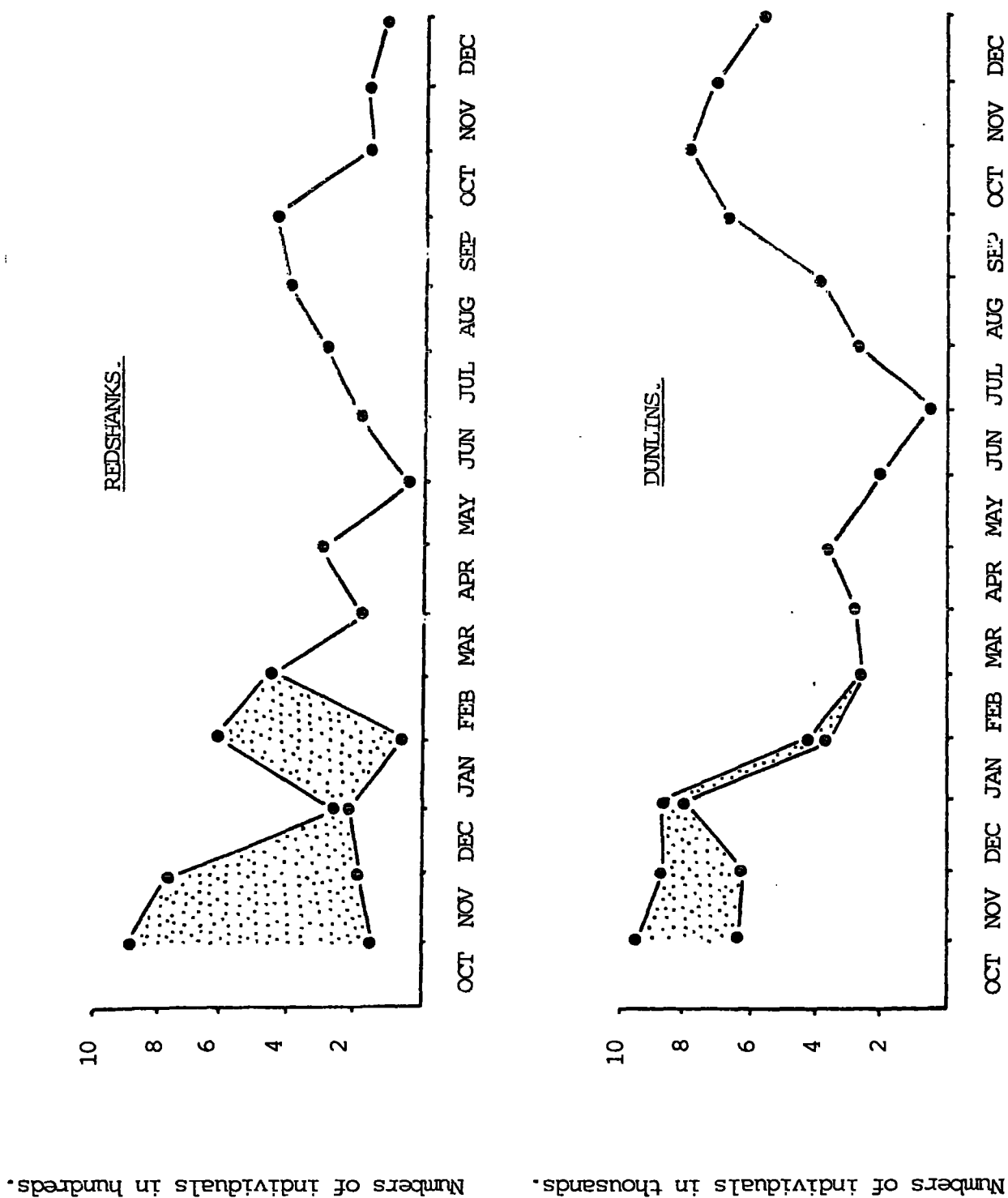
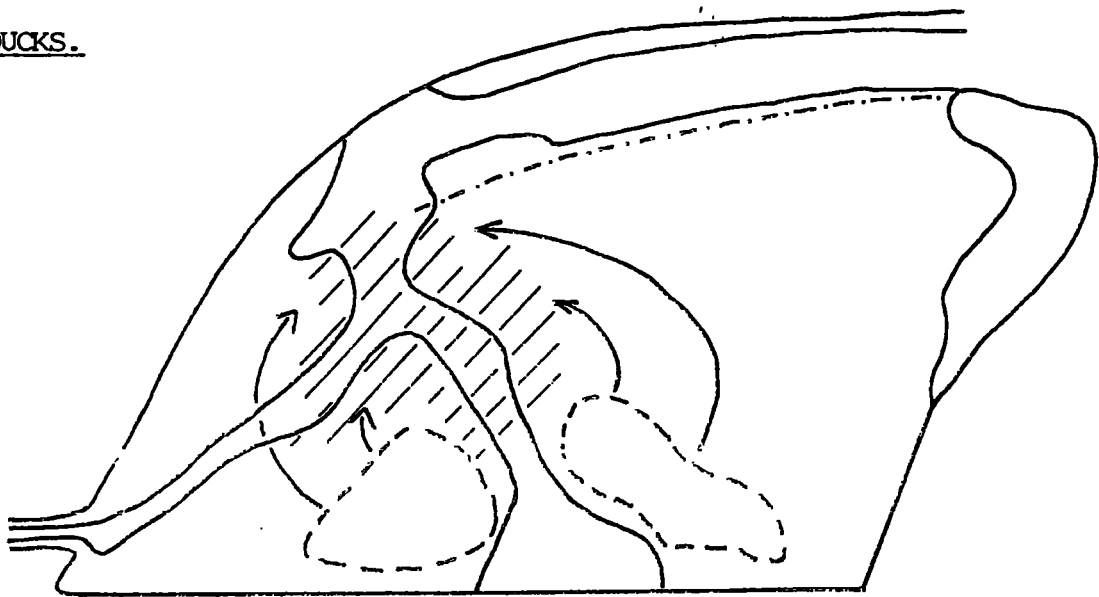


FIGURE 12: THE CHOSEN FEEDING GROUNDS OF SHELDUCK AND GREY PLOVERS WITHIN
THE NORTH AREA OF SEAL SANDS.

SHELDUCKS.



Notation:



Initial feeding areas on the ebb tide.



Main feeding areas used at low water.



Indication of the routes of movement to L.W. feeding areas.

GREY PLOVERS.

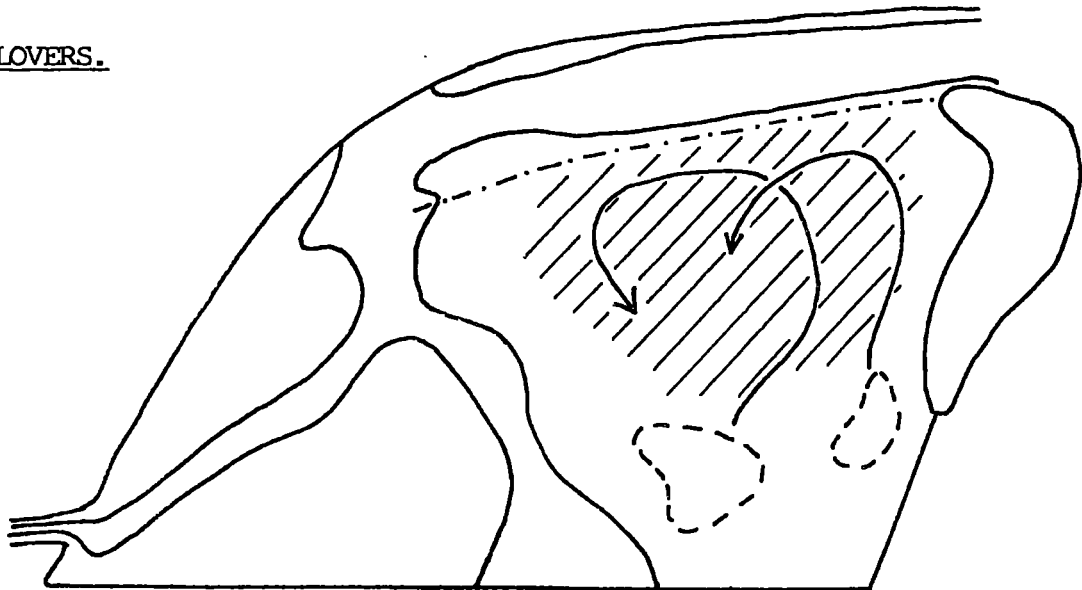
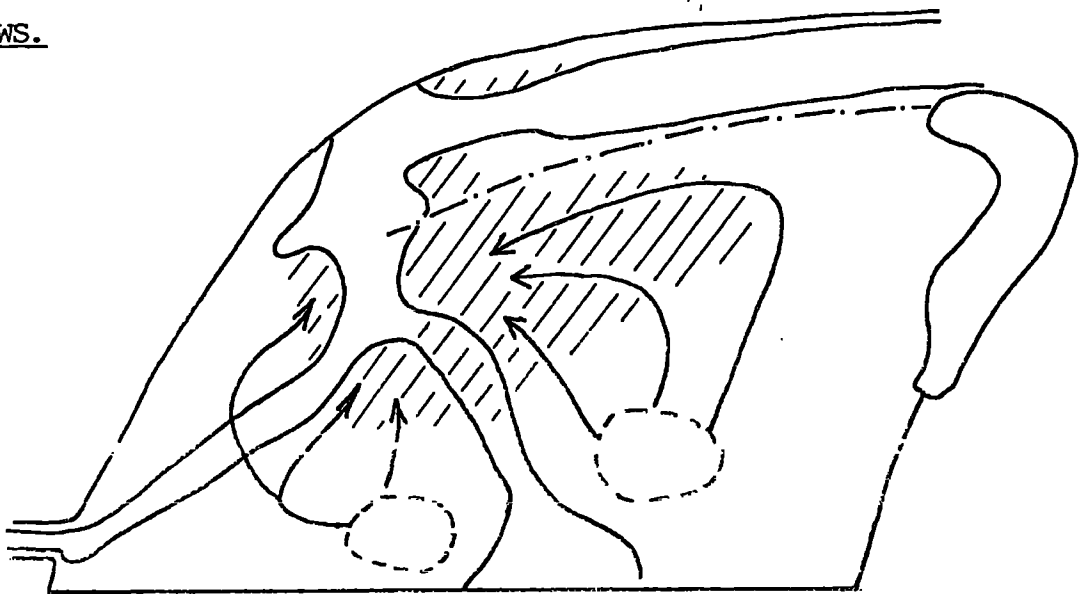


FIGURE 13: THE CHOSEN FEEDING GROUNDS OF CURLEWS AND BAR-TAILED GODWITS WITHIN
THE NORTH AREA OF SEAL SANDS.

CURLEWS.



Notation:

-  Initial feeding areas on the ebb tide.
-  Main feeding areas used at low water.
-  Indication of the routes of movement to L.W. feeding areas.

BAR-TAILED GODWITS.

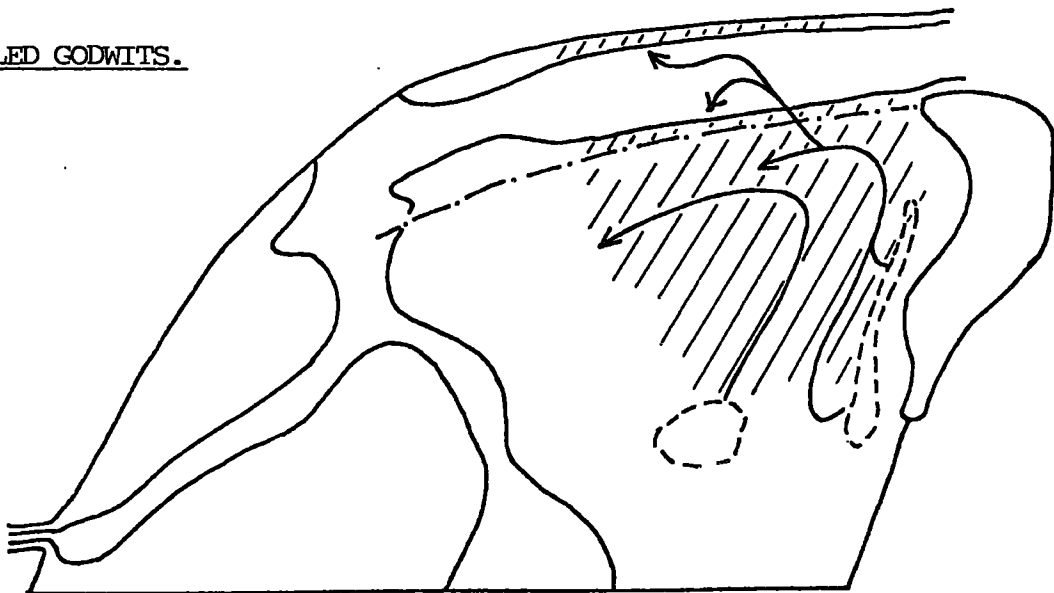
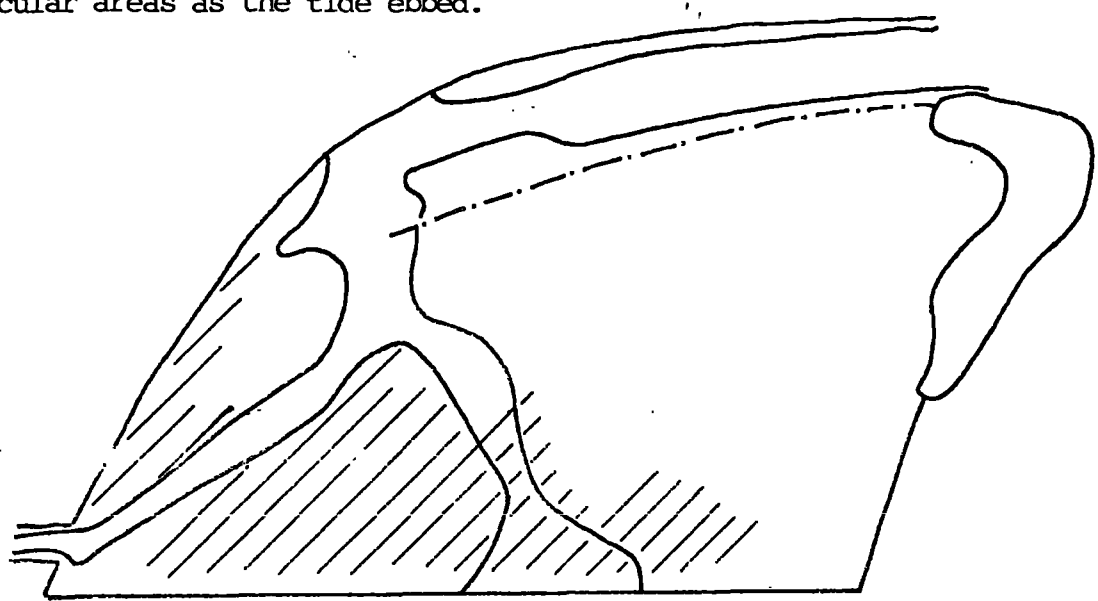


FIGURE 14: THE CHOSEN FEEDING GROUNDS OF REDSHANKS AND DUNLINS WITHIN THE
NORTH AREA OF SEAL SANDS.

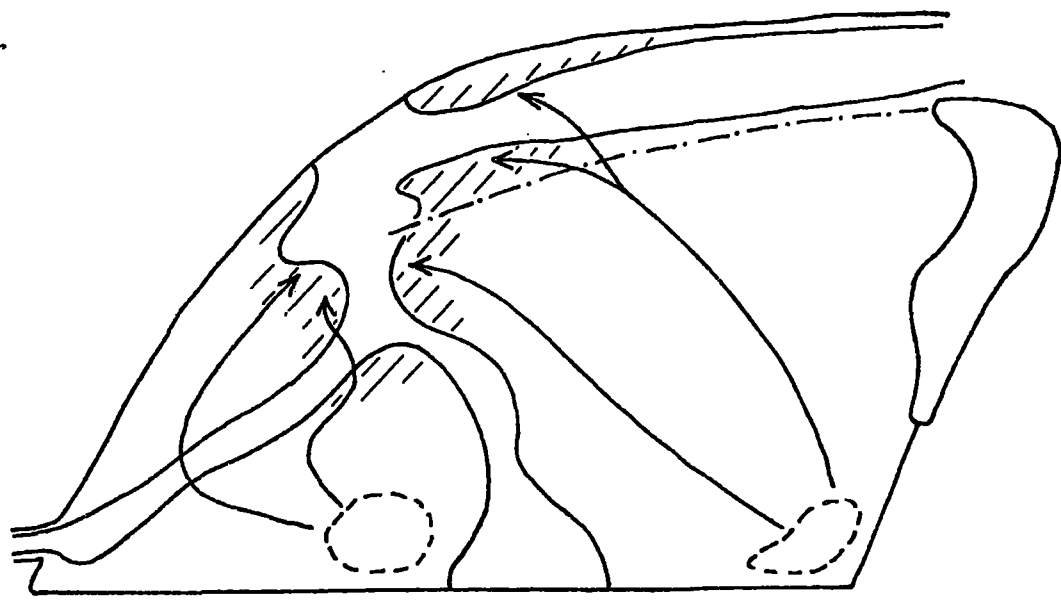
REDSHANKS. In this species there were no definite movements of birds to particular areas as the tide ebbed.



Notation:

-  Initial feeding areas on the ebb tide.
-  Main feeding areas used at low water.
-  Indication of the routes of movement to L.W. feeding areas.

DUNLINS.



SHELDUCKS.The use of different portions of Seal Sands for feeding at low water in the 1973/74 winter.

During the early stages of reclamation in autumn 1973 the West Enclosure was used only occasionally. At most, it held around 200 Shelducks at low water, but more usually only 50 - 60 individuals were to be found there. Most Shelducks therefore fed on North Area at low water from the beginning of my study, and in October 1973 this involved around 1,000 birds. Around 80% of the birds using North Area usually moved to the west Enclosure at high water. This movement did not appear to be directly related to feeding within the enclosure since movement usually occurred when most portions of the North Area were covered. By that time, despite the tidal delay caused by the slag walls, the muddy areas of substrate within the West Enclosure were also covered. By the end of November almost all Shelducks remained on North Area over high water and all feeding took place there.

The reclamation of the South-East Enclosure did not provide satisfactory feeding for Shelducks, no birds being present there at low water and only small numbers moving there to roost at high water.

The pattern of use of the South Area even at the beginning of my study was very different from that recorded by Pienkowski (1973) in spring 1973. At that time the South Area was more important for feeding, although up to 60% of the population moved to and from the North Area as it was exposed and submerged. The numbers of birds involved in movements and the timing of movement was very variable but nonetheless this was clearly an important part of this species' feeding strategy. The North-East Enclosure was the preferred feeding site of

Shelducks in spring 1973 with between only 47 - 251 birds using the West Enclosure.

It would appear that the reclamation of the North-East Enclosure had effectively removed the South Area as a viable feeding ground. The West Enclosure had not been a favoured feeding site and movement there over high water during reclamation occurred only for roosting, since it still provided an element of shelter and security. The active reclamation of the enclosures did not provide favourable feeding conditions as it appeared to do for several wader species.

The use of fields and marshes.

Although small groups of Shelducks regularly moved to field areas at high water, particularly to the former channel of Greatham Creek within the Brinefields and also to the Reclamation Pond, the majority of the Seal Sands population roosted on the estuary in both the 1973/74 winter and in autumn 1974. In the 1973/74 winter the highest recorded use of the fields was in January 1974 (96 birds), and throughout the spring records frequently exceeded 30 birds. Generally when numbers using the fields were high, the proportion of birds feeding there was also high, thus it seems possible that after reclamation and towards the end of the overwintering period when prey populations were probably at their lowest levels of availability, some Shelducks were having to feed over the high water period on the fields and pools. However, although the lowest level of use of field areas in the 1973/74 winter occurred in autumn (when the West Enclosure was available for feeding over part of the high water period), equally small numbers visited the fields after reclamation in autumn 1974 (maximum records of 25 individuals). There appeared to be no direct relationship between the level of use of the fields and climatic factors, although the high record of 96 birds within the 'standard walk' in January 1974 did coincide with a particularly cold spell during that winter.

The record of 87 birds using the Reclamation Pond in May 1974, almost the entire population at that time, was exceptional. Also at this time many paired resident breeding Shelducks were present in widely dispersed field areas.

Areas used for feeding within North Area. (Fig. 12).

Shelducks on North Area fed most intensively as the flats were exposed and covered by the tide, feeding by upending and dredging food from the submerged surface of the flats. Feeding in this manner was most concentrated over the central portion of North Area, the Central Bank, and, as this became exposed, most of the population settled on this section and thereafter fed by swishing (or scything).

Around low water the majority of feeding Shelducks were located in the water or along the margins of Seaton Channel and on areas of wet mud bordering the Central Bank, areas exposed after HW+5. Only small groups continued to feed over low water in the muddy channels and slacks at higher tidal levels. In all months of my study, the majority of the population ceased to feed over low water and a large roosting flock of Shelducks developed on the Central Bank. These birds would typically begin to feed again as the tide flooded over the roosting area.

Shelducks always showed preference for feeding in areas of 'sticky' mud, avoiding areas of liquid mud such as developed in those portions of North Area where fine outwashed sediment was accumulating (the preferred feeding sites of Redshanks) due to the reclamation of South Area.

Seasonal fluctuations and numbers using Seal Sands.

In the 1973/74 winter there was a progressive decline in the numbers of

Shelducks using Seal Sands from a peak in October 1973. There seemed to be no relationship between this fall in numbers and particular stages in the reclamation programme.

In autumn 1973 and 1974 the peak numbers and overall levels of the populations were reasonably similar although peak numbers in autumn 1974 were achieved rather later than in 1973.

GREY PLOVERS.

The use of different portions of Seal Sands for feeding at low water in the 1973/74 winter.

In spring 1973 low water counts showed that just over 220 Grey Plovers made regular use of Seal Sands, feeding being concentrated on North Area and within the North-East and West Enclosures of South Area (Pienkowski, 1973).

When my study began, therefore, two principal feeding sites for this species remained. At the end of October 1973, 75% of Grey Plovers (190 birds) used the West Enclosure at low water whereas the maximum count there in spring 1973 had been only 98 birds. This suggests that, as for some other wader species, the process of active reclamation provided particularly favourable feeding conditions. Within the West Enclosure feeding occurred in all areas of firm, sandy mud but was particularly concentrated around the margins of the deltas of dredged material. This concentration became more pronounced as fine sediment covered the original flats. By the end of November 1973 the number of Grey Plovers using the West Enclosure had dropped to 90, this being associated with a reduction in the total Grey Plover population of Seal Sands. Numbers on North Area also fell slightly during November.

When active reclamation of the West Enclosure ceased the number of Grey

Plovers feeding there at low water fell rapidly, such that by the end of December 1973 only five birds were present at that stage of tide. Those birds displaced were accommodated on North Area with the result that a peak in the numbers using North Area for feeding was recorded in December, namely 98 birds. This figure is, however, substantially lower than highest low water count on North Area in spring 1973, namely 195 birds in early March.

In late January 1974 the distribution of Grey Plovers was again reversed with birds previously feeding on North Area transferring to the South-East Enclosure during the period of its reclamation.

The differential use of the North Area and the enclosures of South Area during reclamation was broadly similar to that of Godwits. This is perhaps not unexpected since for both species the preferred prey at Teesmouth was Nereis and both favoured feeding sites comprising firm mud/sand substrates. However, Grey Plovers, unlike Godwits, retained the pre-reclamation pattern of movement between the North and South Areas, that is with up to 80% of the population beginning to feed on the ebb tide on North Area, but with a substantial and progressive movement thereafter to the South Area. Before reclamation this movement had the important effect of enabling individuals to feed for longer periods of time due to the delay in the tidal cycle caused by movement of water through the enclosing slag walls. During reclamation, however, the raised nature of the deltas of dredged material and the manner of infilling, which provided feeding throughout the tidal cycle in the West Enclosure, may have removed this advantage of movement at least for Godwits. A possible reason why Grey Plovers adhered to their established pattern of movement may be related to the high density at which waders fed on the West Enclosure deltas at high water. In these situations the feeding success of Grey Plovers using their traditional run-stop-peck feeding technique is likely to be greatly reduced (Pienkowski, 1973) sufficient at least perhaps to make movement away from an otherwise very

attractive feeding site the most beneficial alternative.

The use of fields and marshes.

During reclamation, when the enclosures of South Area provided valuable feeding at high water, only occasional individuals were seen to feed within adjacent field areas, although up to 25 were seen to roost there. After reclamation was completed in early February 1974, and contrary to expectations at the time, no more than four individuals were seen on the fields at high water. Grey Plovers were seen most frequently on the Brinefields in the channel of the former Greatham Creek, but occasional birds frequented Seaton Common, the Reclamation Pond and Dormans Pool, which are further from Seal Sands.

In autumn 1974, the favoured area was again the Brinefields near the cut-off Greatham Creek, but there appeared to be no increase in the overall use of field areas for feeding.

Areas used within North Area. (Fig. 22) .

The majority of Grey Plovers using North Area in October 1973 fed in the Eastern Channel, with a distribution similar to that of Godwits, that is birds fed throughout its length with no special preference for feeding at the edge of the retreating tide. In November and December 1973 there was an increasing tendency to follow the water's edge closely on ebb tides, the majority of birds tending to remain in the Eastern Channel until its complete exposure between HW+4-5. Thereafter birds moved to the Central Bank where feeding was concentrated on the higher northern and eastern margins, that is areas of firm sandy muds. This almost circular movement of the population through each tidal cycle became more pronounced in January 1974, but in February the previously strong preference for feeding in the Eastern Channel diminished, with birds

tending to move more directly to the Central Bank as it became exposed.

With loss of the South Area for feeding over high water, Grey Plovers remained on North Area until finally forced to move by the flooding tide.

In September and October 1974 the Eastern Channel was again the most favoured feeding location and the circular pattern of feeding established in mid-winter 1973/74 was repeated. At the end of October 1974 this pattern again broke down, as noted in February of the previous winter, to be replaced by rapid dispersal to preferred portions of the Central Bank.

While the changes in the pattern of feeding amongst the whole population of Grey Plovers were distinct in both winters, not all individuals were involved. During almost the whole day of observation between late September and December 1974 a single Grey Plover, individually identifiable by a limp, was seen feeding in one portion of Eastern Channel throughout the tidal cycle; this bird was reluctant to move from its chosen feeding station and quickly returned if disturbed, defending it against members of the same species. A similar observation was made of Curlews (p. 202).

Seasonal fluctuations and numbers using Seal Sands.

Although peak population levels occurred in early autumn in both years, in autumn 1974 this peak reached only 30% of the numbers in the previous autumn. (This might be an underestimate if the true peak in autumn 1973 had occurred in September, that is before the beginning of my study, as it did in 1974).

In both winters the decline in numbers following the autumn peak paralleled similar changes in the use of Seal Sands by Godwits and culminated in the establishment of a 'stable' overwintering population which was maintained with only a slight, although steady, decline until April. There were no changes in numbers which coincided with the temporary loss in the attractiveness of the enclosures

for feeding in December 1973 nor with their complete demise in February 1974.

The 'stable' population level recorded on North Area in autumn 1974 was below that established on Seal Sands in autumn 1973 and below the levels achieved on North Area alone in spring 1974 when reclamation was completed.

CURLEWS.

The use of different portions in Seal Sands for feeding at low water in the 1973/74 winter.

The use of the West Enclosure by Curlews during reclamation never approached the levels recorded for other Nereis feeders. The highest level of use occurred in November 1973 when over 70 birds (30% of the population at that time) fed there at low water. Before reclamation began, that is, in early October, less than 20 Curlews fed here regularly, and in spring 1973 Pienkowski (1973) recorded a maximum of 64 individuals. All birds showed preference for those parts of the West Enclosure covered by fine sediment, that is, areas similar to those favoured by Redshanks, rather than those chosen by Godwits or Grey Plovers, but usually Curlews fed where the fine sediment was too deep for Redshanks to feed (over 10 cm.), thereby achieving a spatial separation of the two species.

The reason why Curlews chose to feed primarily in areas of deep sediment was not apparent. On the contrary, since areas of deep sediment developed first at lower tidal levels within the enclosure and were thus only exposed for a relatively short period, it might have been expected that these would be the least attractive of feeding sites. Furthermore, since the sediment had to pass through a 'thin' stage before it became deep, it is possible that Redshanks might have previously extracted many of the Nereis which were present there before reclamation (that is, the worms present in the original substrate which were

driven to the surface of the fine sediment).

During reclamation between 15 - 30 Curlews using North Area at low water would move initially to the West Enclosure; as the tide flooded, the majority flew directly to the adjacent marshes and fields. Only occasional birds stayed throughout the high water period on the West Enclosure.

Although Curlews, like other waders using the West Enclosure, appeared to take the majority of prey items from within the fine surface sediment, many large Nereis were taken by probing deeply, presumably into the original flats.

The reclamation of the South-East Enclosure did not create attractive feeding for Curlews, as it did for Godwits and Grey Plovers. In this, Curlews were again more similar to Redshanks, and indeed small numbers fed in the West Enclosure along the outflow from the South-East Enclosure during its active reclamation.

Use of field areas.

The fields and marshes in the vicinity of Teesmouth provided particularly attractive feeding for Curlews in both years of my study. The extent of field feeding was suggested by the occasional use of North Area by a large flock of Curlews additional to those normally present. Invariably the second flock remained discrete and few individuals fed; and all birds in the flock left together after staying on North Area for perhaps only two hours. This flock, which first appeared in November 1973, returned on a number of occasions until March 1974 at which time large numbers of Curlews ceased using Seal Sands.

This 'non-feeding' flock generally comprised over 100 individuals, the number declining through the winter from a peak of about 150 birds in November 1973, when its appearance on North Area was most frequent. It is assumed that these birds were feeding exclusively on field areas north of the estuary, beyond the

areas included in the 'standard walk'. Although it was expected that this flock would have made use of intertidal areas when the flooded pasture areas were unavailable in severe weather, this was never recorded.

A similar non-feeding flock did not appear on North Area in autumn 1974, although the location and quality of feeding in field areas appeared similar. However, occasional checks on field areas within the standard walk at low water revealed the presence of small groups of Curlews, comprising 20 - 30 birds. Clearly, there was once again no necessity for some Curlews to use intertidal areas for feeding.

During autumn and mid-winter 1973 Curlews, like Redshanks, tended to remain on North Area only while preferred feeding areas were available. A steady movement to fields took place after HW+7 and a return movement between HW+2½-3. In autumn 1974 and in late spring 1974 movement from North Area was more concentrated around HW+8½ although this did not necessarily imply an increased period of feeding on North Area.

In both years of study, Greenabella Marsh and the Brinefields were favoured for use at high water by birds feeding on Seal Sands; frequently counts here included 80% of birds present on the flats at low water. Small numbers also used Seaton Common or Dormans Pool, but more frequently Cowpen Marsh was used as an alternative to the Brinefields and Greenabella when these areas were subject to disturbance.

The presence of an exclusively field feeding flock of Curlews in the winter of 1973/74 and the prolonged use of field areas for feeding over high water in both years - frequently exceeding 6 hours for birds using Seal Sands - suggests that at Teesmouth the availability of suitable field areas was of great value to Curlews and might be a major factor determining total overwintering numbers around the estuary.

Areas used within North Area. (Fig. 13).

Movement to North Area on the ebb tide occurred most frequently around HW+2½-3 as preferred feeding areas became exposed. This movement typically included the majority of birds in a single flock. Only slight variation in the timing of arrival on North Area occurred between spring and neap tides - major variation being the result of disturbance of field areas.

Between October - December 1973 two principal feeding areas were easily distinguished within North Area: the 'Greenabella Bank' where over 100 birds fed regularly at low water and, therefore, representing the single most important feeding site, and subsidiary to this, the Central Bank. In January 1974 the Greenabella Bank was used by progressively fewer Curlews and in February and March perhaps only 3 birds fed here at low water. During this time all feeding became concentrated on the Central Bank.

The western portion of the Central Bank, comprising soft deep mud, was preferred for feeding. Birds followed the water's edge closely on the ebb tide and then dispersed more widely around low water over the Central Bank. At this time, it was frequent to find small numbers of Curlews, which had stopped feeding, roosting on the higher drier parts of the flats.

The Central Bank was again a principal feeding area in autumn 1974, whereas Greenabella Bank was only used by occasional individuals. The reason for its popularity in autumn and early winter 1973 is not clear, although its use did coincide with the period of active reclamation of the West Enclosure. It is possible therefore, although there is no firm evidence for this, that Greenabella Bank, like the portions of the North Area immediately adjacent to the West Enclosure where Redshanks fed heavily during reclamation, was subject to the deposition of fine sediment which again made prey particularly available, albeit temporarily. It was assumed initially that the distance of Greenabella Bank from the outflow from West Enclosure - over 200 yards - although in the direct line of

water flow, would mean that very little new sediment would accumulate on this section. However, the intensity and timing of use was closely similar to those of other waders for which reclamation more clearly provided very favourable feeding.

Although only small numbers of Curlews fed in the Eastern Channel of North Area (the preferred feeding location of Godwits), the regular presence of single birds in the same sites both during the day and at night suggested that some individuals at least had a great tenacity to a chosen feeding site. It was not established if these feeding territories were defended.

Seasonal fluctuations and numbers using Seal Sands.

In the 1973/74 winter there was a marked autumn peak in the numbers of Curlews on Seal Sands (268 birds in October). Numbers fell steadily thereafter until January 1974 when the lowest population level (82 birds) was recorded. In late spring 1974, although there was great week to week variation in the numbers, there was an overall increase in the use of North Area. It was not possible in my study to determine whether these seasonal changes in numbers were associated with movement of birds to or from other estuaries, or whether movement between Seal Sands and adjacent field areas was more important. The presence in the vicinity of Teesmouth of a large field feeding flock of Curlews, which frequented Seal Sands on occasions throughout the winter, gives some support for the latter hypothesis. Furthermore, the abrupt decline in numbers using North Area between October and November coincided with the development of the non-feeding flock of Curlews on Seal Sands. High counts of Curlews on North Area at low water in spring 1974 coincided with high numbers of Redshanks visiting intertidal areas, and a large proportion of the population of this species was also suspected of feeding exclusively in the fields. It seems likely that both species would respond similarly to changes in the profitability of feeding in the fields and thus that their occurrence on Seal Sands would follow a similar pattern.

While it was expected that peak numbers in autumn 1974 might again occur in October, it was at the end of this month that the lowest level of use was recorded, there being 200 fewer birds present than in the same month of 1973. However, more usually, just over 100 were present when hourly measures of F.I. were made - therefore, the monthly count may be regarded as exceptional. Nonetheless, the difference in October levels is considerable. By late November 1974, however, numbers had increased although they decreased again slightly in December. The counts in these two months of 1974 were slightly lower than in the same months of 1973 when considering Seal Sands as a whole, but with respect to the numbers using North Area alone they are reasonably similar and this is so for respective October counts also (using the 'adjusted' figure based on F.I. counts). The small differences between the levels of use of North Area in 1973 and 1974 are perhaps to be expected in a situation where an attractive alternative feeding site also exists, i.e. the field areas, and with which there must have been some interchange of individuals. The difference in numbers using Seal Sands as a whole between the two years appears to result from a loss of those birds which fed on South Area in autumn 1973.

Before reclamation, in spring 1973, the numbers of Curlews using North Area at low water had varied from 47 to 168 (mean of four counts being 105 birds), while Seal Sands as a whole had supported between 196 and 340 birds (the mean being 268) (Pienkowski, 1973). The level of use of North Area during and after reclamation had thus remained broadly similar to that recorded before reclamation. There had been no increase in use and those birds previously using Seal Sands had moved elsewhere, although not necessarily outside the Teesmouth area.

BAR-TAILED GODWITS.

The use of different portions of Seal Sands for feeding at low water in the 1973/74 winter.

In spring 1973, Pienkowski (1973) recorded that Godwits preferred to feed on the North-East and West Enclosures of South Area. Between 13 - 28% of the population moved from the main roosts on South Area to feed on North Area as the latter became exposed (mudflats being exposed earlier on North Area than on South Area because of the tidal lag. see p. 141) but some returned to South Area before low water. The numbers of birds feeding on North Area at low water varied from 51 (26% of the population at that time) to 175 (25% of the population), the mean of counts on four occasions in February and early March 1973 being 113.

The reclamation of the West Enclosure (between October and early December 1973) and of the South-East Enclosure (late January to early February 1974) created particularly favourable feeding conditions for Godwits and despite the loss of the North-East Enclosure, the South Area remained the preferred feeding location for this species during periods of active reclamation. Between 310 (83% of the population) and 145 (74% of the population) Godwits fed in the South Area at low water during reclamation, while the numbers of birds on North Area at these times varied from 65 (17%) to 52 (26%), lower numbers, therefore, than recorded on most occasions before reclamation. In contrast to the situation recorded by Pienkowski, those birds which started to feed on North Area as it became exposed remained there throughout the exposure period. There was little or no return movement of birds to South Area before low water nor was there a progressive movement to the enclosures after low water.

As has been noted, the process of reclamation of the West Enclosure created deltas of coarser debris around the inflow points of the 'liquid' dredged material and it was on the margins of these deltas that feeding Godwits concentrated.

Before reclamation, in spring 1973 and at the beginning of my study in early October 1973, feeding birds were well distributed over all sections of the enclosure. Possible reasons for the attractiveness of feeding in the deltas are considered on p.155. Few Godwits fed in areas of fine outwashed silt and as the depth of this sediment increased so feeding became increasingly concentrated on the deltas. No birds were seen to feed in mud over 5 cm. in depth, although the feeding success of Redshanks in deeper mud suggested Nereis were abundant near to the surface in such situations.

In the South-East Enclosure, which was completely filled with water from mid-October 1973, all feeding, of necessity, occurred on the immediate edge of the deltas and here most birds fed in the water.

In early December 1973 active reclamation of the West Enclosure ceased and there was a dramatic fall in the numbers of Godwits using this section of Seal Sands. At the end of December only 48 birds fed there. All Godwits displaced at this time appeared to be accommodated on the North Area, 175 birds being present there at low water at the end of December. At high water in late December and early January, a few Godwits continued to feed in the West Enclosure, the raised deltas of debris being available for feeding throughout the high water period. When the reclamation of the South-East Enclosure was completed by early February, the South Area ceased to be a viable low water or even high water feeding area. Thereafter all Godwits were restricted to feeding on the North Area and 118 birds were recorded there at low water at the end of February, that is between 60 - 70 more birds than used this section of Seal Sands during reclamation but similar to the mean of numbers recorded there before reclamation (113) in spring 1973 (Pienkowski, 1973).

The use of fields and marshes.

During reclamation only occasional Godwits were seen to move to field areas at high water: the majority remained on the enclosures of South Area where the raised deltas of dredged debris enabled feeding throughout the high water period. In late February and March 1974, when the enclosures provided no additional feeding over high water, small numbers did move to the Brinefields and to Greenabella Marsh (adjacent to North Area) and a few birds did feed there. However, this use was not regular and most of the population roosted on the partially reclaimed West Enclosure.

From September to early November 1974, the entire population of Godwits feeding on North Area at low water moved south of the River Tees to roost near Bran Sands. During this period no Godwits were seen in the fields north of the estuary. In November, however, small numbers began to move to the Brinefields at high water and in mid-December 1974 45 birds were present there, 50% of the population using North Area at this time. On all occasions some birds were seen to feed in the cut-off channel of Greatham Creek, this being a tidal, although predominantly brackish, body of water. During this period, small numbers of Godwits also fed, just before high water, in Greatham harbour.

Before reclamation Pienkowski (1973) recorded single birds using the field areas on two occasions.

Areas used for feeding within North Area. (Fig. 13).

The principal feeding site of Godwits within North Area was the Eastern Channel, an area of firm muddy sand which retained a surface film of water, even after low tide. Between October - December 1973 and October - December 1974 there was no apparent concentration of feeding towards the tide edge, except at higher tidal levels, for example HW+2 and HW+9 when some birds regularly fed in

the water. During these periods it was common to find between 50 - 75% of those Godwits using North Area to be spread along the entire length of the Eastern Channel even when it was fully exposed. Generally, those birds feeding in the higher sections of the Eastern Channel were smaller, male birds.

In January 1974 there was an increasing tendency for Godwits to move from the Eastern Channel before low water to other portions of North Area, in particular to the Central Bank.

The same sections of North Area were used for feeding by day and night, and the pattern of dispersion on the ebb tide was similar, but there appeared to be a preference at night for feeding in channels and gullies rather than on the open flats which was usually the case in the day.

Seasonal fluctuations and numbers using Seal Sands.

In autumn 1973 the peak numbers of Godwits using Seal Sands were in October. A marked fall in numbers occurred in late October and early November, a loss of birds largely from those feeding in the West Enclosure. Population levels established in late November 1973 (197 - 223 birds) were maintained with only a slight decline until February 1974 when a further decline in numbers occurred, and this coincided with the complete loss of feeding even at high water in the enclosures. This decline appeared to be separate from the more complete emigration in April and May, although Godwits do begin to leave other estuaries on the north-east coast of Britain, e.g. Lindisfarne, in late February and March (Smith, 1975).

In autumn 1974 there was no early peak in numbers nor any drop in numbers in early autumn. From late September until the end of my study in December, a reasonably 'stable' population of between 55 - 78 birds fed on North Area. Thus numbers were around $\frac{1}{3}$ of those I recorded using Seal Sands during reclamation in the 1973/74 winter, and lower also than the numbers present in February and

March 1974 when the final post reclamation situation was achieved.

REDSHANKS.

The use of different portions of Seal Sands for feeding at low water in the 1973/74 winter.

The peak numbers of this species at Teesmouth are usually in September (Prater, 1972). During early October 1973, before reclamation of West Enclosure commenced, Redshanks were widely distributed over both that enclosure and North Area. By the end of October however, 780 Redshanks were present on the West Enclosure and only 117 fed on the North Area at low water. Larger numbers moved initially to feed on the North Area, but rarely more than 250 individuals and, as numbers at low water show, many of these returned quickly to the West Enclosure.

In spring 1973, before any reclamation of South Area, when the overall numbers of Redshanks using Seal Sands were considerably lower than in early autumn 1973, the numbers on North Area varied from 17 - 144, while on South Area there were between 75 - 250, of which a maximum of 116 fed in the West Enclosure (Pienkowski, 1973). Numbers using North Area were larger as it became exposed by the ebbing tide, but many of these birds moved to the enclosures before low water. It would appear, therefore, that the numbers of Redshanks using North Area before reclamation and during the early part of reclamation were similar and that in both periods there was a similar pattern of movement between the open and enclosed parts of Seal Sands. During reclamation the West Enclosure clearly provided very favourable feeding for this species and the level of use of this area was very much greater than it had been previously.

Between October and December 1973, however, the use of the West Enclosure diminished and at the end of December only 74 birds were present there at low

water. The process of reclamation, although initially creating a very attractive feeding site, ultimately made it useless for feeding. Of the 700 Redshanks displaced from the West Enclosure, around 80 moved to the North Area but the majority disappeared from Seal Sands. In October and November, most Redshanks using North Area moved to West Enclosure at high water, but in December greater numbers moved to the fields directly and this continued in spring 1974. In part, the reduction in numbers may have involved emigration from Teesmouth which was usual at this time of year (see later) but it was not possible to distinguish this from emigration which might have been directly attributable to the loss of West Enclosure for feeding. It seems likely that large numbers of Redshanks forced from the West Enclosure were in fact feeding exclusively in the wet and flooded pasture around the estuary. This is suggested by the immediate increase in numbers using Seal Sands when, in January 1974, the reclamation of the South-East Enclosure again created favourable feeding for this species, mainly along the outflow channel from the South-East Enclosure into the West Enclosure. The numbers recorded here at low water at the end of January were similar to those in November 1973, and included all those Redshanks previously using North Area.

Coincident with the end of reclamation of the South-East Enclosure in early February, a large reduction occurred in the numbers of Redshanks using Seal Sands, but again this was temporary. Subsequently, the use of North Area varied greatly from day to day. A maximum record of 470 birds fed there at the end of February. The presence or absence of Redshanks on North Area did not appear to be related to the timing of the tidal cycle (and thus the period of mudflat exposure) in relation to daylight, but may have been associated with variation in the profitability of feeding on the fields and marshes. The maximum use of North Area in spring 1974 greatly exceeded that in spring 1973, although the regular use of North Area in these two periods was possibly similar.

Within the West Enclosure Redshanks fed almost exclusively in areas of newly

deposited 'liquid mud' where all birds adopted a 'swishing' feeding technique (described later: see Foraging Behaviour). Most prey were taken from within the new sediment, rather than by probing into the original flats. Redshanks showed preference for feeding in areas where the 'liquid mud' was between 4 - 7 cms. in depth but some birds continued to feed when the mud was 10 cms. deep.

Use of field areas.

In both winters of my study, rainfall was considerably higher than average and caused extensive flooding in pasture areas north of the estuary. These areas of surface water were frozen only temporarily and, therefore, prey availability was greatly reduced only in November 1973 and January 1974. At these times, feeding away from the estuary at high water was restricted to brackish pools, such as the Reclamation Pond and the former Greatham Creek in the Brinefields, e.g. HW on 15/1/74. During November 1973 movement to field areas was slight since the West Enclosure was available for feeding throughout high water. The cold period in this month did not seem to make it difficult for Redshanks to collect sufficient food.

When mild wet weather prevailed after reclamation, it was frequently found that most Redshanks, which normally fed on North Area as the tide fell, had left by HW+7. Generally, these birds moved to field areas immediately adjacent, that is, areas included within the 'standard walk', notably the former channel of Greatham Creek and the Reclamation Pond, but birds also dispersed widely throughout the Brinefields. However, it was in fields beyond the 'standard walk' that most flooding occurred and large numbers of Redshanks were seen here on occasions at low water by members of the Teesmouth Bird Club (pers. comms.), although I did not undertake counts there. The great day-to-day variation in the numbers of Redshanks on Seal Sands after reclamation also suggests that a substantial portion of the Teesmouth population of this species remained in the locality and fed almost

exclusively on fields.

In autumn 1974 large numbers of Redshanks again fed exclusively on field areas. However, the degree of flooding was less than in the 1973/74 winter and this may have been an important factor in determining the overall wintering population level.

Areas used within North Area. (Fig. 14).

During the early part of autumn in both 1973 and 1974 feeding birds were well dispersed throughout North Area despite some preference for feeding on wet, muddy substrates, particularly on the flood tide when most areas had dried out.

As the process of reclamation continued, fine outwashed sediment was deposited on certain portions of the North Area immediately adjacent to the points of outflow from the West and North-East Enclosures. This accumulation of liquid mud appeared to create particularly attractive feeding conditions for Redshanks, similar to those of the preferred areas within the enclosures. In these sites Redshanks fed by swishing, as in West Enclosure, and again the use of these parts of North Area fell dramatically when active reclamation ceased. This was particularly true of the area adjacent to West Enclosure. During reclamation this had attracted several hundred birds, yet within a week of active reclamation ceasing it held only one or two Redshanks, as it had done before reclamation. In contrast, the wide channel from the North-East Enclosure, which had been a popular feeding site before reclamation began, although similarly attracting great numbers of Redshanks during reclamation, remained a preferred feeding site after reclamation, but the reason for this is not known. In addition, Redshanks regularly used the channels and gullies within the central part of North Area after reclamation.

In early autumn 1974 Redshanks fed widely over North Area for a few weeks, but throughout November and December feeding was concentrated in gullies and

other areas of soft mud especially within the Central Bank of North Area.

Seasonal fluctuations and numbers using Seal Sands.

The peak in numbers of Redshanks using Seal Sands in autumn 1974, namely 466, was recorded in September. Thereafter, numbers fell sharply to a level at the end of October which was nearly maintained until the end of December. Day-to-day variation in the use of North Area during this period could account for the difference between the October, November and December low water counts and my general impression was that a relatively stable number of Redshanks used North Area at this time.

The numbers of Redshanks using Seal Sands in autumn 1974 were lower than in respective months of autumn 1973, the difference being greatest in October (a difference of 580 birds) and least (134 birds) in December. The use of North Area alone, however, was more closely similar. In spring 1974 the considerable day-to-day variation in the use of North Area which has been attributed to the changing profitability of feeding in field areas makes it impossible to identify a stable population level similar to that in autumn 1974 when feeding in field areas was less attractive.

Although I was unable to study quantitatively the extent to which Redshanks (and other species, e.g. Curlews) used the extensive pastures north of the River Tees, it seems likely that the availability and quality of feeding there (which must have been closely equivalent to that of intertidal areas in terms of net energy intake) played an important role in supporting the population at Teesmouth, especially in the 1973/74 winter.

DUNLINS.

The use of different portions of Seal Sands for feeding at low water in the 1973/74 winter.

Before reclamation between 40 - 86% of Dunlins using Seal Sands began feeding on the North Area as this became exposed (Pienkowski, 1973). Usually, the majority of those birds would remain there until the flood tide forced them to move to the South Area, although occasionally (and particularly on neap tides) there was a tendency for this movement to occur shortly after low water. In spring 1973 Pienkowski recorded between 14,300 - 6,700 Dunlins on North Area (81% - 74% of the population) at low water compared with 6,100 - 2,000 on South Area. The great majority of Dunlins (3,700 - 1,800) using South Area were found in the West Enclosure and this valuable feeding site was still available at the beginning of my study.

During the initial stages of reclamation, when the West Enclosure was as yet little affected by the deposition of silt from the dredgings used to fill the site, movement of Dunlins between the South Area and North Area continued to be an important feature of this species' feeding strategy. The West Enclosure remained an important feeding site with almost 3,000 birds present at low water at the end of October 1973. Between October - December 1973 over 90% (8,700 - 7,700) birds moved to North Area to feed as it was exposed. In contrast to the situation recorded by Pienkowski in spring 1973, in October 1973 and to a lesser extent in November, a progressive movement of Dunlins took place from North Area to West Enclosure before low water. However, as reclamation progressed, this tendency disappeared. The numbers of Dunlins using West Enclosure at low water decreased from around 3,000 in October to only 335 in December 1973, although over 70% of the population moved there to roost over high water. By the end of

January 1974 the number there at high water had fallen to around 1,800.

The movements of Dunlins between the North and South Areas of Seal Sands during reclamation and the increasing movement of birds to the fields at high water was clearly a complex phenomenon. This changing distribution of Dunlins is summarized in tabular form in Table 3, based on a combination of monthly observations of the birds' movements to and from North Area and the monthly counts.

In contrast to Grey Plovers and Godwits, feeding Dunlins showed no tendency to concentrate on the perimeter of the deltas of dredged debris. Perhaps for this reason, the pattern and nature of sedimentation had a more immediately adverse effect on the numbers of Dunlins feeding within the West Enclosure. The reclamation of the South-East Enclosure provided a feeding situation similar to that of the deltaic deposits within the West Enclosure and only just over 500 Dunlin fed within these two enclosures of South Area at the end of January 1974.

The use of field areas at high water.

Following the reclamation of the West Enclosure in December 1973 and in autumn 1974, large numbers of Dunlins fed in the field and pool areas north of the estuary at high water. Preferred feeding areas included the Reclamation Pond and the Monsanto Option, both of which were similar in that they contained extensive areas of shallow brackish surface water, especially after heavy rain. While large areas of pasture north of the estuary were flooded in both seasons of my study, particularly in spring 1974, only small numbers of Dunlin visited these at high water.

In October and November 1973 the pool and field areas were used by a remarkably consistent number of birds representing between 20 - 30% of the population at this time. The highest number of Dunlins I recorded using pool and field areas was around 3,000 (in January 1974), but on 2/12/73, when surface water was frozen, less than 500 Dunlins were found there. Such conditions occurred

temporarily in late December 1973 but more particularly in early January 1974, although I managed to undertake no counts on these occasions.

In September and early October 1974, although the numbers of Dunlins using Seal Sands was high, only a few hundred individuals moved to field areas, the majority of birds moving south of the River Tees along with other waders, and it is not known whether these birds fed or roosted. In November and December, however, the use of the pools increased, and involved up to 2,800 birds, then 45% of the population using Seal Sands. On only a few occasions were the fields and pools frozen and unavailable for feeding; the weather was never as severe as in the previous winter. In general it appeared that similar numbers of Dunlins moved away from Seal Sands at high water in both spring and autumn 1974 but in the latter period this represented a higher proportion of the population.

In February and March 1974 up to 250 Dunlins used field areas at low water, but this was seen only under conditions of warm weather when pasture land north of the estuary was waterlogged.

Areas used within North Area. (Fig. 14).

In all months of my study Dunlins moved to North Area in large numbers between HW+1½-2 and began feeding at the extreme south-eastern portion. This site typified the preferred feeding substrates in North Area, comprising particularly soft, 'sticky' mud.

Although small groups of up to one hundred Dunlins remained feeding in gullies and other pockets of sticky mud within the main sections of flats, the majority of the population closely followed the water's edge on the ebb tide. At low water the majority of birds would then be found feeding along the edges of Seaton Channel. This tenacity, both to the water's edge on ebb tides and to favoured low water feeding sites, was similar in both the 1973/74 winter and in autumn 1974, although in March and April 1974 Dunlins appeared to feed in more

widely dispersed flocks.

The feeding pattern on the flood tide was again similar both during and after reclamation. Rather than feeding on the immediate tide edge, Dunlins moved well in advance of the flood tide, concentrating more exclusively on areas of 'sticky' mud.

Movement away from North Area after low water became increasingly delayed after reclamation and the majority of birds remained there until at least HW+9 after the end of December 1973.

Seasonal fluctuations and numbers using Seal Sands.

Between October - December 1973 the numbers of Dunlins using Seal Sands fell only slightly, despite the fact that during this time the value of the enclosures for feeding at low water was much reduced, and that feeding at high water was also becoming less attractive. During January 1974, however, numbers fell by approximately 50%. It is perhaps significant that this decline coincided with the longest periods of cold weather, during which the enclosures were not suitable for feeding and that on a number of occasions the surface water in field and pool areas was frozen for several days. However, the further halving of the population in February cannot be attributed to unfavourable weather conditions since this period was unusually mild and wet. Probably this represented the start of the normal spring departure.

Movement away from Teesmouth in late spring, that is after April 1974, was preceded by a slight increase in population levels.

In autumn 1974, peak population levels again occurred in October, although at some 2,000 less than in the previous autumn. Throughout November and December 1974 there was a steady decline in the numbers of Dunlins using Seal Sands (i.e. North Area) to a population of around 4,000 birds at the end of my study. This population level was similar to that in January of the previous winter.

TABLE 3.

A SUMMARY OF THE MOVEMENT OF DUNLINS BETWEEN DIFFERENT FEEDING AREAS
DURING THE COURSE OF ONE TIDAL CYCLE, OCTOBER 1973 - JANUARY 1974.

This table shows the proportion of the population in each of the areas used by this species in each hour during the tidal cycle.

<u>Hours after</u> <u>high water</u>	<u>Percentage Distribution of the Population</u>											
	O C T			N O V			D E C			J A N		
	N. Area	S. Area	Fields	N. Area	S. Area	Fields	N. Area	S. Area	Fields	N. Area	S. Area	Fields
1	40	50	10	17	63	20	10	60	30	10	35	55
2	78	22	-	83	17	-	85	15	-	80	20	-
3	90	10	-	90	10	-	96	4	-	90	10	-
4	79	21	-	85	15	-	96	4	-	90	10	-
5	75	25	-	80	20	-	96	4	-	90	10	-
6	72	28	-	75	25	-	96	4	-	90	10	-
7	68	32	-	70	30	-	92	8	-	90	10	-
8	65	35	-	62	33	5	81	18	1	90	10	-
9	38	45	17	40	40	20	54	33	13	77	15	8
10	4	78	18	4	71	25	4	70	26	5	37	58
11	-	82	18	-	75	25	-	74	26	-	42	58
12	-	82	18	-	75	25	-	74	26	-	42	58

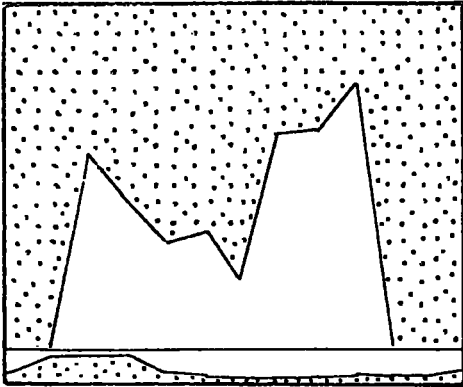
THE FEEDING ACTIVITY OF SHOREBIRDS ON SEAL SANDS.

Measurements of feeding intensity (FI), taken at hourly intervals during observation of feeding behaviour and weighted according to the distribution of birds between different feeding areas and roosts, provide a reasonable estimate of the time spent feeding by the average individual of each species during the course of a tidal cycle in daylight. The calculation of time spent feeding and its expression as a proportion of time available in a tidal cycle and as a mean value for each month - the 'Percentage Feeding Time' (PFT) - is given in the description of methods (p. 173).

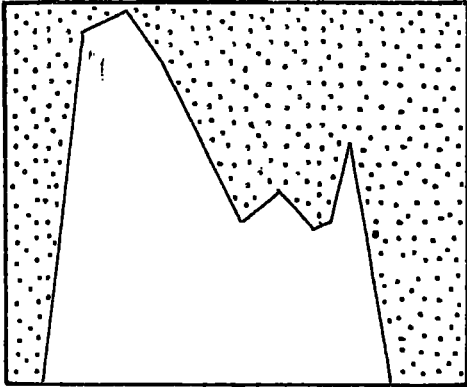
While the composite nature of a monthly mean PFT does not allow precise relationships to be drawn with short term changes in the environment, e.g. brief cold periods, which might temporarily induce a change in daily PFT, the records which I have compiled do provide a means of detecting changes associated with a developing feature or pattern within the environment of shorebirds at Teesmouth.

In Figs. 15 - 20 the weighted mean feeding intensities for each hour during the tidal cycle are shown graphically for each species on a monthly basis. It is from these diagrams that PFT has been calculated; their inclusion here serves to show the pattern and intensity of feeding activity particularly within North Area. The construction and interpretation of these diagrams is shown in Fig. 8, (p. 174).

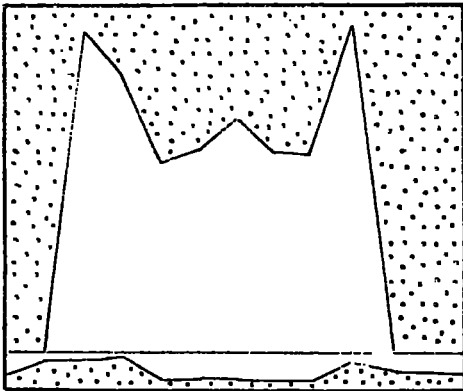
FIGURE 15 : THE DISTRIBUTION OF FEEDING TIME OF SHELDUCKS AT TEESMOUTH
DURING THE 1973/74 WINTER.



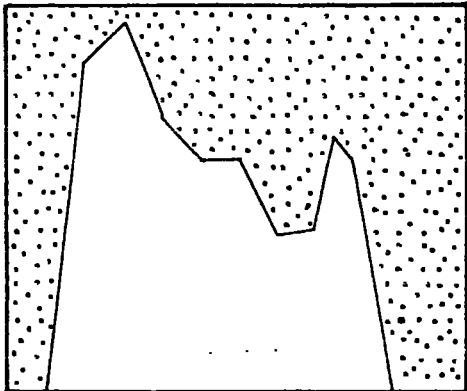
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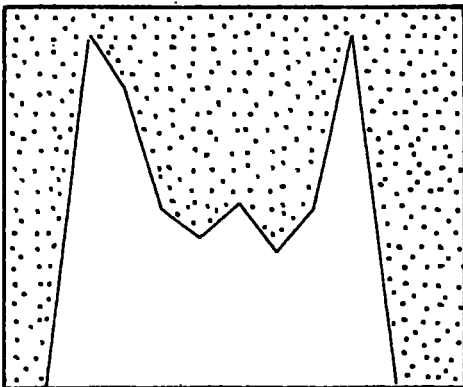
JANUARY



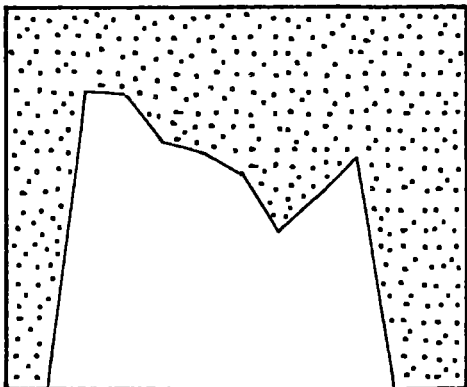
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FEBRUARY



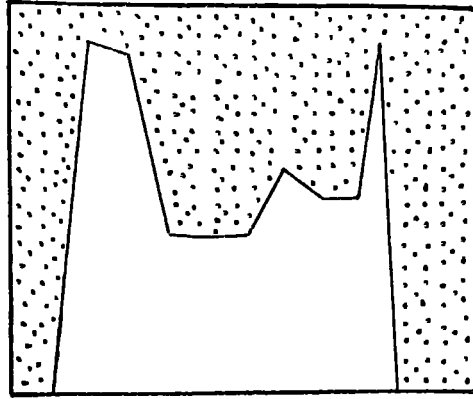
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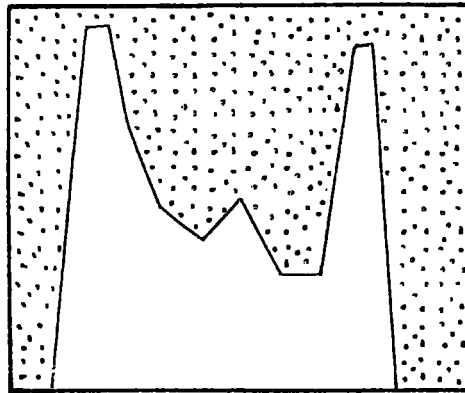
MARCH

FIGURE 15 : THE DISTRIBUTION OF FEEDING TIME OF SHELDUCKS AT TEESMOUTH

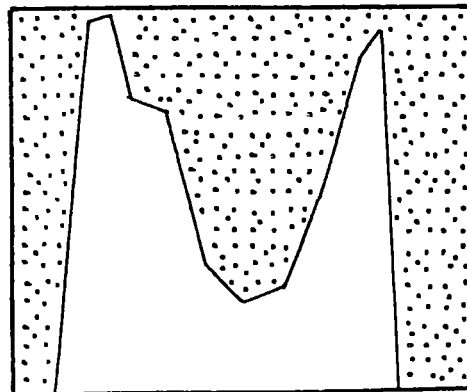
IN AUTUMN 1974.



OCTOBER

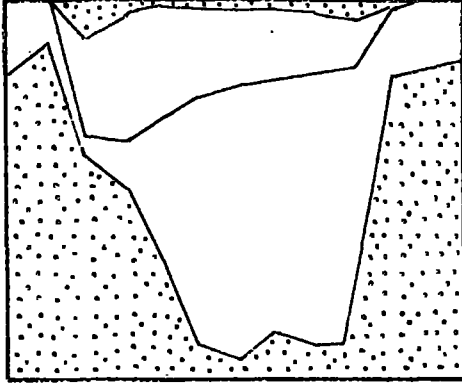


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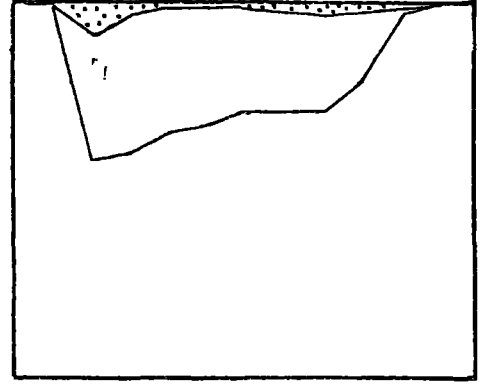


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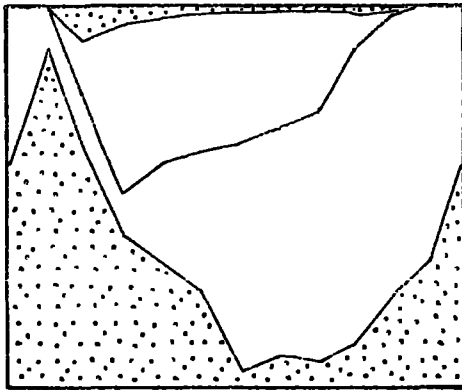
FIGURE 16 : THE DISTRIBUTION OF FEEDING TIME OF GREY PLOVERS AT TEESMOUTH
DURING THE 1973/74 WINTER.



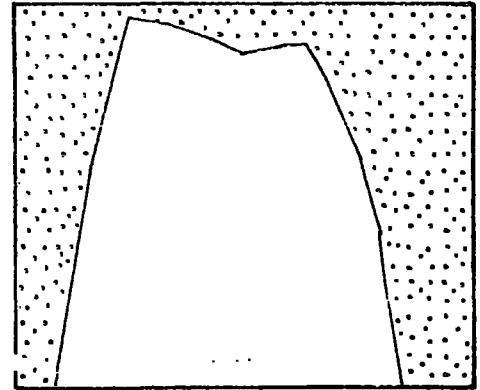
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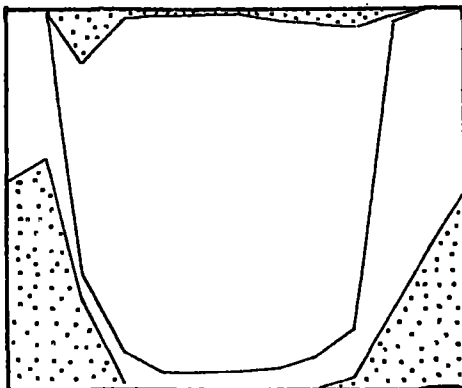
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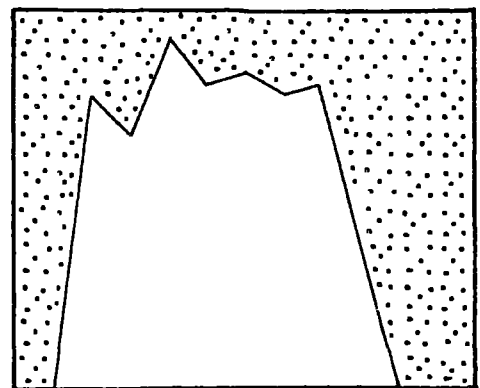
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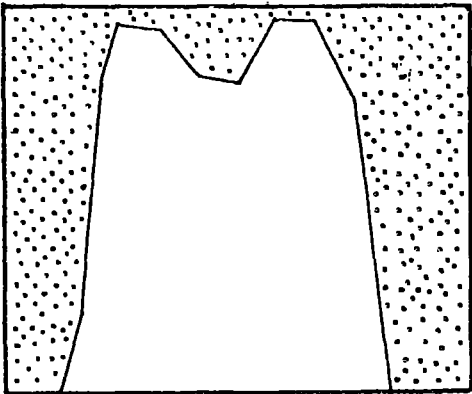


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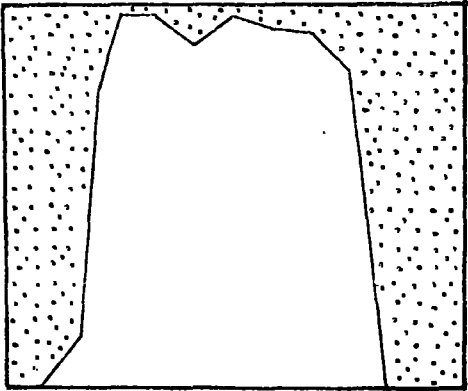


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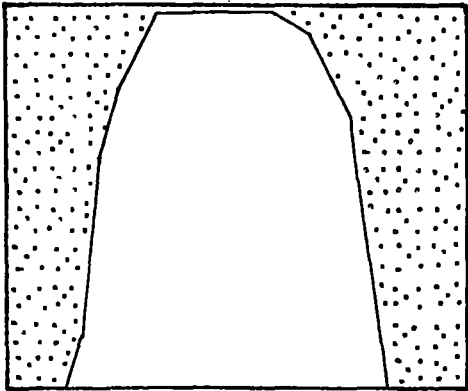
FIGURE 16: THE DISTRIBUTION OF FEEDING TIME OF GREY PLOVERS AT TEESMOUTH
IN AUTUMN 1974.



OCTOBER



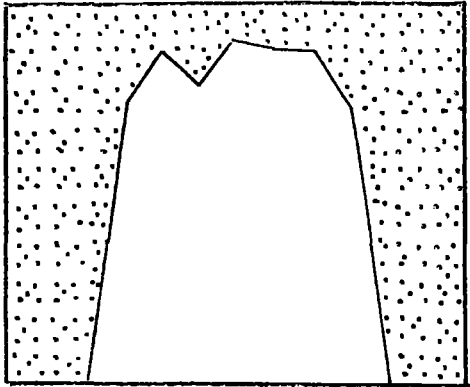
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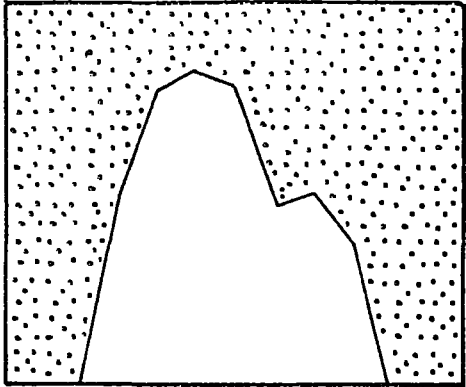
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FIGURE 17 : THE DISTRIBUTION OF FEEDING TIME OF CURLEWS AT TEESMOUTH

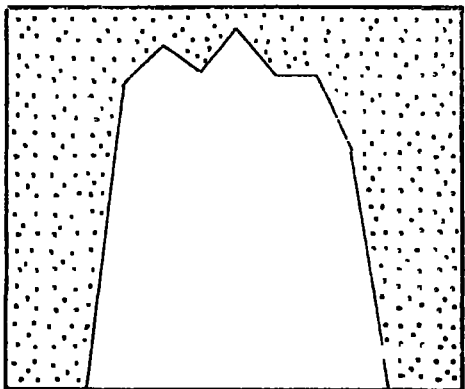
DURING THE 1973/74 WINTER.



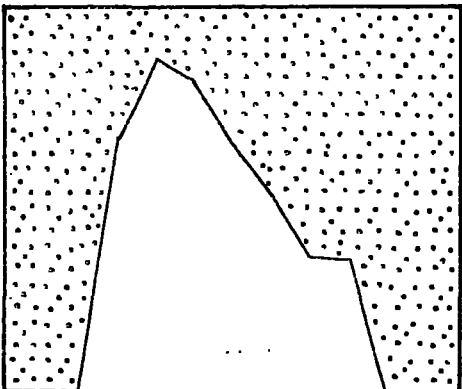
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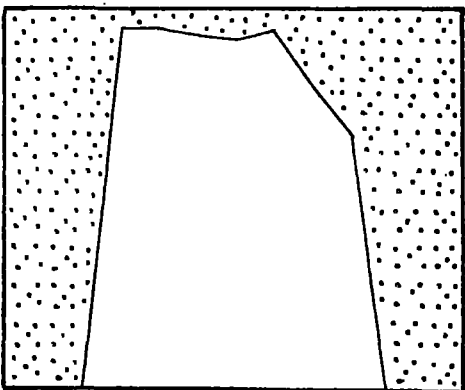
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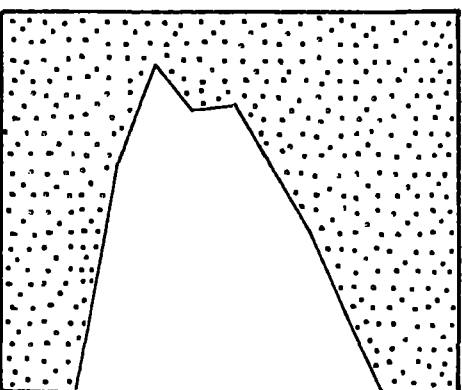
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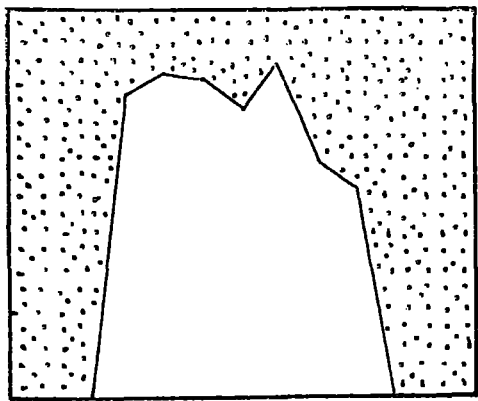
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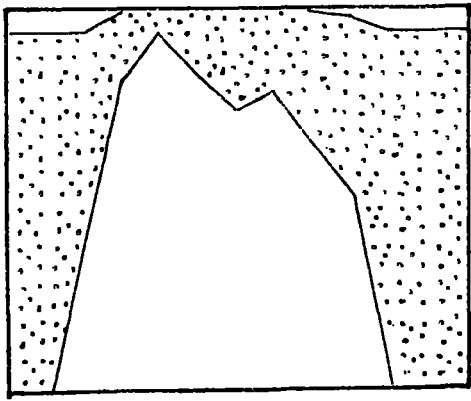
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FIGURE 17 : THE DISTRIBUTION OF FEEDING TIME OF CURLEWS AT TEESMOUTH IN

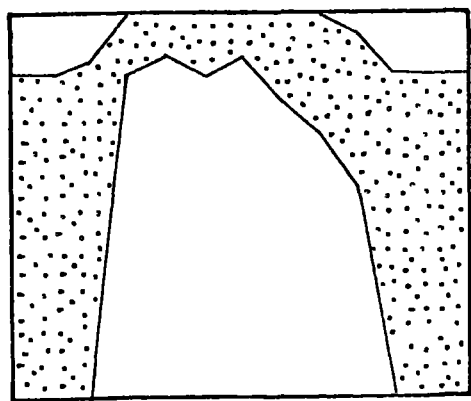
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OCTOBER

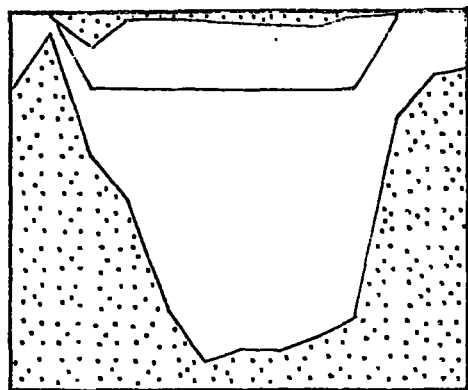


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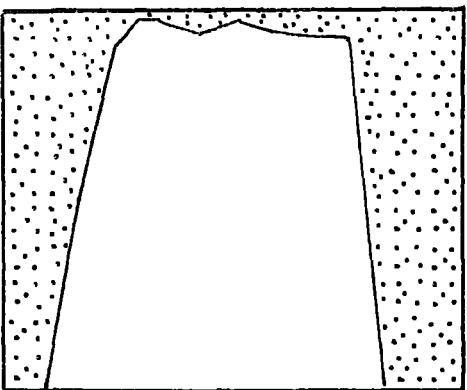


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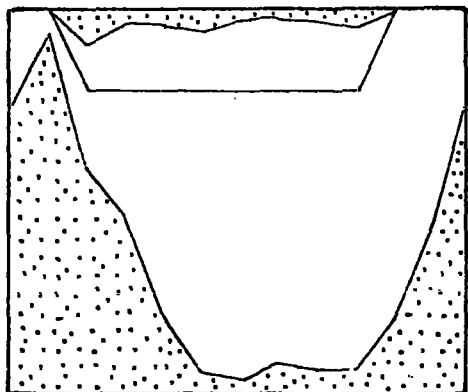
FIGURE 18 : THE DISTRIBUTION OF FEEDING TIME OF BAR-TAILED GODWITS AT
TEESMOUTH DURING THE 1973/74 WINTER.



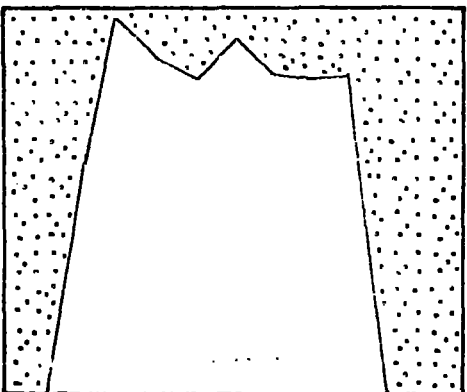
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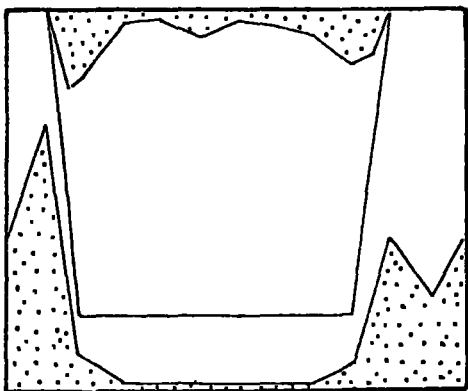
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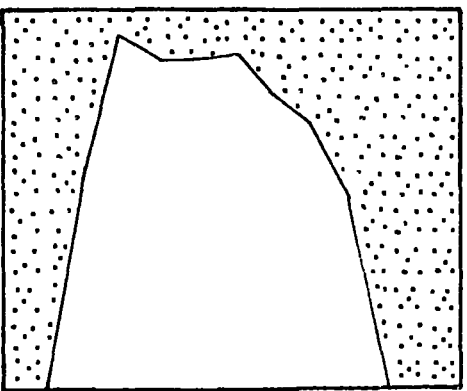
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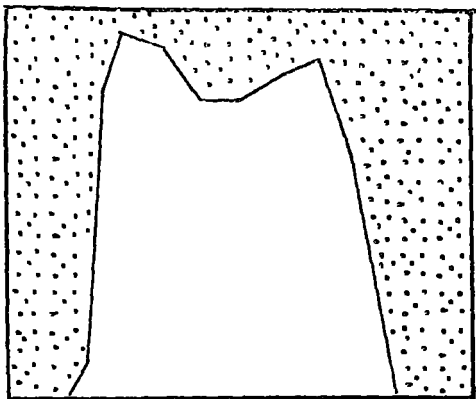


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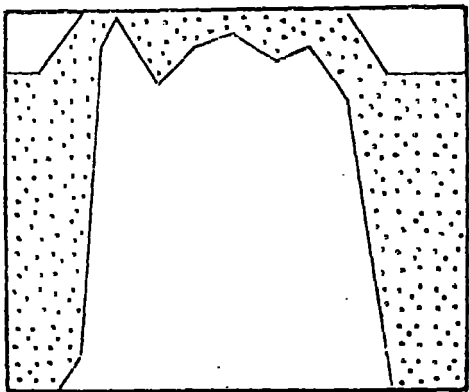


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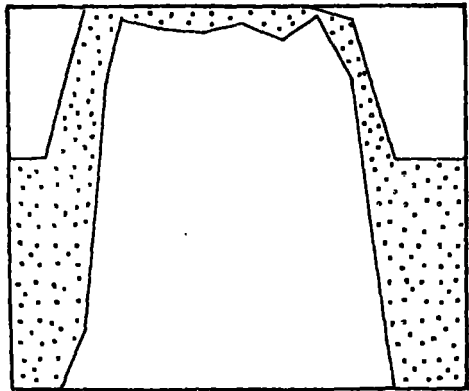
FIGURE 18 : THE DISTRIBUTION OF FEEDING TIME OF BAR-TAILED GODWITS AT
TEESMOUTH IN AUTUMN 1974.



OCTOBER

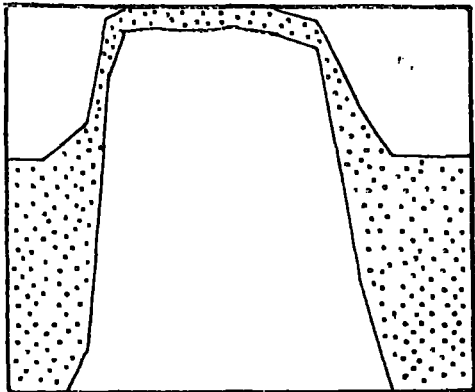


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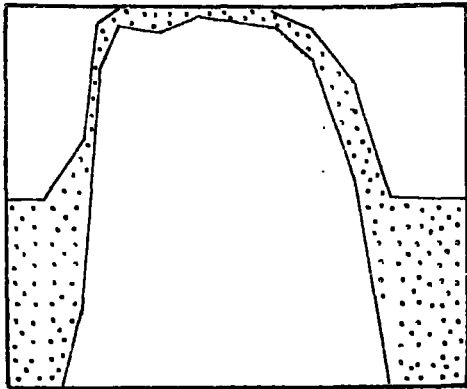


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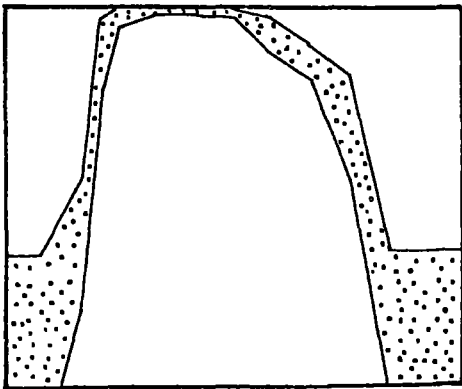
FIGURE 19 : THE DISTRIBUTION OF FEEDING TIME OF REDSHANKS AT TEESMOUTH IN
AUTUMN 1974.



OCTOBER

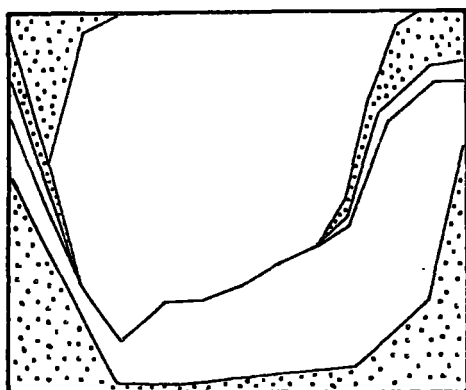


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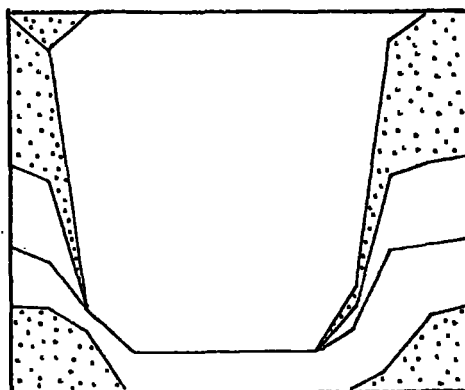


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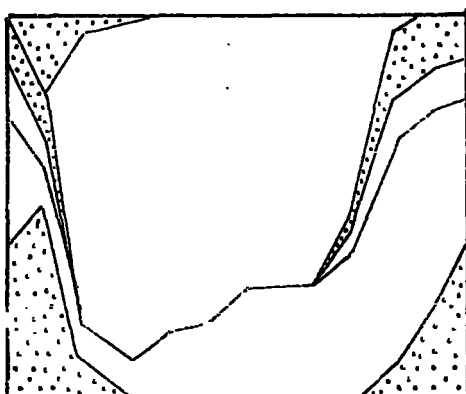
FIGURE 20 : THE DISTRIBUTION OF FEEDING TIME OF DUNLINS AT TEESMOUTH
DURING THE 1973/74 WINTER.



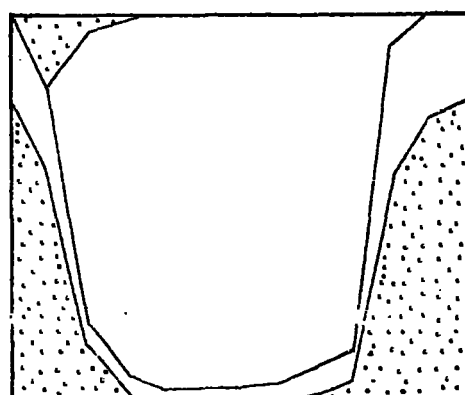
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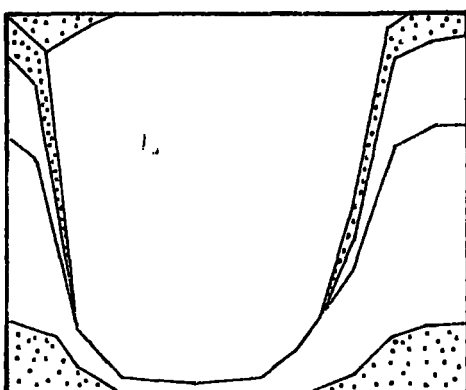
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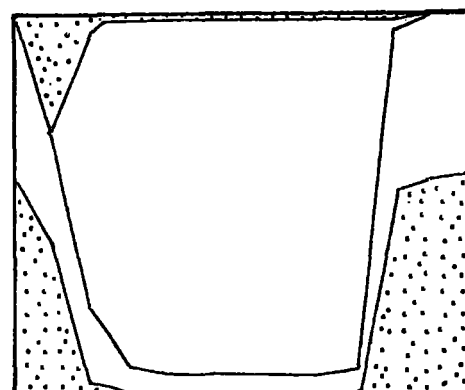
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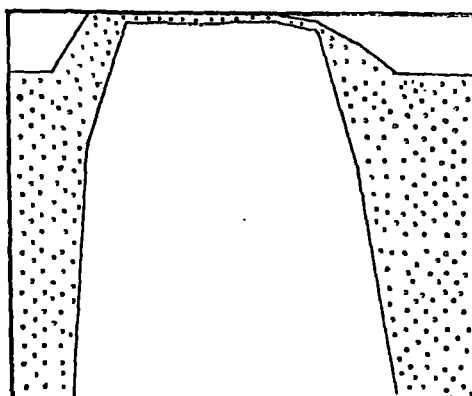
DECEMBER



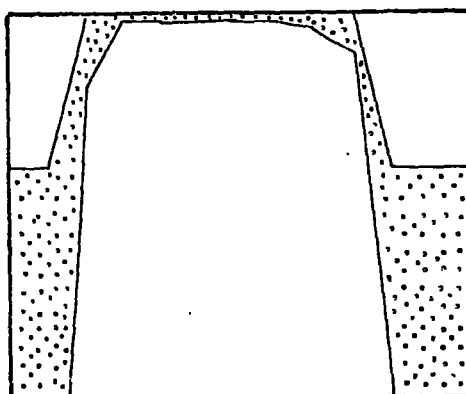
MARCH

FIGURE 20 : THE DISTRIBUTION OF FEEDING TIME OF DUNLINS AT TEESMOUTH IN

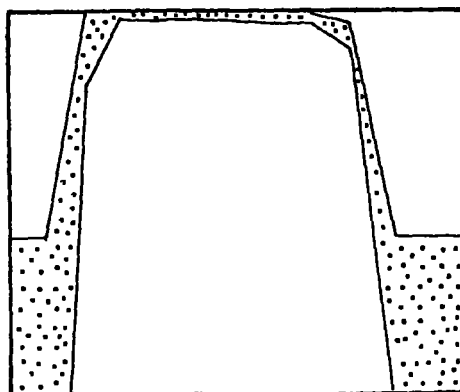
AUTUMN 1974.



OCTOBER



NOVEMBER



DECEMBER

Table 4. presents the monthly PFT values for each species between October 1973 - March 1974 and October - December 1974 inclusive. That portion of the PFT which derived from time spent feeding in the enclosures of South Area and from feeding at high water in the fields is given separately. Table 5. shows the proportion of the eight hour period of exposure of the North Area which was used for feeding by different shorebirds during the two winters of my study.

Only for Shelducks, Dunlins and Curlews were complete records of feeding activity obtained. Although the numbers of birds using the South-East Enclosure during January 1974 were checked on a number of occasions, at no time was the FI in that enclosure recorded on a systematic basis, with the result that the PFT of Godwits and Grey Plovers, for which this was a particularly important feeding area, cannot be calculated completely. Throughout the 1973/74 winter the immense day-to-day variation in the use of intertidal areas by Redshanks, for reasons discussed later, confounded attempts to establish a reliable PFT for this species. In autumn 1974 the numbers of Redshanks using Seal Sands were more stable and PFT values have been calculated, although again they are undoubtedly subject to considerably greater error than for any other species.

THE PATTERN OF FEEDING ACTIVITY.

The FI of most shorebird species was highest on the ebb tide, as preferred feeding areas became available, usually around HW+2-4. Exceptions to this generalisation were evident with Shelducks in October 1973 and Grey Plovers in March 1974, that is at the beginning and end of the overwintering period for most individuals of these two species at Teesmouth.

Dunlins and, in most months, Redshanks sustained a high FI, with no regular fluctuations, during the principal period of exposure of North Area, i.e. HW+3-9. For other shorebird species there was a reduction in feeding activity over the low

TABLE 4.

THE PERCENTAGE FEEDING TIMES OF ALL SPECIES, INCLUDING SEPARATELY THAT PORTION OF

THE PFT WHICH WAS SPENT IN SOUTH AREA DURING RECLAMATION AND IN THE FIELDS AT HW.

	Shelduck			Curlew			Godwit			Grey Plover			Redshank			Dunlin		
	Total	S. Area	Fields	Total	S. Area	Fields	Total	S. Area	Fields	Total	S. Area	Fields	Total	S. Area	Fields	Total	S. Area	Fields
OCT	35	6	-	47	10	*	57	47	-	56	41	-	-	-	-	72	25	2
NOV	44	7	-	47	12	*	64	52	-	59	50	-	-	-	-	84	33	5
DEC	39	-	-	51	-	*	77	29	-	77	22	-	-	-	-	89	23	8
JAN	43	-	-	35	-	*	57	?	-	?	?	-	-	-	-	78	6	10
FEB	42	-	-	34	-	*	56	-	-	54	-	-	-	-	-	75	-	17
MAR	43	-	-	35	-	*	48	-	-	50	-	-	-	-	-	79	-	21
OCT	41	-	-	42	-	*	48	-	-	54	-	-	68	-	18	63	-	6
NOV	40	-	-	46	-	2	59	-	5	55	-	-	74	-	20	73	-	13
DEC	41	-	-	52	-	7	66	-	12	54	-	-	80	-	26	80	-	20

N.B. * Occasional sightings indicate very small numbers of Curlews fed on field areas during these months.

? For Godwits and Grey Plovers, that portion of the PFT spent in the South Area during the reclamation of the S.E. Enclosure is not known.

TABLE 5. THE PROPORTIONS OF THE 8 HOUR PERIOD FOR WHICH NORTH AREA WAS AVAILABLE IN EACH TIDAL CYCLE (67% OF THE TIDAL CYCLE) WHICH IS UTILIZED FOR FEEDING BY DIFFERENT SPECIES OF SHOREBIRDS.

	Shelduck		Grey Plover		Curlew		Godwit		Redshank		Dunlin	
	%	hrs.	%	hrs.	%	hrs.	%	hrs.	%	hrs.	%	hrs.
OCT	52	4.2	23*	1.8	55	4.4	15*	1.2	-	-	72	5.8
NOV	66	5.3	29*	2.3	52	4.2	18*	1.4	-	-	72	5.8
DEC	58	4.6	82	6.6	76	6.1	72	5.8	-	-	87	7
JAN	64	5.1	-	- +	52	4.2	85	6.8	-	-	85	6.8
FEB	63	5	80	6.4	51	4.1	83	6.6	-	-	87	7
MAR	58	4.6	75	6	52	4.2	72	5.8	-	-	87	7
OCT	61	4.9	79	6.3	63	5	72	5.8	75	6	85	6.8
NOV	60	4.8	82	6.6	66	5.3	81	6.5	80	6.4	90	7.2
DEC	62	5	80	6.4	68	5.4	80	6.4	80	6.4	90	7.2

N.B. * These values for Grey Plovers and Godwits represent the proportion of the exposure period of North Area used by the average individual of the whole population. In fact a large proportion remained exclusively on the South Area while those individuals present on North Area at LW probably fed there for 70 - 80% of the exposure period.

+ For Grey Plovers the use of North Area on the date of the January count was so small as to make a calculation of feeding time meaningless.

water period with a second, but lower and more short-lived, peak in activity on the flood tide. Increases in FI during the low water period occurred as winter progressed and this contributed to the higher PFT's recorded in mid-winter - this feature is clearly shown in the patterns of feeding activity of Godwits and Grey Plovers in autumn 1974, Figs. 16 and 18).

The manner in which the peak in feeding activity on the ebb tide developed showed variation amongst shorebird species. This variation appeared to be related to the timing of exposure of different feeding areas and to their relative value for different species. Thus feeding activity of Shelducks on North Area rapidly achieved a high intensity probably because the whole of their preferred feeding areas, the Central Bank, lies at approximately the same tidal level and therefore becomes available for feeding simultaneously by large numbers of birds. Another possible reason for this brief peak in FI, is that Shelducks' crops may become so full of Hydrobia (one of the more important prey species on Seal Sands, see p. 242) that they could not eat any more until those had been digested. This situation was found to occur at the Ythan (Buxton, 1977). By contrast, Curlews had a number of subsidiary feeding sites on North Area which were used by some individuals before their preferred areas at lower tidal levels became exposed. The result was that a peak FI was achieved only gradually. In Dunlins the overall pattern of feeding activity was more straightforward, in that, as soon as exposure of North Area occurred, the majority of individuals present fed, particularly in the south-east corner.

For most species the peak (weighted) hourly value of FI exceeded 90% in most winter months and around mid-winter was usually in excess of 95%. However, for both Shelducks and Curlews a peak FI of around only 80% was recorded in October 1973 and March 1974 and for Curlews in January and February 1974 also. The October and March records are perhaps not surprising in view of the higher mean temperatures in these months. However, the January and February records for Curlews are unusual and, although these may have arisen from incorporating in the

hourly counts individuals of the non-feeding Curlew flock (see p. 199), it is possible that the high profitability of field feeding at this time depressed their activity on Seal Sands. In both Curlews and Shelducks there was great individual variation with respect to the time spent feeding - some individuals were seen to feed hardly at all throughout the exposure period of North Area, especially in mild weather. This behaviour was conspicuous also in some Grey Plovers in March 1974.

Only for Dunlins was an FI of 100% recorded, this occurring regularly, although temporarily, in all months of my study.

For no shorebird species did the basic rhythms of feeding activity within North Area show any substantial change as the result of reclamation of South Area despite the large changes in the proportion of feeding time spent there by some species, for example Godwits and Grey Plovers.

TIME SPENT FEEDING IN DAYLIGHT.

For all species except Shelducks the PFT (Table 1) was slightly higher in mid-winter than in spring or autumn. While the increase in PFT in each winter coincided with a decrease in mean daily temperatures calculated for the whole of each month, it is impossible to distinguish the contributions to variation in PFT associated with other features of the environment. Decreasing daylength, through its effect on the availability of intertidal feeding in daylight, is probably of considerable significance in the Seal Sands situation where feeding time had already been reduced through reclamation. Increases in PFT were achieved in part by an increase in feeding intensity over the low water period (for example, by Grey Plovers, Fig. 16, in October - December 1974) but for several species, for example Godwits and Dunlins, the use of field feeding at high water clearly contributed more to the overall PFT.

Comparison of PFT's in corresponding autumn months of 1973 and 1974 suggests

that in general birds were not feeding for a longer period during daylight after reclamation of South Area was completed. In fact, for Grey Plovers, Dunlins and also Godwits (although rather less marked in this species) PFT's were consistently lower in autumn 1974 than in 1973. Only in Shelducks and Curlews were PFT's closely similar in these two years. In spring 1974, following completion of reclamation, there was no tendency for PFT's to increase, as might have been expected when the North Area alone was available for feeding. In fact, in both Shelducks and Godwits there appeared to be a decrease in PFT from January - March 1974 but this coincided with an increase in mean daily temperatures.

Only for Curlews was there a marked increase in PFT between spring 1974 and autumn 1974. This was linked with an increase in the use of North Area by this species, but the PFT's in autumn 1974 were no higher than those in autumn 1973. For other shorebirds there appears to have been no distinct increase in PFT in the second winter after reclamation was completed. Comparison of the records for time spent feeding on North Area alone (Table 5.) shows remarkably constant levels of use in months immediately after reclamation and in the following winter, in Grey Plovers, Godwits and Shelducks. This suggests that for these species either further feeding time on North Area during the day was unnecessary or that on balance the profitability of utilizing the additional feeding time available there was not as great as could be achieved by exploiting other feeding areas (e.g. fields) or adapting in other ways (e.g. feeding rates, feeding at night, etc.) For Shelducks which had concentrated their feeding on North Area almost from the beginning of my study, there was no tendency to feed for longer periods on North Area after reclamation.

For Redshanks, as has already been noted (p. 230), it was impossible to calculate a meaningful PFT for any months in the 1973/74 winter, during which the different portions of Seal Sands and adjacent fields were used to varying extents, presumably in response to changes in the profitability of feeding in those areas.

I have no data for autumn 1973, therefore, which are comparable with the PFT's I calculated for each month in autumn 1974. However, it is of interest that, although Redshanks had a higher PFT than either Godwits or Grey Plovers, the average individual of each species spent a similar amount of time feeding on North Area after reclamation was completed. (The extra PFT for Redshanks was derived from field feeding). This raises the possibility that a feeding time on North Area (for the average individual of each species) of around $6\frac{1}{2}$ hours (i.e. 54% PFT) may in some way represent an upper limit for the profitable exploitation of North Area by these species. This level of use was reached in spring 1974 after reclamation and was reached also in autumn 1974.

In contrast to Grey Plovers and Godwits, Curlews spent more time feeding on North Area in autumn 1974 than immediately after reclamation in spring 1974, although the highest feeding time on North Area was recorded in December 1973. The reason for this exception to the general difference between the two years is not clear. In view of the importance of field feeding for this species, and the probability that some Curlews in the vicinity of Teesmouth fed almost exclusively on fields, it seems likely that the profitability of feeding on non-tidal sites determined the differences in time spent on Seal Sands. Most Curlews fed for a relatively small proportion of the time for which North Area was exposed. Some birds stayed on Seal Sands for the entire period of exposure, whether or not they were feeding, but many birds left for the field areas well before North Area was covered by the tide, and returned only when the favoured feeding sites were available. This is evident in the monthly graphs of PFT for this species, and it may be assumed that, on balance, feeding in the fields was more profitable than continued feeding on North Area. Most Godwits and all Grey Plovers satisfied their energy requirements by feeding on North Area alone - only small numbers of Godwits fed in field areas. However, most Godwits and Grey Plovers, unlike Curlews, fed on North Area for most of the time which was

suitable for feeding before seeking additional feeding elsewhere, if this were necessary.

NIGHT FEEDING.

Throughout both winters of my study Shelducks fed on North Area at night, in similar areas and in approximately similar numbers to those observed during daylight. Similarly, Grey Plovers made regular use of preferred daytime feeding areas at night and, although these sites were higher and therefore drier and less easily observed (less reflective), the numbers of birds present were frequently similar to equivalent daytime records in both winters. For the other wader species, feeding at night was most often seen during the period of active reclamation, i.e. October - December 1973, and at this time the distribution and behaviour of feeding birds (including the division between North Area and the enclosures) was closely similar to that seen by day. However, the numbers of birds in any preferred feeding site were usually slightly less than in the day.

From late December 1973 onwards there was a reduction in the numbers of each wader species (with the probable exception of Grey Plovers) feeding at night. In Redshanks, the reduction in night feeding was abrupt and coincided with the fall in use of Seal Sands during daylight which occurred in association with the cessation of active reclamation. Thus, within less than a month, the numbers of feeding Redshanks visible at night fell from in excess of 300 to less than 30. In Curlews, Godwits and Dunlins the overall reduction in night feeding was progressive and was accompanied by changes not only in the number of birds present but also in the timing of feeding in relation to the exposure of the flats and in the distribution of feeding birds.

In Curlews, reduced night feeding coincided with diminishing use during daylight of an important feeding site (the Greenabella Bank). At night, Curlews

fed less at the tide edge, as was also true of Godwits. Until mid-winter 1973/74, Dunlins began feeding at night around HW+2 and continued until HW+9 in a similar manner to the pattern of feeding in daylight. In early 1974 the arrival time on North Area became delayed and, frequently almost all Dunlins had moved off the flats by HW+8.

Occasionally groups of Redshanks and Curlews were seen roosting at night both on North Area and on the enclosures in spring 1974, but the majority of non-feeding birds moved elsewhere.

In autumn 1974 the proportion of the Seal Sands populations of these waders feeding at night was less than in autumn 1973 but higher than in spring 1974. In Godwits and Dunlins the pattern of use of North Area at night, established in spring 1974, i.e. a tendency to arrive later and leave earlier than during a daylight tidal cycle, was retained, while the majority of Curlews often departed for field areas at around dusk, irrespective of the state of the tide.

FIELD FEEDING.

Although small numbers of Shelducks regularly visited certain pools north of the Tees at high water, feeding off the intertidal areas was unusual at any time during my study. Similarly very few Grey Plovers were found to feed over high water, although a few were present regularly on some marsh and pool areas. Up to 10 Grey Plovers did feed, however, in portions of Greatham Creek adjacent to the Brinefields and Cowpen Marsh, (the highest portion of intertidal flats within my study area), on both the flood and ebb tides. Since this area was difficult to observe, the significance of this and its possible contribution to the PFT is not known. It is possible that some individuals found feeding in this location did not feed on Seal Sands at any stage of the tidal cycle but stayed in Greatham Creek.

For other wader species field feeding became a regular feature of feeding

activity following reclamation of South Area. It was the principal means by which Redshanks and Dunlins were able to maintain their PFT which, before reclamation, had exceeded the exposure period of North Area alone. For the Godwit, although the exposure period of North Area was sufficient for it to maintain its pre-reclamation PFT, some individuals of this species chose to feed at high water in the brackish pool within the Brinefields, rather than attempting to feed for longer periods on North Area.

In Dunlins the extent of field feeding in autumn 1974 was similar to the levels recorded immediately after reclamation, but for Godwits regular use of the fields was recorded only in autumn 1974. For those Curlews feeding on Seal Sands at low water, the field areas within the 'standard walk' were used only sporadically during and immediately after reclamation, despite the fact that this species is particularly adept at feeding within marsh and wet pasture. Only in autumn 1974 did the numbers of feeding Curlews reach levels which might be considered more than a 'trace'.

FORAGING BEHAVIOUR

The measurement of feeding rates and searching rates of shorebirds at Teesmouth occupied the majority of the time available during my study. These aspects of foraging behaviour are particularly appropriate for quantitative assessment and at Teesmouth were relatively easily measured, since feeding birds could be watched from a Land Rover from raised vantage points provided by the slag walls which almost enclosed the feeding areas. Furthermore, it was anticipated that these parameters would provide a sensitive indicator of the birds' ability to maintain themselves in the post-reclamation situation at Seal Sands.

When my study began it was known that completion of phase I of the reclamation programme would reduce the feeding time available to shorebirds by approximately 30%, from $12\frac{1}{2}$ to just over 8 hours, in each tidal cycle. In addition it seemed a reasonable assumption that any increase in numbers of birds feeding on North Area, after South Area had been reclaimed, would depress prey densities more rapidly than had occurred before reclamation. Other features associated with an increase in shorebird density on North Area, for example aggression or interference, might have further reduced prey availability. If this were the case, then those birds using North Area would have had to adapt their feeding strategy so as to maintain an adequate net intake of food each day. Any, or all, of the following changes might have taken place. Birds

might have fed for longer periods each day; and this was tested by the calculation of PFT (see p. 173); or they might have modified their searching rate or the rate at which prey were captured; or they might have changed the species and sizes of prey selected so as to increase their intake rates.

On those days which I devoted to observations of feeding behaviour, I attempted to obtain a series (and preferably more than one series) of measurements of both feeding rate and searching rate for as many species as possible (see Method's p. 175). Unfortunately, because several shorebird species had to be studied simultaneously rather than a single species, the data for each species are not sufficient to allow any sophisticated analysis, e.g. of feeding and searching rates in relation to temperature change or time available for feeding during daylight. I have depended heavily on univariate analysis and, in an attempt to establish even simple relationships, I have generally had to lump data to achieve reasonable sample sizes. Even by doing this, there are still deficiencies for some species at certain periods during my study. For example, the feeding behaviour of Redshanks could not be analysed in detail for the period when the numbers of this species were small, or on occasions when the majority of birds had left Seal Sands just after low water.

Low temperatures were rare and very temporary during both winters of my study, with the result that some of the potentially most interesting conditions in which to determine the effects of this important modifier of feeding behaviour could not be examined.

My data on the feeding rates of Curlews, Godwits and Shelducks are more satisfactory since for each species the principal feeding areas were clearly visible at all stages of the tide, the birds showed no tendency to hide or feed in creeks or gullies and, being large birds, their behaviour could be observed over long distances and, therefore, from all chosen observation points. For Curlews and Godwits the proportion and sizes of Nereis diversicolor within the diet could be determined with a high degree of accuracy, but similar records,

in terms of the overall numbers of observations, were obtained rather less frequently for Grey Plovers which, although confirmed Nereis feeders, also took a large number of small unidentified prey. Similarly, a breakdown of the diet of Redshanks was not always possible when birds fed by 'swishing', a technique which predominated on North Area during, and for several months after, reclamation of the West Enclosure. For Shelducks and Dunlins, which fed almost exclusively on small prey items, the diet could not be assessed by direct observation. Also the absence of any distinctive swallowing movements by both species (when observed at distances greater than 50 metres), and the speed of feeding movements of Dunlins, did not allow feeding rate and searching rate to be distinguished. For those two species, therefore, the measurements presented here combine these two components.

Below, aspects of foraging behaviour, and when possible the composition of the diet, are considered for each species.

SHELDUCKS.

In agreement with findings elsewhere (Olney, 1965) Shelducks at Teesmouth fed in part on the small gastropod mollusc Hydrobia ulvae which occurs at high densities on the North Area of Seal Sands (Evans et al., 1979). However, small oligochaetes and polychaetes of eleven species (see p.153), which Gray (1976) found to occur in some parts of Seal Sands at densities of 300,000/m², are probably an important part of the diet of Shelducks here. Because of their delicate structure, their contribution to the diet has proved difficult to quantify by gizzard analysis. Small Nereis are undoubtedly taken but are probably not specifically sought.

Shelducks use a number of different feeding techniques depending primarily on the state of the tide - these have been well documented in other studies, for example, Olney, (1965) and Bryant and Leng, (1975). Similar methods were used by Shelducks at Teesmouth. Thus, birds fed in the water on both ebb and flood tides by 'head-dipping' and upending, sieving the mud just below the surface of the water. After the mudflats were exposed, birds fed using a scything or swishing motion of the bill, held just below the mud surface. These two methods were sharply delineated and fewer examples were noted of the intermediate stages observed by Bryant and Leng (1975). In further contrast to this Scottish study, although at Teesmouth the use of head dipping and upending coincided with the peaks of feeding intensity, these peaks were of short duration. Between HW+3-8 most birds fed on the exposed mud surface. The reason for this appears to be that most of the mudflats of the North Area lie at about the same tidal level, so that the period for which feeding was possible on the submerged mud surface was limited. In contrast, for surface feeding the time available was extensive. It is perhaps important for this species, therefore, that large parts of North Area comprise very soft and 'liquid' mud - the substrates preferred for surface feeding by Shelducks on the Forth (Bryant and Leng, 1975).

Measurement of feeding rate could be made of only those birds using the scything technique of feeding. I quantified this in terms of the pacing rate of individuals recorded over a period of 30 seconds. Since these values represent a combination of feeding and searching behaviour, a wide range of results was obtained; individual measurements ranged from 14 paces/minute to 95 paces/minute and, correspondingly, the variance about means was high. Daily mean values varied from 24 paces/minute to 63 paces/minute. Generally, birds scything the bill through a wider angle appeared to be feeding more intently, perhaps having found a dense patch of prey, and the pacing rates of these

individuals were slower. This graded into a faster walking pattern in which the bill was held straight out in front of the birds and it seems likely that this represented largely a searching technique. During any 30 seconds of observation both patterns of movement might be used.

In the 1973/74 winter all records were included in the calculation of pacing rates but in autumn 1974 I excluded (at the time of observation) those individuals which were exclusively or predominantly fast moving birds, that is, those essentially not feeding. As a result of this change in my recording technique, monthly mean pacing rates for the two years appear to be significantly different in November and December, as shown in Table 6. which includes monthly means throughout my study. The records for North Area and West Enclosure, both by day and at night, have been separated for the winter of 1973/74. In autumn 1974, the preferred feeding areas of Shelducks were not illuminated sufficiently well at night for any reasonable data to be obtained. A single series, i.e. measurements of more than 20 individuals, obtained at night in October 1974, has been included with daytime records for that month (since there was no significant difference) to give a single mean value. The mean daily values are plotted in Fig. 21.

I found no significant difference in pacing rates recorded in the same months on North Area and West Enclosure. Pacing rates in daylight and at night were also similar. While there appears to be no evidence in my records of a progressive increase in pacing rate during the 1973/74 winter of South Area, pacing rate was certainly slower in October 1973 than in spring 1974. It is tempting to see in this an indication that perhaps birds were spending more time searching and/or scything more quickly in spring, since prey densities were reduced towards the end of the overwintering period.

The pacing rate of Shelducks in October 1974 was similar to that in October 1973, but values in November and December 1974 were significantly slower than

TABLE 6.

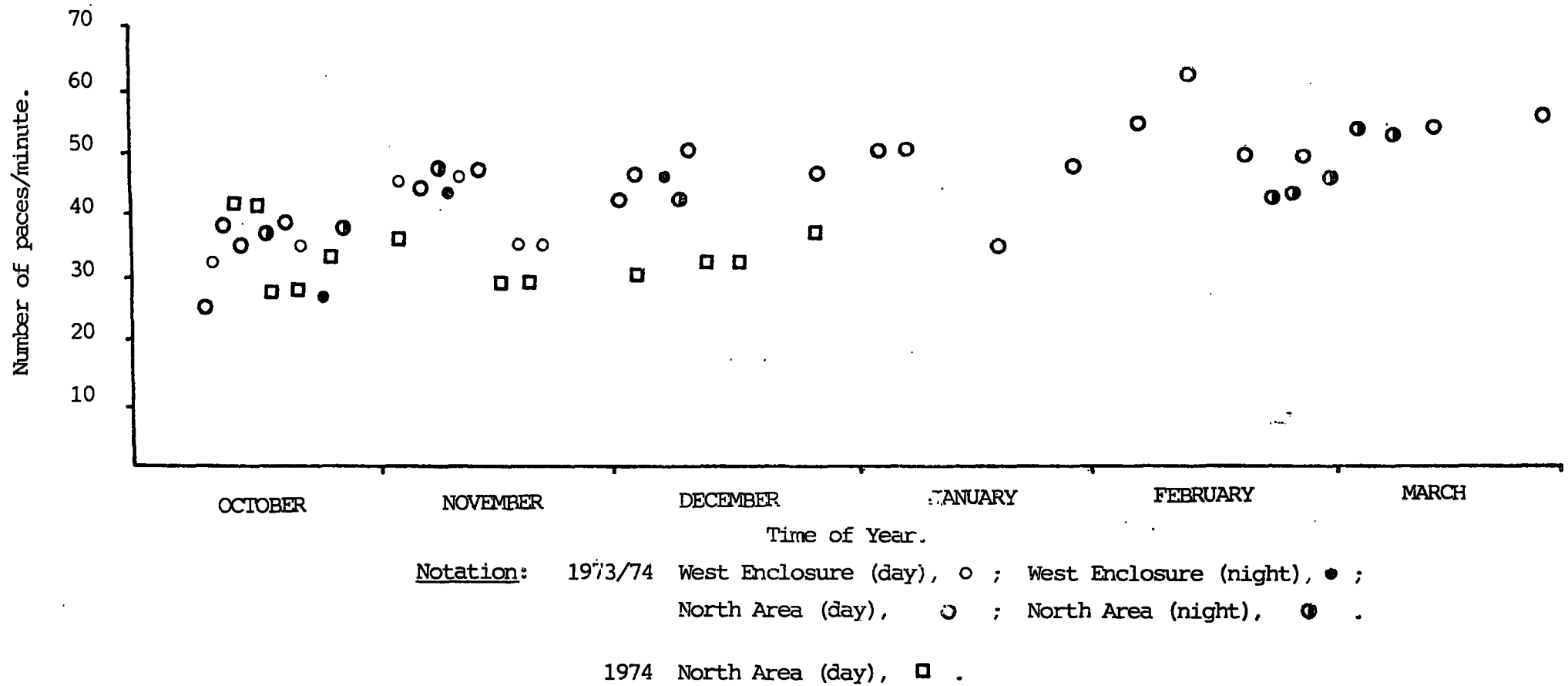
MONTHLY SUMMARY OF SHELDUCK PACING RATES.

Values are expressed as the mean number of paces per minute $\pm$ S.E.
The number of individual measurements are given in parenthesis.

1973/74	OCTOBER	NOVEMBER	DECEMBER	JANUARY	FEBRUARY	MARCH
North Area						
(daylight)	34.8 $\pm$ 1.68 (100)	46.4 $\pm$ 2.78 (43)	47.2 $\pm$ 1.84 (93)	45.8 $\pm$ 2.12 (87)	54.5 $\pm$ 2.28 (81)	51.0 $\pm$ 3.2 (40)
North Area						
(night)	36.8 $\pm$ 1.55 (72)	49.6 $\pm$ 3.4 (25)	44.6 $\pm$ 2.4 (28)	-	42.8 $\pm$ 2.58 (34)	51.2 $\pm$ 2.35 (71)
West Enclosure						
(daylight)	34.6 $\pm$ 2.2 (41)	37.8 $\pm$ 1.68 (91)				
West Enclosure						
(night)	33.4 $\pm$ 2.12 (47)	41.0 $\pm$ 4.40 (23)	49.0 $\pm$ 2.4 (23)			
1974						
North Area						
(daylight)	31.5 $\pm$ 2.65 (71)	32.6 $\pm$ 2.54 (77)	31.2 $\pm$ 2.02 (70)			

FIGURE 21 : THE VARIATION IN MEAN PACING RATE OF SHELDUCKS DURING THIS STUDY.

Each value represents the mean of approximately 20 measurements. Pacing rate on the West Enclosure and the pacing rate at night in the 1973/74 winter is distinguished.



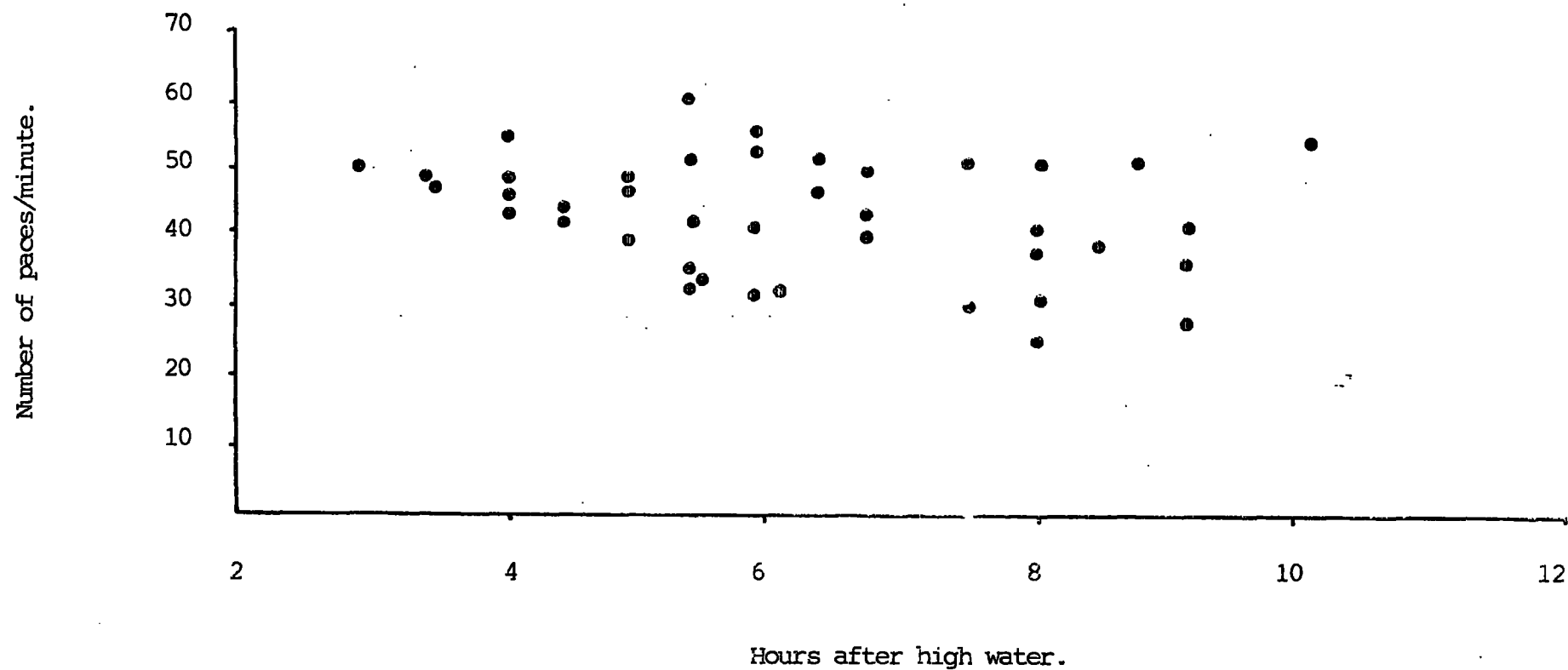
for respective months in autumn 1973. As noted earlier in this section, these differences might be attributed to the exclusion of fast-moving and effectively non-feeding birds when I was taking measurements in autumn 1974.

There was no relationship between pacing rate and air or mud temperatures, nor one with wind speed, but a significant correlation ($p = 0.05$) was found with the stage of the tide in the 1973/74 winter (Fig. 22), with birds pacing more slowly as the period of exposure of North Area increased, that is, they spent less time in searching and/or scythed more deliberately at HW+8 than at HW+3. In general, birds seemed to feed with more haste, almost feverishly, shortly after the exposure of the mudflats while after low water those birds which continued to feed did so in what appeared a more leisurely fashion.

Since the availability of Hydrobia may be expected to be highest just as the mudflats become exposed, and at this time Shelducks must be having a high feeding success, this conflicts with my suggestion earlier that Shelducks having a slower pacing rate and a wider scything movement were feeding within a high density patch of prey. Both observations might be true, however. For example, it might be expected that just after the flats are exposed Hydrobia and other prey are on, or very near, the mud surface, physically enabling Shelducks to scythe more rapidly and, furthermore, it might be beneficial for individuals to change their feeding site more frequently as the tide recedes, with the result that overall I recorded higher pacing rates. On the other hand, at lower levels of the tide prey are more deeply buried in the mud and their collection requires more deliberate feeding movements with the result that pacing rate was slower. Clearly more detailed study would be necessary to resolve this. In autumn 1974, however, a similar relationship was not established, but it will be remembered that birds spending more time searching than feeding were excluded from the samples.

FIGURE 22 : VARIATION IN THE PACING RATE OF SHELDUCKS DURING THE 1973/74 WINTER
IN RELATION TO THE TIME AFTER HIGH WATER.

This relationship is significant, $p = 0.05$.



GREY PLOVERS.

At Teesmouth this species was seen to employ two broadly separable feeding techniques:-

1. The run - stop - peck method - being that more typical of all Plovers and comprising a series of short runs separated by pauses during which the immediate locality was scrutinized and after which prey might be taken. Generally 2 - 3 pauses were recorded in a one minute period of observation, the individual moving about 10 metres in that time.
2. Fast pecking method - being similar to that used by Knots in which individuals usually covered only 3 metres in one minute, pecking almost continuously and taking small prey, none of which were identifiable.

Although distinct in their extremes there was gradation between these techniques and intermediate variants were particularly evident in autumn 1974. However, during reclamation there was separation of these techniques with respect to feeding area. Thus in the West Enclosure, the most important feeding site for this species between mid October - December 1973, and also on the S.E. Enclosure in January 1974, method 1 was used exclusively. The faster pecking technique was used on North Area only and throughout the 1973/74 winter birds using both techniques, in a distinct form, could be seen at any one time. Fast pecking was most frequently used by birds feeding in the Eastern Channel, in situations where a certain amount of surface water remained. This gave the impression that groups of feeding Grey Plovers tended to use one method or the other. In my records of feeding activity for the 1973/74 winter the extent of 'fast pecking' is underestimated in terms of the proportion of observations which comprised this technique, since for purposes of comparison with

Pienkowski's work at Teesmouth, I sought primarily to watch birds which used slow pecking, from which I could obtain some indications of intake rates of Nereis.

At no time were Grey Plovers sufficiently close to allow accurate determination of swallowing movements, but on the basis of Pienkowski's (1973) observations at Teesmouth which indicated that feeding success approached 100%, I have assumed for the purposes of calculation that this was so in my study also, i.e. pecking rate = success rate.

Mean monthly pecking rates for the slow and fast pecking methods of feeding are shown in Table 7. A small number of records of pecking rate were obtained at night in the 1973/74 winter and these have been combined with respective daytime records. For the 1973/74 winter, separation of the two methods was reasonably straightforward, since groups of birds tended to feed by one or other method (as mentioned above) with the result that respective means are clearly distinct. In autumn 1974, however, birds using both feeding methods were present in the same area so that each daily mean was compiled from a mixture of the two. Furthermore, some individual birds also employed a combination of 'fast' and 'slow' pecking during any one minute of observation. The daily means plotted graphically show this difference between the two years (Fig. 23). In autumn 1974 it was apparent that birds making over 20 feeding movements per minute were taking no prey of visible size whereas birds making fewer than 20 pecks/minute were consistently taking numbers of small worms, probably Nereis. On the basis of this observation I have made an arbitrary separation at about this level of feeding rate, so as to provide the monthly mean values presented in Table 7. The mean numbers of visible Nereis taken per minute by the slow pecking feeding method is also shown in Table 7. The sample size for these is generally very small and the variance about these mean values high.

TABLE 7.

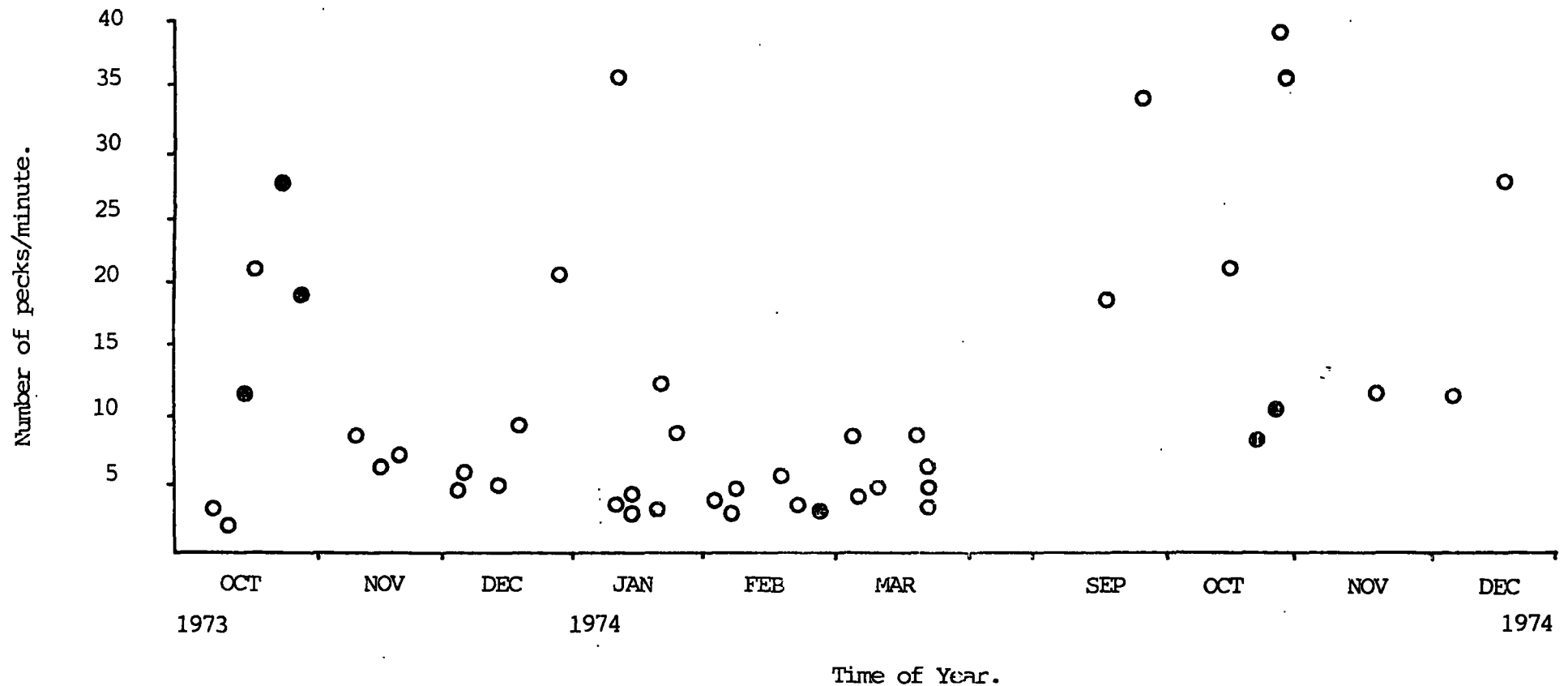
SUMMARY OF MONTHLY FEEDING RATES OF GREY PLOVERS.

Values are expressed as means $\pm$ S.E. and the number of measurements is given in parenthesis.

1973/74	OCTOBER	NOVEMBER	DECEMBER	JANUARY	FEBRUARY	MARCH
<u>North Area</u>						
Slow pecking method:						
pecks/min. (N)	6.00 $\pm$ 0.51 (51)	6.96 $\pm$ 0.45 (51)	5.82 $\pm$ 0.37 (66)	5.52 $\pm$ 0.42 (104)	4.33 $\pm$ 0.23 (106)	5.1 $\pm$ 0.28 (138)
worms taken/min.	-	-	0.22 $\pm$ 0.05	0.39 $\pm$ 0.08	0.26 $\pm$ 0.06	0.33 $\pm$ 0.05
Fast pecking method:						
pecks/min. (N)	24.53 $\pm$ 1.13 (59)	-	31.36 $\pm$ 2.05 (36)			
<u>West Enclosure</u>						
Slow pecking method:						
pecks/min. (N)	3.08 $\pm$ 0.29 (36)	2.66 $\pm$ 0.18 (103)				
worms taken/min.	0.59 $\pm$ 0.09					
1974		SEPTEMBER	OCTOBER	NOVEMBER	DECEMBER	
<u>North Area</u>						
Slow pecking method:						
pecks/min. (N)		9.41 $\pm$ 1.06 (26)	7.38 $\pm$ 0.60 (61)	11.21 $\pm$ 0.95 (19)	10.13 $\pm$ 0.76 (24)	
worms taken/min.		0.44 $\pm$ 0.17	0.79 $\pm$ 0.15	2.74 $\pm$ 0.52	1.26 $\pm$ 0.29	
Fast pecking method:						
pecks/min. (N)		44.17 $\pm$ 4.14 (24)	49.79 $\pm$ 3.32 (30)	42.40 $\pm$ 6.72 (10)	35.14 $\pm$ 2.81 (21)	

FIGURE 23 : VARIATION IN THE MEAN PECKING RATE OF GREY PLOVERS FEEDING ON NORTH AREA
DURING THE COURSE OF THIS STUDY.

Open circles represent means for birds feeding in daylight, solid circles being for birds feeding at night.



In the 1973/74 winter pecking rates for the 'slow' method were significantly faster in the months of November and December than in February 1974 only - otherwise mean monthly rates were similar. There was no relationship between pecking rate of birds using feeding method 1 and daily air or mud temperatures, nor were any consistent changes found in relation to wind speed.

Of particular interest is the fact that the pecking rate of birds on the West Enclosure was significantly slower than for birds on North Area in the months of October and November 1973. In view of the distribution of Grey Plovers between these two sections of Seal Sands at this time, with 60% in the West Enclosure at low water, it had been expected that the rate at which prey were captured would have been higher in the West Enclosure. However, the rate at which large items, chiefly Nereis, were captured was substantially higher on the West Enclosure in autumn than on the North Area in other winter months, and it seems likely that it was the higher rate of biomass intake which made the West Enclosure so attractive for Grey Plovers.

The rate of slow pecking (feeding method 1) in autumn 1974 was consistently higher than in the same months of 1973 and values differ significantly in the months of November and December. Additionally, the rate at which visible Nereis were taken by slow-pecking Grey Plovers in autumn 1974 was substantially higher than I recorded in spring 1974, immediately after reclamation of the West Enclosure and also higher than occurred in the West Enclosure itself in autumn 1973. It must be noted, however, that the autumn 1974 data are based on small samples of birds and that the proportion of the Grey Plover population which captured Nereis at this rate was small - the majority of the Grey Plover population were feeding by the fast pecking technique and were dependent largely on small prey to satisfy their energy requirements. The separation of the slow pecking technique was arbitrary and the group would tend to include those birds which were most successful at capturing Nereis. The rate of fast pecking was

TABLE 8.

THE COMPOSITION OF THE DIET OF GREY PLOVERS EMPLOYING THEIR MORE
TYPICAL RUN - STOP - PECK (SLOW PECKING) TECHNIQUE OF FEEDING.

Percentage contribution to the diet.						
<u>1973/74</u>	Small items	Nereis Under 20 mm	Nereis 20-35 mm	Nereis Over 35 mm	Macoma	Crabs
North Area	94.1	1.4	1.9	2.0	0.5	-
No. of prey	1771	27	36	38	10	
West Enclosure	81.7	0.8	2.5	14.9	-	-
No. of prey	192	2	6	35		
<u>Autumn 1974</u>						
North Area	86.5	9.7	2.1	0.7	0.7	0.1
No. of prey	726	82	18	6	6	1

significantly faster in October 1974 than in October 1973 but December values (the only other month for which I have comparable data) were similar.

For birds feeding by slow pecking, Nereis were a consistent item of the diet and Macoma were also taken regularly in both years by birds feeding on portions of the Central Bank and on the sandy parts of the Eastern Channel. In autumn 1974 small crabs were taken on occasions. However, assuming a success rate around 100%, then small items of food such as Hydrobia and small polychaetes were numerically the most important component of the diet, comprising over 80% of the diet even in the West Enclosure. The composition of the diet of those Grey Plovers feeding by the slow pecking method is shown in Table 8. For birds feeding in the West Enclosure a greater proportion of the diet comprised Nereis than for birds on North Area and these were of a larger size than those taken on North Area. A greater proportion of the diet in autumn 1974 consisted of visible Nereis than in spring 1974, although these tended to be of a rather smaller size.

Grey Plovers appear to have a broadly similar diet on other British estuaries. For example, in Essex, Burton (1966) found Nereis and Hydrobia were the most important prey with numbers of crabs being taken in autumn. These prey were also important on the Wash (Goss-Custard et al., 1977a) where Macoma were also taken frequently, although here the single most important prey was probably Ianice conchilega, a potential prey species not occurring on Seal Sands although present on the sandy areas of Bran Sands around the low water mark.

CURLEWS.

On North Area Curlews fed almost exclusively on exposed mud flats, only occasionally (and always temporarily) on submerged substrates. Visible-sized

Nereis (quarter bill length = 26-35 mm.) contributed between 81-100% of the diet during the 1973/74 winter, and in autumn 1974 94-98% of the diet. The lowest percentage contribution of Nereis occurred when some numbers of crabs, Carcinus maenus, were taken over a period of 2-3 weeks in the months of November and December 1973 and again in November 1974. The West Enclosure was not a favoured feeding site at any time during my study. However, the small number of records which I did obtain indicated that the diet there also included in excess of 90% Nereis.

Most prey were taken by probing to at least half the depth of the bill. As a rule two or three separate probes (between which the bill was removed almost completely from the mud) appeared necessary to locate and capture the prey. While searching for food, individuals made a number of pecks at the mud surface. These appeared to be involved only in the detection of prey, since only very rarely were even small items seen to be taken using this movement. On the basis of this observation and for the purpose of obtaining a true measure of the rate at which birds attempted to catch prey, I chose to record only those feeding movements involving probing to a depth of half bill length and over - that is, those likely to have been directed at a definite item of food.

My records of feeding activities of Curlew on North Area during the 1973/74 winter were obtained from the Greenabella Bank on all occasions except in January 1974. This site was the single most important area for feeding until the end of December 1973, regularly containing up to 80 birds at low water (around 25% of the Seal Sands population at this time), but thereafter its attractiveness diminished and was particularly low in January 1974, when I resorted to obtaining records from the Central Bank of North Area. However, even in spring 1974, I attempted to obtain most records in the vicinity of Greenabella Bank so as to maintain some consistency of approach. In autumn 1974 the Central Bank was the primary feeding area of Curlews and of necessity

my records were taken exclusively from that site.

The composition of the diet of Curlews on North Area in the two years of my study are shown in Table 9. These records suggest that the worms taken in the 1973/74 winter were generally larger than those taken in autumn 1974. This is also shown in Table 11 where I have grouped data for the periods before and after low water within each season. It seems quite probable that this difference is attributable to the difference in feeding areas studied in the two years, i.e. the Central Bank in autumn 1974 rather than the Greenabella Bank where most measurements were taken in 1973/74 winter. During the 1973/74 winter there appeared to be a smaller proportion of small items and a larger proportion of large worms (half bill length and over) taken in mid-winter than in either early spring or late autumn.

Additionally in spring 1974 my results indicate that there was a tendency for Curlews to collect a larger proportion of worms of about a third bill length and fewer worms over half bill length than earlier in that winter, although admittedly the sample size is small. If this was a real change in behaviour, then this might be connected with the fact that the later observations were from an area (the Greenabella Bank) which was clearly less attractive for feeding than it had been in autumn 1973. Perhaps it was the reduced availability of larger worms in this section of North Area which induced a movement of birds to the Central Bank where, although the diet comprised an even greater proportion of smaller size classes of Nereis, Curlews were able to collect more worms per minute (see later in this section).

There appeared to be no significant change in the proportions of different size classes of Nereis taken between September and December 1974. The measurements I made in autumn 1974 were reasonably well spread throughout the exposure period of North Area and these records are separated for each hour in Table 10. Although there appear to be no dramatic changes, there is a tendency for a greater percentage of worms taken to be of a larger size class after than

TABLE 9. THE COMPOSITION OF THE DIET OF CURLEWS FEEDING ON

NORTH AREA OF SEAL SANDS.

The size classes of *Nereis* are given as a proportion of bill-length, with the length this represents in millimetres being shown in parenthesis.

1973/74 Winter: Percentage contribution of different prey in each month.

Type of prey		OCT	NOV	DEC	JAN	FEB	MAR
Small items (< $\frac{1}{4}$ bill-length)		7.5	3.9	1.7	4.7	-	10.5
Sizes of <i>Nereis</i>	$\frac{1}{4}$ (26-35)	30	7.9	3.4	4.7	10.2	10.5
	$\frac{1}{3}$ (36-49)	50	56.8	52.5	64.3	83.0	73.7
	$\frac{1}{2}$ (50)	12.5	19.6	25.4	26.3	6.8	5.3
Crabs		-	11.8	16.9	-	-	-
Total No. of items		40	51	59	42	59	19
% visible worms		92.5	84.3	81.3	95.3	100	89.5

Autumn 1974: Percentage contribution of different prey in each month.

Type of prey		SEP	OCT	NOV	DEC
Small items (< $\frac{1}{4}$ bill-length)		8.5	4.1	-	14.7
Sizes of <i>Nereis</i>	$\frac{1}{4}$ (26-35)	44.1	42.3	22.1	39.8
	$\frac{1}{3}$ (36-49)	42.4	43.3	66.9	42.8
	$\frac{1}{2}$ (50)	5.0	10.3	5.5	2.7
Crabs		-	-	5.5	-
Total No. of items		59	97	163	299
% visible worms		91.5	95.9	94.5	85.3

TABLE 10.

THE COMPOSITION OF THE DIET OF CURLEWS FEEDING ON NORTH AREA OF
SEAL SANDS IN RELATION TO THE STATE OF THE TIDE IN AUTUMN 1974.

The size classes of Nereis are given as a proportion of bill-length with the length this represents in millimetres being shown in parenthesis.

Type and Size of Prey	The percentage of different prey captured in each hour after high water for which Curlews fed.					
	3 - 4	4 - 5	5 - 6	6 - 7	7 - 8	8 - 9
Small items (< $\frac{1}{4}$ bill-length)	10	7	19	11	1	4
$\frac{1}{4}$ (26-35)	40	38	40	32	28	37
Sizes of <u>Nereis</u> $\frac{1}{3}$ (36-49)	45	48	34	52	61	49
$\frac{1}{2}$ (50)	4	5	6	4	8	7
Crabs	1	2	1	1	2	3
Total No. of items	80	150	67	191	59	75
% visible worms	89	91	80	88	97	93

TABLE 11.

THE PERCENTAGE OF DIFFERENT SIZE CLASSES OF NEREIS IN THE DIET
OF CURLEWS FEEDING ON NORTH AREA BEFORE AND AFTER LOW WATER IN
THE TWO WINTERS OF THIS STUDY.

HW+3 to +6:

Percentage of different size classes of Nereis.

OCTOBER 1973 - MARCH 1974

OCTOBER - DECEMBER 1974

Sizes of Nereis

$\frac{1}{4}$ (26-35)	17.9	45.2
$\frac{1}{3}$ (36-49)	62.6	48.3
$\frac{1}{2}$ (50-70)	19.5	6.5
$\frac{2}{3}$ (over 70)	-	-
Total No. of items	123	230

HW+6 to +9:Sizes of Nereis

$\frac{1}{4}$ (26-35)	5.6	35.7
$\frac{1}{3}$ (36-49)	72.2	59.6
$\frac{1}{2}$ (50-70)	21.3	4.7
$\frac{2}{3}$ (over 70)	0.9	-
Total No. of items	108	277

before low water. This is shown more strikingly when data are grouped for the periods before and after low water (Table 11). This division of data allows comparison with my 1973/74 data which cannot be separated so effectively on an hourly basis, owing to the small sample sizes available for some hours.

However, by this grouping the results are biased in favour of those hours with larger sample sizes, i.e. HW+4-5 and HW+6-7 respectively, and these are records which differ quite widely. Grouping data for the 1973/74 winter into HW+3-6 and HW+6-9 periods in Table 11 also suggests that a larger proportion of worms taken after L.W. were of a $\frac{1}{3}$ bill-length or longer. My results suggest, therefore, that there was a selection by Curlews of larger size classes of Nereis after L.W., although whether this was a passive or active selection is not known.

A complete summary of the feeding rates and searching rates of Curlews using North Area in each month of my study is presented in Table 12. Records for the West Enclosure are insufficient to tabulate in this manner and are considered in the text.

Curlews appeared to search for prey at approximately similar rates throughout my study, although searching rate in November 1973 was significantly higher than in November 1974. The difference between searching rates in this instance might be attributed, in part, to the fact that observations were obtained from different parts of North Area in autumns 1973 and 1974. However, since similar differences are not apparent between other autumn months, it seems probable that some other features of the environment were involved. Although I suspect that the very low temperatures in November 1973 (air temperatures at night frequently falling below zero for a period of over one week) might have been responsible for the faster searching rate in this month, no correlation between pacing rate and air or mud temperatures was found when all my observations were analysed.

TABLE 12.

MONTHLY SUMMARY OF THE FEEDING ACTIVITY OF CURLEWS ON NORTH AREA IN DAYLIGHT.

Data are expressed as means $\pm$ S.E. with the number of observations in parenthesis.

	Searching Rate (N)* (Seconds)	Mean No. of probes/min. (N)	Mean No. of successes/min.	Mean No. of worms/min.**
OCTOBER 1973	2.64 $\pm$ 0.23 (10)	8.17 $\pm$ 0.64 (17)	1.47 $\pm$ 0.21	1.47 $\pm$ 0.21
NOVEMBER	3.00 $\pm$ 0.13 (28)	9.84 $\pm$ 0.55 (37)	1.43 $\pm$ 0.15	1.21 $\pm$ 0.15
DECEMBER	2.4 $\pm$ 0.33 (42)	11.80 $\pm$ 0.49 (67)	0.93 $\pm$ 0.11	0.73 $\pm$ 0.10
JANUARY 1974	2.6 $\pm$ 0.15 (39)	8.35 $\pm$ 0.52 (53)	0.79 $\pm$ 0.11	0.73 $\pm$ 0.11
FEBRUARY	2.5 $\pm$ 0.15 (42)	8.77 $\pm$ 0.56 (62)	0.95 $\pm$ 0.12	0.95 $\pm$ 0.12
MARCH	2.7 $\pm$ 0.26 (48)	10.40 $\pm$ 0.91 (20)	0.95 $\pm$ 0.19	0.85 $\pm$ 0.17
SEPTEMBER 1974	1.8 $\pm$ 0.24 (16)	11.85 $\pm$ 0.70 (20)	3.00 $\pm$ 0.31	2.75 $\pm$ 0.28
OCTOBER	2.4 $\pm$ 0.10 (23)	12.78 $\pm$ 0.53 (46)	2.13 $\pm$ 0.19	2.04 $\pm$ 0.18
NOVEMBER	2.38 $\pm$ 0.13 (63)	11.94 $\pm$ 0.29 (107)	1.57 $\pm$ 0.11	1.47 $\pm$ 0.11
DECEMBER	2.4 $\pm$ 0.12 (13)	11.97 $\pm$ 0.25 (140)	2.17 $\pm$ 0.11	1.81 $\pm$ 0.09

N.B. * Searching rate being the time, in seconds, for birds to make five paces.

** These are 'visible' Nereis, that is, $\frac{1}{4}$ bill-length (25 mm.) and over.

In the 1973/74 winter the rate at which Curlews attempted to capture prey (probing rate) was higher in November and December than in other months with the exception of March 1974 (when the sample size was small and the variance high). The probing rate was significantly higher in December 1973 than in January or February 1974. The success rates in the 1973/74 winter, and particularly the rate at which visible sized Nereis were captured, appeared to be rather lower over the mid-winter period than in autumn or spring. However, a significant difference exists only with respect to the autumn value, the overall success rate being significantly higher in October and November 1973 than in January 1974, while the rate at which visible Nereis were taken was higher in October than in either December or January.

During autumn 1974 there were no differences in searching rate or probing rate between months. As in autumn 1973, however, success rates appeared to be higher in early autumn. Curlews captured significantly fewer prey of all kinds in November than in either September or December, and significantly fewer visible Nereis in both November and December records than in September. The difference between November and December in terms of the overall numbers of prey captured is surprising and my qualitative records during this period give no indication why this should be, apart from the fact that it was in November that crabs (most in excess of 2 cms. in width) featured in the diet of Curlews on North Area. It seems likely that these prey would provide a disproportionately large contribution in terms of biomass, which would compensate for a deficiency in terms of numbers of prey taken and the numbers of Nereis taken. This would also account for the low intake rates of prey and particularly of Nereis in November and December 1973. Depending on the extent to which crabs might compensate in terms of biomass, there could be a totally different interpretation of the monthly changes in intake rates in the 1973/74 winter. Thus there might have been a gradual decrease of the biomass intake rate from autumn to spring or

there might have been a higher intake rate over the mid-winter period, since not only were crabs taken at that time but also the average size of Nereis captured was greater.

Although my records suggest that Curlews captured more prey and also more worms per minute in autumn 1974 than in respective months of 1973, only values for December are significantly different. Again comparison would best be made in terms of biomass intake since in addition to the greater contribution of crabs to the diet of birds in 1973 the Nereis taken in 1974 were generally smaller (Table 11). On this basis, a higher numerical intake rate would be required if birds were to satisfy their daily energy needs by feeding for the same number of hours when restricted to North Area alone.

A small number of records of searching rate and feeding rate were made of birds using the West Enclosure over low water in October and November 1973. During daylight, searching rate in this part of Seal Sands varied from 2.15 ± 0.07 seconds for 5 paces ($N = 22$) to 2.9 ± 0.18 seconds ($N = 10$), a similar range, therefore, to my records for North Area at this time. Feeding rates (all recorded in November 1973) were 1.75 ± 0.2 items (chiefly large Nereis) per minute ($N = 24$), 2.1 ± 0.3 ($N = 11$) and 1.14 ± 0.2 ($N = 22$) - again these are within the range of feeding rates recorded on North Area.

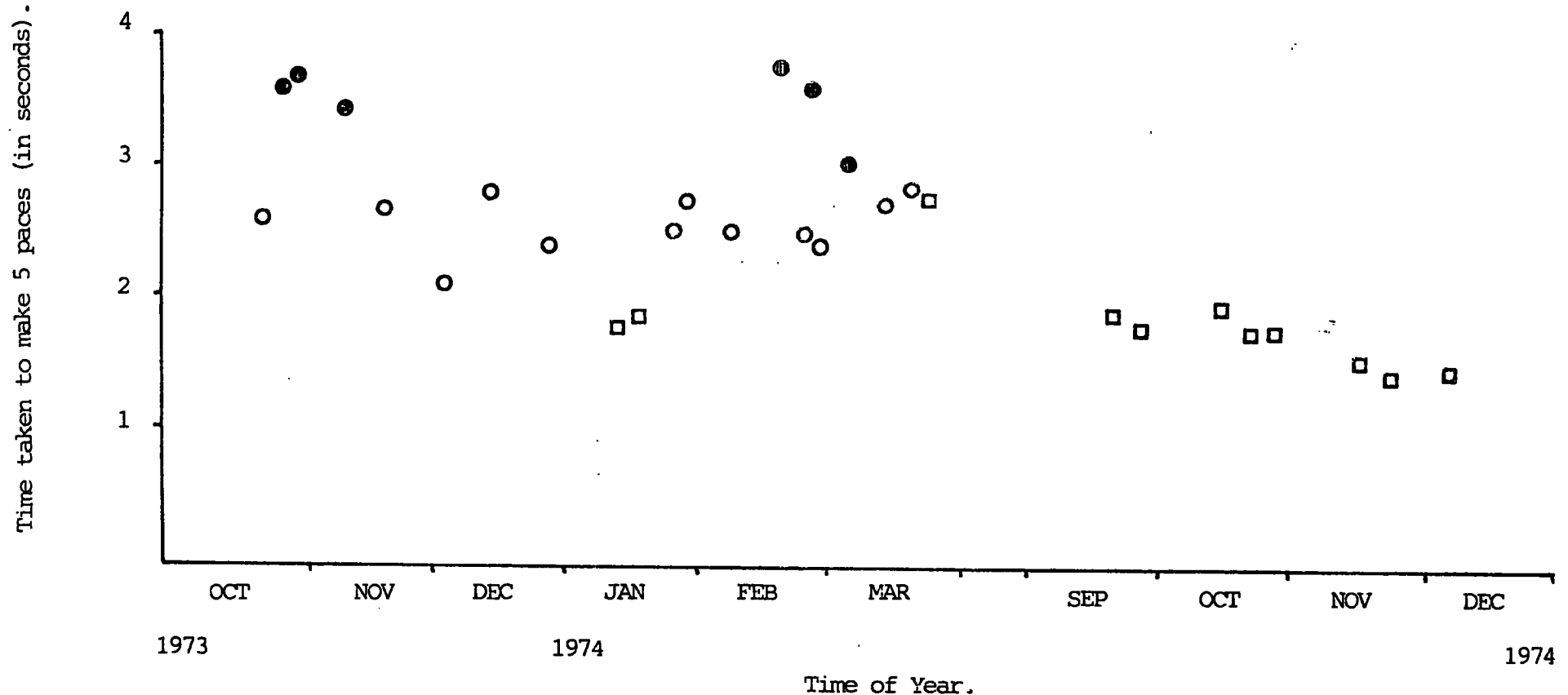
The high level of illumination by night over the Greenabella Bank and West Enclosure in the 1973/74 winter enabled me to measure searching rates of Curlews on a number of occasions. These are plotted graphically in Fig. 24 along with all daytime records made during that winter. Searching rates at night on North Area and West Enclosure were similar, just as they had been during daylight, but in both sites they were significantly slower than the majority of daytime records. The mean time taken for 5 paces at night on Seal Sands in 1973/74 was 3.6 ± 0.18 seconds ($N = 120$) compared with a mean value of 2.58 ± 0.21 seconds by day ($N = 250$). In autumn 1974 it was possible to make a small number of records at night despite the reduced level of industrial

FIGURE 24 : VARIATION IN THE SEARCHING RATE OF CURLEWS FEEDING ON NORTH AREA

DURING THE COURSE OF THIS STUDY.

Each value is derived from measurements of approximately 20 individuals.

Values shown as circles are of birds feeding on the Greatham Creek area of North Area - open circles being recorded in daylight and the solid circles being night records. The squares depict the searching rate of birds feeding on the Central Bank.



lighting and the drier, non-reflective nature of sediments on the Central Bank; the mean for these was 3.1 ± 0.21 seconds ($N = 40$), and as in the previous winter this is slower than searching rate in daylight. It was a consistent observation that birds feeding at night tended to hesitate occasionally while searching (being most marked before probing), but during the day, walking, surface pecking and probing seemed to flow in a single movement. It seems likely that this behaviour accounted for the slower rate of pacing observed at night. However, my measurements at night were under conditions of lower wind speeds than occurred during the day, and this might have accounted in part for the difference in pacing rates. There was no correlation, however, between pacing rate and wind speed when all observations were considered.

The feeding rates of Curlews for the months October - December 1973, January - March 1974 and October - December 1974 are separated for the periods before and after low water in Table 13. Although between October and December of both 1973 and 1974 feeding rate was faster before than after low water, this difference was not significant. In the months January - March 1974 there appeared to be a lower feeding rate before than after low water, but again this difference was not significant. In autumn 1974 sufficient data are available to provide a reasonable measure of feeding rate in each hour for which Curlews fed (Table 14) but there appears to be no consistent trend. There is a suggestion that success rates between HW+6-8 were rather lower than before low water, and lower also than between HW+8-9. This is given some support statistically since, in terms of overall success, the HW+7-8 value is significantly lower than all values except for the HW+6-7 record which itself is significantly lower than that in the HW+5-6 period. The differences are less when considering the intake rate of worms alone, the value for HW+7-8 being lower than for the periods HW+5-6 and HW+8-9 only.

The rate at which Curlews captured prey and probed for prey did not vary consistently in relation to air or mud temperatures nor with wind speed.

TABLE 13. THE FEEDING RATES OF CURLEWS IN RELATION TO THE TIME
AFTER HIGH WATER.

Data are summarized in relation to the three main divisions of my study. Each record represents a mean $\pm$ S.E. with the number of observations in parenthesis.

<u>HW+3 to +6:</u>	OCT - DEC 1973	JAN - MAR 1974	OCT - DEC 1974
No. of successes /minute	1.24 $\pm$ 1.0 (79)	0.67 $\pm$ 0.12 (42)	2.14 $\pm$ 0.12 (128)
No. of <u>Nereis</u> taken/minute	0.75 $\pm$ 0.10	0.67 $\pm$ 0.12	1.88 $\pm$ 0.10
 <u>HW+6 to +9:</u>			
No. of successes /minute	1.00 $\pm$ 0.14 (42)	0.99 $\pm$ 0.09 (93)	1.78 $\pm$ 0.09 (165)
No. of <u>Nereis</u> taken/minute	0.88 $\pm$ 0.13	0.96 $\pm$ 0.09	1.62 $\pm$ 0.09

TABLE 14.

THE FEEDING RATE OF CURLEWS ON NORTH AREA IN AUTUMN 1974 IN RELATION TO THE TIME AFTER HIGH WATER.

Data expressed as means $\pm$ S.E. with the number of observations in parenthesis.

Mean success rates in each hour after high water.

	3 - 4	4 - 5	5 - 6	6 - 7	7 - 8	8 - 9
Total No. of successes/minute (N)	2.27 $\pm$ 0.26 (30)	2.19 $\pm$ 0.16 (72)	2.9 $\pm$ 0.29 (21)	1.84 $\pm$ 0.13 (86)	1.4 $\pm$ 0.14 (43)	2.16 $\pm$ 0.20 (36)
Nos. of visible <u>Nereis</u> taken/minute	2.0 $\pm$ 0.22	1.93 $\pm$ 0.14	2.3 $\pm$ 0.3	1.61 $\pm$ 0.13	1.3 $\pm$ 0.15	2.03 $\pm$ 0.19
Total No. of probes made/minute	11.60 $\pm$ 0.37	13.22 $\pm$ 0.33	11.6 $\pm$ 0.63	12.24 $\pm$ 0.32	10.6 $\pm$ 0.21	11.4 $\pm$ 0.61

BAR-TAILED GODWITS.

Two feeding techniques were seen to be used by Godwits at Seal Sands:

1. On firmer substrates which were either fully exposed or only shallowly covered by water or soft wet mud, birds fed in the same way as Curlew, that is by surface pecking followed by probing (i.e. the insertion of the bill into the substrate to at least a quarter of its length - see Methods p. 175) to obtain prey.
2. In deeper water or areas of very fine water-saturated mud (liquid mud) more than 4 cms. deep, birds used surface feeling, a continuous pecking over the submerged surface with the bill open, followed eventually by probing for any item of prey detected.

Although Godwits showed a tendency to move to lower tidal levels as these were exposed, only at higher states of the tide on North Area (e.g. HW+1½-2½ and HW+9-10) were groups of birds seen to feed for any extended time in the water, employing method 2 above. Between HW+3-9, feeding method 1 predominated on North Area. Within the West Enclosure where, as reclamation progressed, the area covered by fine mud and its depth increased, all Godwits preferred to feed on the margins of the dredged material. Here, birds again employed method 1. Only in the final stages of reclamation were large numbers of birds seen to feed in the deeper areas of fine sediment where they then fed by method 2. In the South-East Enclosure, where the water level remained high throughout its reclamation, method 2 was used almost exclusively, but observations of feeding rates were not conducted here.

All my records of foraging activity were made of birds feeding by method 1, since this predominated on North Area, which was destined to be the sole remaining portion of Seal Sands after completion of phase I of the reclamation

programme. Furthermore, only for birds using this technique could the size of prey and the numbers of feeding movements be counted accurately.

On North Area, although I observed some slight changes in the composition of the diet of Godwits with the state of the tide, and also seasonally, Nereis diversicolor predominated both in terms of absolute numbers of prey taken and biomass. This was also the case before reclamation (Pienkowski, 1973), but contrasts with the known diets of Godwits on some other major overwintering sites on the east coast. For example at Lindisfarne, Smith (1975) found Arenicola marina to form the bulk of the diet in terms of biomass, while on the Wash Lanice conchilega was the most important prey (Goss-Custard et al., 1977a). However, some Nereis were also taken at both sites but particularly on the Wash. The contribution of different prey species and different size classes of Nereis (as measured against bill length) to the diet of Godwits feeding on North Area is shown in Tables 15 - 19. In Tables 15 and 16 the composition of the diet before and after low water is separated for the periods October - December 1973 (during reclamation), January - February 1974 (immediately after reclamation) and October - December 1974 (the first winter following reclamation). This grouping is necessary since sufficient data are not available for each tidal period in each month. The diet of birds for the principal period for feeding, that is HW+3-9, can however be presented on a monthly basis with greater accuracy - Table 17. Data relating to the diet of Godwits at higher tidal levels has not been included in this monthly summary in view of the disproportionate quantity of small prey taken at these stages of tide (see Table 18) and the relatively small proportion of the bird population involved (see Percentage Feeding Times p.234). Table 18 relates only to the period HW+2-3, since Godwits fed only sporadically after HW+9-10 and then frequently in the water, using method 2, which was not recorded in view of its incompatibility with records of feeding rates from method 1. A small number of records

of birds feeding by method 1 after HW+9 were obtained, chiefly in spring 1974, but are not included here in view of the lack of comparable data for autumn 1973 or 1974.

My findings, in Table 17, show that for Godwits on North Area visible Nereis (that is, those over quarter bill-length = over 15 mm.) constituted in excess of 90% of all items taken, in all months except October and December 1973 and September and October 1974, the December record being unusually low because of the large numbers of crabs taken in this month. The contribution of small prey species was highest in autumn of each year. These prey were not identifiable but probably included Hydrobia ulvae, small Macoma balthica and small worms, no doubt mostly Nereis but possibly other polychaetes such as Scoloplos armiger which occur in small numbers at Teesmouth (Gray, 1976; Herdson pers. comm.). A larger proportion of Macoma occurred in the diet of birds feeding at higher tidal levels, especially between HW+2-3, and almost exclusively in autumn. Macoma were usually taken in the vicinity of the Peninsula where the substrate is firm and sandy. Records of Macoma taken in December 1973 are probably unusual; they coincide with a period when small groups of Godwits were feeding on shore crabs, Carcinus maenas, towards the upper part of the foreshore (where Macoma were most frequently taken at other times of year). These were areas rarely frequented during most of the tidal cycle when preferred feeding sites lying at and around the mid-tidal level were exposed. Crabs were taken by Godwits only in December 1973 and then only for a period of 2 - 3 weeks. Although the same general feeding area (mainly the Eastern Channel and adjacent parts of the Central Bank) was observed in autumn 1974, a similar change in the dietary pattern was not noted. Crabs were also taken by Godwits in late autumn at Lindisfarne (Smith, 1975) but similarly only in small numbers.

The high contribution of Macoma and small prey, the majority of which were presumed to be Hydrobia, in autumn coincides with a period when the abundance of these molluscs is highest at Teesmouth (Evans et al., 1979) and

TABLE 15.

SEASONAL VARIATION IN THE COMPOSITION OF THE DIET OF GODWITS ON
NORTH AREA BEFORE LOW WATER (HW+3-6) .

The sizes of prey are given as a proportion of bill-length with the length this represents in millimetres being shown in parenthesis.

Type and Size of Prey	Percentage contribution to the diet.		
	OCT - DEC 1973	JAN - MAR 1974	OCT - DEC 1974
Small items (< $\frac{1}{4}$ bill-length)	1.3	32.4	8.8
$\frac{1}{4}$ (15-25)	2.6	14.7	12.0
$\frac{1}{3}$ (25-37)	41.0	50.0	30.4
Sizes of <u>Nereis</u> $\frac{1}{2}$ (38-55)	35.9	2.9	44.0
$\frac{2}{3}$ (55-70)	3.8	-	4.0
Crabs	10.3	-	-
<u>Macoma</u>	5.1	-	0.8
Total No. of items taken	78	34	250
% contribution of visible worms (i.e. 15-70 mm. in length).	83.3	67.6	90.4

TABLE 16.

SEASONAL VARIATION IN THE COMPOSITION OF THE DIET OF GODWITS ON
NORTH AREA AFTER LOW WATER (HW+6-9):

The sizes of prey are given as a proportion of bill-length with the length this represents in millimetres being shown in parenthesis.

Type and Size of Prey	Percentage contribution to the diet.		
	OCT - DEC 1973	JAN - MAR 1974	OCT - DEC 1974
Small items (< $\frac{1}{4}$ bill-length)	48.8 *	3.0	2.9
$\frac{1}{4}$ (15-25)	7.0	5.1	14.5
$\frac{1}{3}$ (25-37)	16.3	60.6	25.6
Sizes of <u>Nereis</u> $\frac{1}{2}$ (38-55)	27.9	29.3	53.5
$\frac{2}{3}$ (55-70)	-	2.0	3.5
Crabs	-	-	-
<u>Macoma</u>	-	-	-
Total No. of items taken	43	99	171
% contribution of visible worms (i.e. 15-70 mm. in length).	51.2	97	97.1

N.B. * October - December 1973 record comes from two series of observations on the 18/10/73 and 21/10/73 when large numbers of small prey were taken.

TABLE 17.

THE COMPOSITION OF THE DIET OF GODWITS ON NORTH AREA BETWEEN HW+3-9 IN EACH MONTH

AND ON THE WEST ENCLOSURE OF SOUTH AREA DURING AUTUMN 1973 FOR ALL STAGES OF THE TIDE.

The sizes of prey are given as a proportion of bill-length with the length this represents in millimetres being shown in parenthesis.

Percentage contribution to the diet in each period.

Type and Size of Prey	West Enclosure Autumn 1973	OCT*	1973 NOV	DEC	1974 JAN	FEB/MAR**	SEP	1974 OCT	NOV	DEC
Small items (< $\frac{1}{4}$ bill-length)	15	49	-	2	2	17	20	11	3	7
$\frac{1}{4}$ (15-25)	16	7	5	2	5	7	7	11	14	13
Sizes of $\frac{1}{3}$ (25-37)	53	16	42	41	56	60	31	26	26	34
<u>Nereis</u> $\frac{1}{2}$ (38-55)	15	28	53	30	34	14	36	47	53	41
$\frac{2}{3}$ (55-70)	1	-	-	5	3	-	3	3	4	5
Crabs	-	-	-	13	-	-	-	-	-	-
<u>Macoma</u>	-	-	-	7	-	-	3	2	-	-
Total No. of items taken	193	43	19	59	59	74	61	109	186	126
% contribution of visible worms (i.e. 15-70 mm. in length).	85	51	100	78	98	83	77	87	97	93

N.B. * The record for October 1973 included an unusually high percentage of small items, this record comprising largely measurements on two days only, that is the 18/10/73 and 21/10/73.

** Since only one series of measurements were made in March 1974, these have for convenience been combined with the February record.

TABLE 18.SEASONAL VARIATION IN THE COMPOSITION OF THE DIET OF GODWITS ONNORTH AREA BETWEEN HIGH WATER +2-3.

The sizes of prey are given as a proportion of bill-length with the length this represents in millimetres being shown in parenthesis.

Type and Size of Prey	Percentage contribution to the diet.	
	1973/74	1974
	OCTOBER - MARCH	OCTOBER - DECEMBER
Small items ($< \frac{1}{4}$ bill-length)	52.2	34.9
$\frac{1}{4}$ (15-25)	11.6	9.5
Sizes of $\frac{1}{3}$ (25-37)	26.1	17.5
<u>Nereis</u>		
$\frac{1}{2}$ (38-55)	4.3	28.6
$\frac{2}{3}$ (55-70)	-	1.6
Crabs	-	-
<u>Macoma</u>	5.8	7.9
Total No. of items taken	69	63
% contribution of visible worms (i.e. 15-70 mm. in length).	42	57.2

N.B. Data are insufficient to divide the period October 1973 to March 1974 as has been possible in Tables 15 and 16.

TABLE 19.

THE PROPORTIONS OF DIFFERENT SIZES OF NEREIS DIVERSICOLOR IN THE DIET OF GODWITS FEEDING

ON NORTH AREA BETWEEN HW+3-9 AND ON THE WEST ENCLOSURE OF SOUTH AREA IN AUTUMN 1973.

The sizes of Nereis are given as a proportion of the bill-length (80-100 mm.) with the length this represents in millimetres being shown in parenthesis.

Percentage contribution to the diet in each period.

Sizes of <u>Nereis</u>	West Enclosure Autumn 1973	1973/74						1974		
		OCT	NOV	DEC	JAN	FEB	SEP	OCT	NOV	DEC
$\frac{1}{4}$ (15-25)	19	14	5	2	5	9	9	11	15	12
$\frac{1}{3}$ (25-37)	63	32	42	52	57	73	40	32	27	39
$\frac{1}{2}$ (38-55)	17	54	53	39	35	18	47	54	54	44
$\frac{2}{3}$ (55-70)	1	-	-	7	3	..	4	3	4	5
Total No. of worms measured	164	22	19	46	58	55	46	95	178	117

when the biomass per individual of these species is likely also to be highest (Goss-Custard et al., 1977a).

The majority of Nereis eaten by Godwits (Table 19) were between 25-50 mm. in length in both years of my study. The proportion of different size classes of Nereis taken between October - December was similar in both 1973 and 1974 in the periods before and after low water, Table 15 and 16, but between HW+3-6 in January and March 1974 a lower proportion of half bill length Nereis was taken than in the October - December periods of either year. The progressive nature of this change, illustrated in Table 19 (monthly separation), suggests that it was real, even though I could not test its significance in the absence of any confidence limits for my measurements of worm size. In the October - December period of both 1973 and 1974 the composition of the diet was similar between HW+3-6 and HW+6-9, but between January - March 1974 my results suggested a rather smaller proportion of worms taken before low water were in the half bill length (38-55 mm.) size class than of those taken after low water. The sample for the period HW+3-6 is very small however.

Although the diet between HW+2-3 (Table 18) included a far larger proportion of small food items than between HW+3-9 (hence its exclusion from Tables 17 and 19 monthly separation) the proportions of different size classes of Nereis were in fact similar. It seems likely that the quite abrupt change in the proportion of smaller prey after the HW+2-3 period is associated with the tidal levels at which the North Area sediments occur, since the majority of feeding areas are exposed and covered very rapidly around HW+3 and HW+9 respectively.

Data for West Enclosure are insufficient to separate on an hourly basis and it seems likely that treatment of data in this manner would not be particularly relevant in view of the rapidly changing conditions for feeding there. Data have, therefore, been grouped for the whole reclamation period (Table 17 and 19), the majority of measurements having been made in November

1973. It is evident that the Nereis taken by Godwits on the West Enclosure were generally smaller than those taken on the North Area during the same period, for example only 17% of worms taken in the West Enclosure in November 1973 (the month from which I have most measurements) were half bill length whereas 52% were of this size class in my records for North Area.

A complete summary of searching and feeding rates for each month of my study is presented in Table 20. Although the searching rate of Godwits on North Area appeared to be generally slower during reclamation of the West Enclosure of South Area (October - November 1973) than after reclamation, insufficient of the monthly records are significantly different to make any general statements concerning the influence of reclamation on the basis of this parameter of foraging behaviour alone. However, searching rates in October and November 1974 were consistently faster than in the respective months of 1973. The fastest searching rates of any period during my study were recorded in the final months of 1974, but only for November is the difference significant. The November record differs from all other records in that almost all measurements were taken during the most prolonged period of cold weather experienced at Teesmouth during my study. It was slowest pacing rate which I recorded; possibly this was associated with the cold, although I found no correlations between the daily pacing rates and the temperatures or wind speeds (and therefore chill factors) on those days. When considering these records of searching rate, it is important to note that all measurements apply only to the Eastern Channel of North Area and do not incorporate variation due to grouping observations for different areas, i.e. they reflect quite accurately the rate at which birds foraged.

The searching rates of Godwits feeding in the West Enclosure were not significantly different from those of birds using the North Area during autumn 1973.

TABLE 20.

SUMMARY OF THE FEEDING ACTIVITY OF BAR-TAILED GODWITS IN DIFFERENT MONTHS.

All records represent means $\pm$ S.E. with the number of observations in parenthesis.

	Searching Rate (Time taken for 5 paces) in seconds (N)	Mean Nos. of probes/min. $\pm$ S.E. (N)	Mean Nos. of successes/min. $\pm$ S.E.	Mean Nos. of visible worms/min. $\pm$ S.E.
West Enclosure Oct-Dec 1973	1.95 $\pm$ 0.14 (56)	8.68 $\pm$ 0.28 (92)	2.25 $\pm$ 0.14	1.91 $\pm$ 0.13
North Area 1973/74 HW+2-3	-	6.06 $\pm$ 0.57 (47)	1.43 $\pm$ 0.21	0.62 $\pm$ 0.13
North Area 1973/74 HW+3-9				
OCTOBER	2.14 $\pm$ 0.17 (18)	7.16 $\pm$ 0.43 (25)	1.72 $\pm$ 0.22	0.92 $\pm$ 0.13
NOVEMBER	2.35 $\pm$ 0.13 (17)	8.41 $\pm$ 0.63 (18)	1.12 $\pm$ 0.22	1.12 $\pm$ 0.22
DECEMBER	1.67 $\pm$ 0.08 (55)	7.73 $\pm$ 0.35 (67)	0.83 $\pm$ 0.10	0.64 $\pm$ 0.08
JANUARY	1.77 $\pm$ 0.06 (80)	6.91 $\pm$ 0.23 (86)	0.73 $\pm$ 0.09	0.71 $\pm$ 0.09
FEBRUARY	1.63 $\pm$ 0.15 (39)	6.63 $\pm$ 0.31 (54)	1.04 $\pm$ 0.11	0.96 $\pm$ 0.11
MARCH	1.69 $\pm$ 0.12 (27)	-	-	-
North Area Autumn 1974				
HW+2-3	-	6.35 $\pm$ 0.36 (55)	1.16 $\pm$ 0.11	0.76 $\pm$ 0.12
HW+3-9				
SEPTEMBER	1.72 $\pm$ 0.1 (31)	8.70 $\pm$ 0.57 (35)	1.82 $\pm$ 0.21	1.37 $\pm$ 0.16
OCTOBER	1.79 $\pm$ 0.09 (39)	8.29 $\pm$ 0.30 (71)	1.56 $\pm$ 0.22	1.37 $\pm$ 0.11
NOVEMBER	1.43 $\pm$ 0.09 (37)	7.88 $\pm$ 0.23 (118)	1.67 $\pm$ 0.15	1.58 $\pm$ 0.10
DECEMBER	1.41 $\pm$ 0.06 (30)	7.37 $\pm$ 0.28 (86)	1.52 $\pm$ 0.18	1.40 $\pm$ 0.12

The probing rate of Godwits feeding on the Eastern Channel of North Area in the 1973/74 winter (Table 20) showed no significant variation from month to month; only the value for total number of successes/minute in October 1973 is significantly higher than the December 1973 and January 1974 records. The significance of even this difference disappears, however, when the comparison is restricted solely to visible worms taken. Despite the lack of significant variation during this winter there was a trend for probing rates to diminish after early autumn and for success rates to be lowest in mid-winter.

The mean monthly rates of capture of all prey items and the rate of capture of visible worms was consistently higher in autumn 1974 than in the same months of 1973, yet a significant difference can be shown only between respective December measurements. The rate of probing in equivalent months of 1973 and 1974 was similar. In autumn 1974, as in autumn 1973, there was a tendency for the probing rate to fall from early autumn onwards. In autumn 1974 there was no indication that the rate of capture of all prey, or of worms alone, fell between October and December as appears to have occurred in 1973. Neither the capture rate of prey nor the probing rate varied in relation to air temperature, mud temperature or wind speed.

Table 21 shows the probing rates and success rates of Godwits on North Area for each hour between HW+2-10. Probing and success rates were consistently higher in 1974 than in 1973, while for each hour between HW+3-5 and HW+7-9 the rate at which visible Nereis were taken was significantly higher in 1974 than in 1973. There appears to be no consistent variation between success rates in each hour during the period HW+3-9 in either the 1973/74 winter or in autumn 1974, and this was true also for the HW+2-3 period in 1973/74 winter. In autumn 1974, however, the overall success rate and the capture rate of visible Nereis between HW+2-3 was significantly lower than in the period HW+3-9.

Since my data on success rates are insufficient for separation for each

TABLE 21.

SUMMARY OF FEEDING RATES AND PROBING RATES OF GODWITS ON NORTH AREA IN RELATION TO TIDAL LEVEL.

The data are expressed as means $\pm$ S.E. with the number of observations in parenthesis.

The number of hours after high water.

	2 - 3	3 - 4	4 - 5	5 - 6	6 - 7	7 - 8	8 - 9	9 - 10
<u>Probes/minute</u>								
Winter 1973/74	6.06 $\pm$ 0.57 (47)	7.73 $\pm$ 0.40 (49)	7.47 $\pm$ 0.36 (59)	-	7.07 $\pm$ 0.34 (42)	6.63 $\pm$ 0.35 (40)	6.58 $\pm$ 0.26 (60)	8.05 $\pm$ 0.7 (19)
Autumn 1974	6.35 $\pm$ 0.36 (55)	8.4 $\pm$ 0.27 (98)	8.51 $\pm$ 0.35 (59)	7.0 $\pm$ 0.35 (16)	6.5 $\pm$ 0.41 (21)	7.11 $\pm$ 0.33 (67)	8.51 $\pm$ 0.29 (49)	
<u>Total no. of successes/min.</u>								
Winter 1973/74	1.43 $\pm$ 0.21	0.98 $\pm$ 0.12	1.02 $\pm$ 0.13	-	1.29 $\pm$ 0.17*	0.85 $\pm$ 0.14	0.90 $\pm$ 0.11	0.87 $\pm$ 0.16
Autumn 1974	1.16 $\pm$ 0.11	1.64 $\pm$ 0.11	1.76 $\pm$ 0.15	1.68 $\pm$ 0.22	1.62 $\pm$ 0.36	1.62 $\pm$ 0.16	1.64 $\pm$ 0.21	
<u>No. of visible worms captured/minute</u>								
Winter 1973/74	0.62 $\pm$ 0.13	0.80 $\pm$ 0.11	0.75 $\pm$ 0.11	-	0.81 $\pm$ 0.11	0.85 $\pm$ 0.14	0.90 $\pm$ 0.11	0.79 $\pm$ 0.14
Autumn 1974	0.76 $\pm$ 0.12	1.46 $\pm$ 0.11	1.46 $\pm$ 0.12	1.68 $\pm$ 0.22	1.62 $\pm$ 0.36	1.47 $\pm$ 0.15	1.38 $\pm$ 0.12	

N.B. * This record from October 1973 included large numbers of small prey.

TABLE 22.

THE FEEDING RATES OF GODWITS ON NORTH AREA BEFORE AND AFTER
LOW WATER IN THE PERIODS OCTOBER - DECEMBER 1973 AND 1974,
AND BETWEEN JANUARY - MARCH 1974.

Each record represents a mean $\pm$ S.E. with the number of observations in parenthesis.

Mean number of prey captured/minute.

Tidal level	OCT - DEC 1973	JAN MAR 1974	DEC - DEC 1974
<u>HW+3 to +6</u>			
No. of successes /minute	0.88 $\pm$ 0.09 (84)	1.37 $\pm$ 0.19 (27)	1.67 $\pm$ 0.08 (173)
No. of <u>Nereis</u> taken/minute	0.71 $\pm$ 0.08	0.95 $\pm$ 0.19	1.51 $\pm$ 0.08
<u>HW+6 to +9</u>			
No. of successes /minute	1.72 $\pm$ 0.22 (25)	0.82 $\pm$ 0.07 (126)	1.62 $\pm$ 0.12 (137)
No. of <u>Nereis</u> taken/minute	0.88 $\pm$ 0.13	0.79 $\pm$ 0.07	1.57 $\pm$ 0.12

hour within each month of my study, in Table 22 I have grouped records for the periods HW+3-6 and HW+6-9 for the three principal divisions of my study as it relates to the reclamation programme. Unfortunately even this grouping seems not to remove the problem of small sample sizes. It is probably for this reason that the unusual, yet significant, differences in total success rates occur, i.e. the higher success rate after low water in autumn 1973 whereas success rate is higher before low water in spring 1974. Capture rates of visible Nereis in these two periods do not differ however, confirming the earlier observation based on Table 21 that capture rates were reasonably similar in each hour between HW+3-9. The grouping of data in Table 22 serves to emphasize the significantly higher capture rates of Nereis in autumn 1971 than in either autumn 1973 or spring 1974. Unfortunately similar generalization is not possible with respect to total success rates because of the two unusual records which have been noted above.

REDSHANKS.

During reclamation the distribution of Redshanks on Seal Sands corresponded to the areas where fine sediment was being actively deposited (see p. 209) - primarily in the West Enclosure and on adjacent sections of North Area, particularly in the channels draining northwards from the East/West wall. Particularly favoured were those areas where the liquid sediments were between Redshank knee and thigh depth (around 4 - 8 cm.) although some birds continued to feed even when this liquid mud was almost up to the lower edge of the wing. In these situations Redshanks fed almost exclusively by swishing, a technique which involved a side to side sweeping motion of the bill which was held between half to fully immersed in the liquid sediment.

There were many variations of the swishing technique and, although I did not attempt to record these in detail, it is interesting to note the more distinct forms which were employed. The most typical method of swishing involved a fast side to side movement of the head, the bill inserted into the mud to about half its length. After several swishes the prey captured would be swallowed and this appeared to occur at very regular intervals. These prey were not visible but it seems likely that the majority were small worms, oligochaetes and small polychaetes including Nereis. No doubt several were captured before swallowing. Most birds swallowed while continuing to move through the mud, the whole behaviour being uninterrupted. In some situations swallowing followed only a single swish. Occasionally the method was modified into a simple forward scooping movement of the bill, followed by swallowing in all cases.

A second important and distinctive form of swishing involved a deeper movement of the bill through the mud and a wider arc of sweeping with many swishes being made before an item of food was encountered and swallowed. The principal prey taken by this method was almost always Nereis. On the North

Area crabs were also taken by this method in the first few weeks of December 1973.

Redshanks fed at extremely high densities while swishing, and considerable grouping of birds occurred within an area. Each bird within a group used one or other of the two swishing variants, rarely both. On occasions groups some 20 yards apart in sediment of similar depth would use a different variant of swishing. A rather tighter grouping of feeding birds was evident at night and the pacing rate appeared faster, but in measurement over 30 seconds this was counteracted by more frequent pauses in pacing. On one occasion a single group of over 200 feeding Redshanks was seen at night and similarly large flocks were seen by Goss-Custard on the Ythan estuary (Goss-Custard, 1970).

Between mid-October and mid-December 1973, almost all Redshanks fed by swishing. In early October, before reclamation had created any substantial areas of fine sediment, and between the end of active reclamation and the end of the 1973/74 winter, the more typical feeding technique of this species, namely discrete pecks and probes, was more prevalent although still subordinate to swishing. This was localized on the better drained firmer substrates, areas used hardly at all during reclamation. In autumn 1974, only in October were small groups of Redshanks seen swishing in the manner recalling their behaviour throughout the reclamation period. Thereafter, surface pecking and probing was the principal feeding method although swishing was used commonly in areas of surface water and patches of liquid mud near the slag walls bounding North Area. In autumn 1974 swishing and pecking/probing appeared freely interchangeable as birds moved from wet to dry substrates respectively. This contrasts with the situation in the 1973/74 winter when birds generally employed either one method or the other, a result of the tendency for individuals to feed more strictly on a single type of substrate.

Because of the predominance of swishing amongst Redshanks in autumn 1973, I decided to record the feeding activity of birds using this method only, during that winter of my study. As for Shelducks and Dunlins, I measured a combined searching and feeding rate in terms of the numbers of paces taken in 30 seconds. This was converted to a rate/minute for presentation in this section.

The daily mean pacing rates of Redshanks feeding by swishing on North Area in daylight ranged from $57.9 \pm 5.8/\text{min.}$ (numbers of observations = 18) to $92.5 \pm 3.7/\text{min.}$ (24) while mean pacing rate at night varied from 58.3 ± 5.4 (31) to 101.6 ± 4.3 (28). Mean pacing rate on the West Enclosure ranged from $57.6 \pm 5.3/\text{min.}$ (20) to $128 \pm 2.1/\text{min.}$ (22) in daylight and from 78.8 ± 3.2 /min. (26) to $97.4 \pm 4.0/\text{min.}$ (15) at night. All daily mean values of pacing rate (swishing) in the 1973/74 winter are plotted in Fig. 25.

The variability of mean pacing rates during reclamation is in part due to differences in the technique of swishing used, as described above. For example, one day in late November 1973, the mean pacing rates of two groups of Redshanks feeding in West Enclosure were 102 ± 2.4 (26) and 57.6 ± 5.85 (20). These two groups of birds were using a different variant of swishing, one taking small unidentifiable prey (fast pacing) and the other taking Nereis. Although it seems likely that differences in the depth of fine sediment might have influenced the choice of a particular style of swishing or rate of pacing, this was not confirmed by my observations. On North Area, where the variant of swishing was similar on all occasions that I took measurements of pacing, differences in mean pacing rate appeared to be related to temperature, Fig. 26. While differences in pacing rate might arise because different prey types are being positively selected as noted above, a graded change with birds tending to pace more quickly as temperatures fall is unlikely to result from this cause. It is possible that as temperatures fall a preferred prey may become less available with the result that birds begin to take other prey

FIGURE 25 : VARIATION IN THE PACING RATE OF REDSHANKS WHILE SWISHING DURING THE 1973/74 WINTER.

Each point represents the mean number of paces per minute based upon approximately 20 measurements obtained on one occasion.

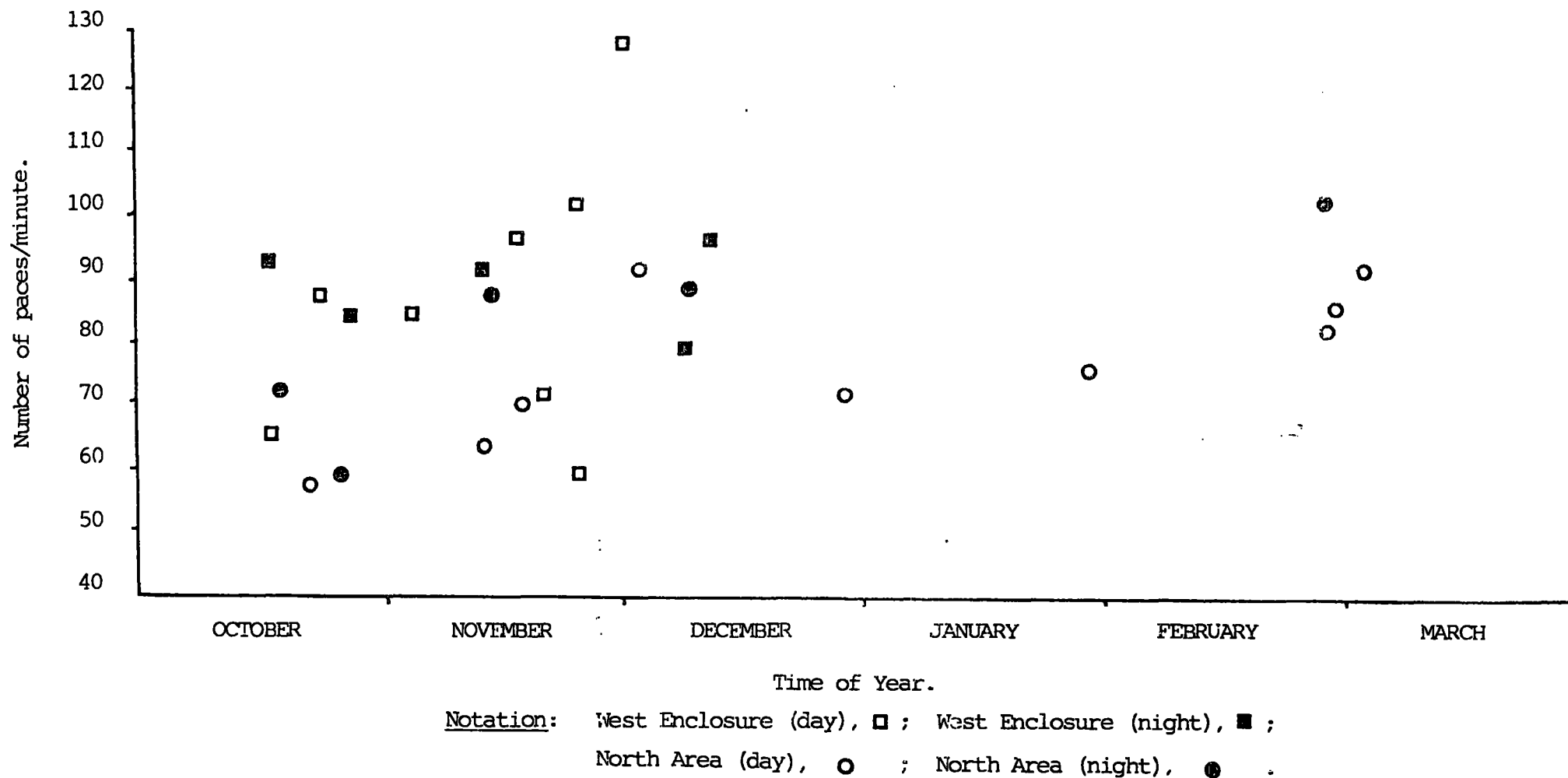
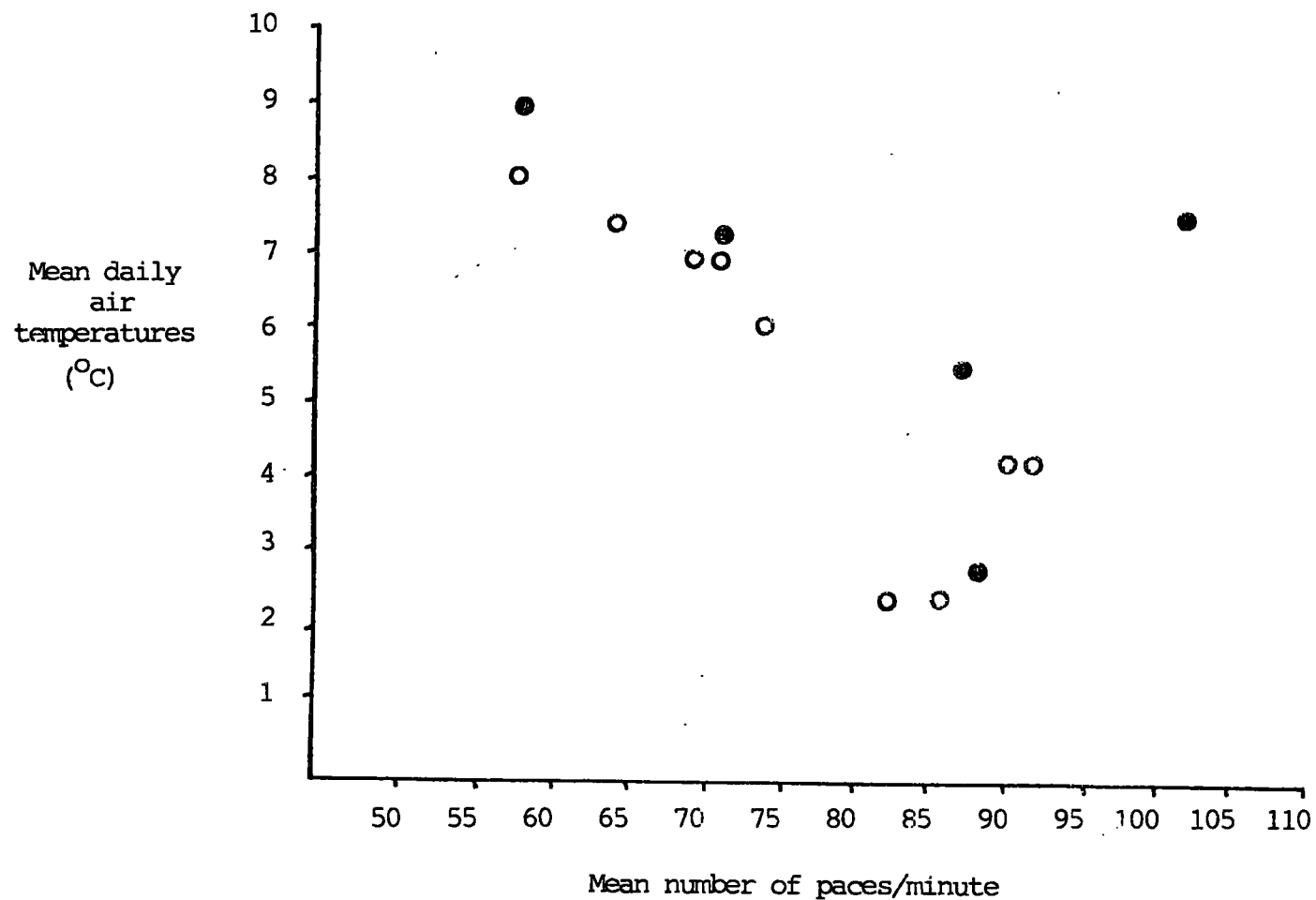


FIGURE 26 : THE RELATIONSHIP BETWEEN THE MEAN PACING RATE OF
REDSHANKS WHEN SWISHING AND MEAN DAILY AIR TEMPERATURES.



Note.

These records are of birds feeding on North Area in the 1973/74 winter.

Open circles represent records obtained in daylight; the solid circles represent records obtained at night.

for which a faster pacing is necessary. Equally, however, faster pacing while swishing, since this includes both searching and feeding movements, might occur as the rate of prey capture decreases and this might well occur due to diminished prey availability as temperatures fall. A lower rate of capture would mean less time spent in swallowing and handling.

Three records diverge considerably from a direct relationship between pacing rate and temperature, two on the 27th February during the day and one on the 25/26th of that month at night, during a period in which mean daily air temperatures were generally very low. The two unexpectedly low records of mean pacing rate on the 27th February occurred when the mean daily air temperature was 2.5°C and when substrate temperature was 3°C . It seems possible that the prey sought by these Redshanks might, like Arenicola at temperatures below 4°C (Smith, 1975), have become less active, and so less easily detected by feeding birds. This might have required Redshanks to search more carefully and, therefore, more slowly.

It seems likely that the faster pacing rate I recorded on the relatively warm night of 25/26th February was related in some way to the feeding performance of birds in daylight during that week. It is tempting, for example, to suggest that a faster searching rate might have occurred so as to compensate for the lower intake rates which probably occurred in the daytime.

In autumn 1974 surface pecking and probing predominated over swishing, and since the use of swishing (i.e. birds feeding singly not in groups) was very different from the 1973/74 winter, I chose to record the feeding rates of birds using the former technique. The aim was to provide data for the period October - December 1974 comparable with the pre-reclamation data collected by Pienkowski (1973). I accepted, therefore, that for this species it would not be possible to provide direct comparison of feeding rates between the two years of my own study. A single record of pacing rate amongst groups of birds

TABLE 23.

THE FEEDING ACTIVITY AND DIET OF REDSHANKS FEEDING ON THE NORTH
AREA OF SEAL SANDS IN AUTUMN 1974.

These records are of birds feeding by 'pecking' and 'probing' only.

Summary of searching rates and feeding rates.

Values are expressed as a mean $\pm$ S.E. with the number of observations in parenthesis.

Searching rate (Time taken for 5 paces) in seconds	OCTOBER	NOVEMBER	DECEMBER
	1.7 $\pm$ 0.06 (18)	1.75 $\pm$ 0.07 (15)	1.63 $\pm$ 0.07 (15)
No. of successes /minute (N)	9.58 $\pm$ 1.53 (12)	11.03 $\pm$ 1.98 (34)	6.33 $\pm$ 0.43 (15)
No. of probes/minute	7.25 $\pm$ 1.07	6.94 $\pm$ 0.55	7.07 $\pm$ 0.38

Composition of the diet.

	Visible <u>Nereis</u>				
	Small items	Crabs	20 mm.	21-35 mm.	Over 35 mm.
Percentage contribution to the diet	43	42	9.5	4	1.5
Nos. of prey captured	156	152	34	11	4

swishing in late September 1974 - the only period when Redshanks behaved in the manner they had used throughout the previous winter - provided a mean of 84.8 ± 4.8 paces/min. (20), significantly higher than for autumn 1973 records on North Area.

During autumn 1974 searching rate and feeding rate were assessed in the same way as for Curlews and Godwits. Mean monthly values are shown in Table 23 and indicate that neither searching rate nor probing rate changed appreciably between October and December. Success rates also were not significantly different, although the November value, when large numbers of small prey were taken, is substantially higher than in December. The sample sizes for these values are, however, small.

The majority of my records of feeding activity in autumn 1974 were of groups of Redshanks feeding on North Area in the channel draining the reclaimed South Area, and which separates the Central Bank from the Scalloped Mud. It was the only portion of Seal Sands where reasonable aggregations of Redshanks occurred at any time in autumn 1974. Elsewhere birds were very scattered. In the 1973/74 winter this channel had been used heavily for feeding by swishing especially in the immediate post-reclamation period; in autumn 1974 most birds feeding here probed for prey. For Redshanks feeding on this site, small items and small crabs (between 5 mm. - 12 mm. in width) contributed equally to the diet (Table 23) together comprising 85% of prey captured. Visible Nereis constituted 15% of the diet by number and the majority of these were of the smaller size class present at Teesmouth. This diet is probably not typical of Redshanks feeding elsewhere on North Area since it refers to only approximately 25% of the population at this time, and on no other parts of North Area were crabs seen to be taken.

DUNLINS.

The North Area of Seal Sands was the most important low water feeding site for Dunlins throughout my study despite the availability of the West Enclosure in a virtually unmodified state in early October 1973. On North Area birds showed a marked preference for feeding on areas of sticky mud, a substratum which, apart from regular use by small numbers of Redshanks, was generally not used by other waders, but which was the preferred feeding substratum of Shelducks also. Only between HW+1½-2, that is, immediately the tide began to fall on North Area, did Dunlins tend to feed on other substrata, and then only along the tide edge. As the tide retreated, progressively fewer birds fed at the water's edge although most followed just behind the retreating tide such that at low water most birds were concentrated at the lowest tidal levels. A similar pattern of feeding was recorded by Prater (1970) on Morecambe Bay although the main feeding areas there were on wet sandy substrates. However, on the Wash, Goss-Custard et al. (1977a) found that Dunlins preferred wet muddy substrates as at Teesmouth.

In areas of sticky mud on North Area, Gray (1976) found high densities of small oligochaete and polychaete worms (see Shelduck) and my observations of Dunlins feeding at close quarters, mainly at around HW+2 on the flats in the extreme south-east corner of North Area, indicated that these were most important in their diet. Only occasionally did I see larger prey taken on North Area and these appeared to be small Nereis. Large Nereis diversicolor were, however, taken consistently by the relatively small numbers of Dunlins which fed on the West Enclosure during the low water period on North Area. Herdson (pers. comm.) found oligochaetes present in the oesophagus of 65% of a sample of 48 Dunlins shot on North Area in winter 1972/73 and these were estimated to comprise 55% of the diet in terms of biomass. At the same time,

Nereis were estimated to comprise 25% and Hydrobia 3% of the diet by biomass and of the Nereis only 0.7% by numbers were thought to exceed 15 mm. in length, that is the size at which they might be identifiable at distances over which my observations were made. This accords well with my observations that very few birds on North Area captured Nereis of the 'visible' size classes, i.e. over 15 mm. Similarly Hydrobia would not have been distinguishable by observation. That Hydrobia contributed so small a percentage to the diet is perhaps surprising in view of the abundance of it on North Area (see p. 152), and also in view of the fact that this is an important prey on other British estuaries (Goss-Custard et al., 1977a; Davidson, 1971) along with Nereis diversicolor.

Dunlins feeding on small prey (presumed to be chiefly oligochaetes) employed a very rapid feeding movement, prey generally being captured by probing to around half the depth of the bill. This was usually preceded by rapid surface pecking which appeared to be exploratory. The overall impression was of a stitching motion which was virtually continuous as the individual moved relatively slowly over the mud surface. Birds feeding in this manner generally travelled only a few yards in a 30 second period of observation and in fact birds tended to feed thus for several minutes on one patch of sticky mud before moving quickly to another patch closer to the retreating tide edge where a further prolonged bout of feeding was repeated. This foraging behaviour contrasted sharply with that employed by birds feeding along the tide edge on firmer, better drained, sandy substrates (for example, those adjacent to the Peninsula). Such birds moved rapidly along the tide edge feeding on items on or very close to the surface.

The preponderance of small prey items in the diet of Dunlins precluded exact measurement of feeding rate alone. As for Shelducks my measurement of pacing rate represents a combination of feeding and searching rates. I collected data only from those groups of birds feeding on areas of sticky mud

since, not only were these the preferred feeding areas for this species, but also the slower rate of pacing was more easily and more accurately measured. For the West Enclosure records were taken of birds employing the same feeding technique.

Within North Area the association of Dunlins with the general vicinity of the tide edge resulted in the rapid disappearance of almost all birds beyond a distance at which measurements of pacing could be made after HW+4. The majority of my records were of necessity, therefore, obtained between HW+2-4. Thereafter, my records were obtained from small groups feeding in pockets or channels of sticky mud within the Scalloped Mud and Central Bank areas or near the water's edge in Greatham Creek.

Mean pacing rates during my study varied from 49 - 138 paces/minute, differences in pacing rate appearing to arise from the frequency of short movements between feeding sites rather than from differences in the rate of pacing while actively pecking and probing for food. For the North Area, pacing rate showed no consistent seasonal change during the 1973/74 winter (Table 24). However, mean pacing rate in October 1973 was significantly slower than for other months in that winter, except February 1974, for which the pacing rate I recorded is also significantly lower than in November and December 1973 and January 1974.

In autumn 1974 pacing rate in October was significantly slower than in November and December suggesting a similar pattern of change to that in 1973. Pacing rates generally were slower in autumn 1974 than in 1973 and the differences are significant between respective November and December mean values. It seems likely that differences in mean monthly pacing rates arise from the fact that observations were not obtained under similar temperature conditions. The significant differences which occurred in both winters are probably explicable in terms of the prevailing temperatures (see below).

TABLE 24.

MONTHLY SUMMARY OF DAYTIME PACING RATES OF DUNLIN ON SEAL SANDS.

The data are expressed as mean values $\pm$ S.E. with the number of observations in parenthesis.

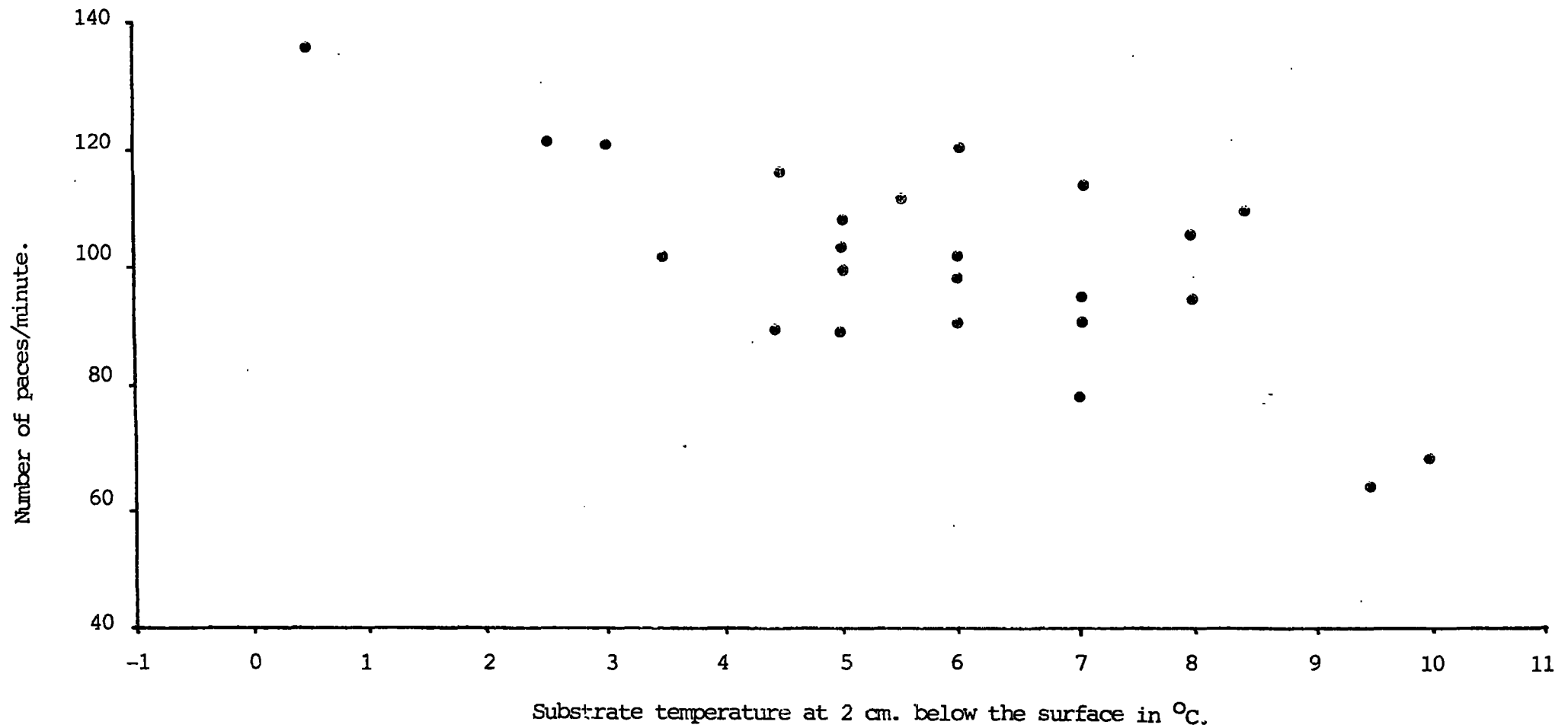
1973/74	OCTOBER	NOVEMBER	DECEMBER	JANUARY	FEBRUARY	MARCH
North Area	74.2 $\pm$ 4.15 (80)	105.4 $\pm$ 1.32 (48)	110.79 $\pm$ 1.44 (114)	104.4 $\pm$ 2.00 (123)	87.6 $\pm$ 4.78 (45)	105.6 $\pm$ 5.3 (61)
West Enclosure	116.0 $\pm$ 2.6 (32)	111.2 $\pm$ 3.4 (68)	120.4 $\pm$ 3.73 (47)			
Autumn 1974						
North Area	58.4 $\pm$ 4.4 (49)	79.5 $\pm$ 4.7 (80)	85.0 $\pm$ 4.68 (51)			

Simple correlations of daily mean pacing rates with climatic variables revealed no consistent relationship with wind speed, but there was an inverse relationship between daily mean pacing rate in the 1973/74 winter and mean daily air temperature ($p = 0.01$; Fig. 27). Since my observations of Dunlins at Teesmouth suggested that increases in pacing rate were due primarily to an increase in the frequency with which birds moved feeding sites, the increased pacing rates at lower temperatures indicates that birds shifted feeding site more frequently then, by moving more rapidly to keep up with the retreating tide edge. This might have been expected if prey were less available at lower temperatures, perhaps because they burrowed deeper or were less active and therefore less frequently detected. A reduction in activity of intertidal polychaetes at low temperatures has been found for Arenicola (Smith, 1975) and Scoloplos (Pienkowski pers.com.) elsewhere in north-east England. The autumn 1974 values do not show a significant relationship, however, although the same range of temperature conditions was not experienced on days for which I made measurements. Perhaps temperatures did not fall below a threshold at which activity is reduced, for example the 3°C threshold which Smith (1975) found for Arenicola.

The pacing rates of Dunlins within the West Enclosure were generally higher than those of birds feeding in North Area but a significant difference was evident only in the month of October 1973. It is possible that these differences were due to differences in substrate type and prey availability, but this could not be checked. Alternatively, since large Nereis were an important component of the diet of Dunlins in West Enclosure, there might have been a tendency for birds to search more rapidly for this relatively scarce prey and therefore pace at a higher rate.

On one occasion in early December 1973, the intensity of lighting and proximity of feeding Dunlins in the West Enclosure allowed measurement of pacing rate at night, over periods of 15 seconds. This single series of 32

FIGURE 27 : VARIATION IN THE PACING RATE OF DUNLINS IN RELATION TO TEMPERATURE DURING THE 1973/74 WINTER ($p = 0.01$).



observations gave a mean rate of 91.4 ± 3.6 paces/minute, significantly slower than the daytime pacing rate, but without a rather larger collection of data no general conclusions can be drawn from this. If it is true, however, perhaps the most obvious explanation is that Dunlins were taking longer to search for and capture prey in darkness, this either giving the direct result of birds pacing more slowly while searching for food in one locality or resulting in birds reducing the frequency with which they moved feeding site.

DISCUSSION AND CONCLUSIONS,

CONCLUSIONS CONCERNING THE CHANGES IN NUMBERS OF BIRDS USING SEAL SANDS DURING AND AFTER THE RECLAMATION OF SOUTH AREA.

Because my study spanned rather less than two winters, it is possible that the changes in numbers which I recorded (p. 180) might represent normal variation in the use of Seal Sands. Fortunately, comparison with counts made by Pienkowski (1973) of birds feeding on Seal Sands in spring 1973, together with monthly counts of birds roosting at high water made by the Teesmouth Bird Club (TBC) for several years before reclamation, make it possible to establish the changes I found with more certainty and to assess the magnitude of these changes.

Since the data from these two sources are extensive and are examined in tabular and graphical form elsewhere (Evans et al., 1979; Knights, 1974), they are not reproduced here. Instead, selected information is used in the following species-by-species comparisons.

Shelducks.

Seal Sands is the principal feeding area at Teesmouth for this species and counts at high water directly reflect its use. Thus, for example, during the period of this study, the TBC data and my own counts of birds feeding at low water are closely similar. In view of this, I have used the TBC counts for the

four winters preceding reclamation to show that the numbers of Shelducks using Seal Sands normally build up through autumn, achieving a peak population around the middle of winter which is usually in the order of 1500 - 1700 birds. In contrast, the numbers overwintering during and after reclamation were lower, the counts in the peak month being 1300 during reclamation and just over 1000 after reclamation (although in most other months counts were closely similar in these two winters). This suggests that there was a reduction in use of the area by between 200 - 500 birds compared with preceding winters. Furthermore, in both winters of my study the peak in numbers occurred one month earlier than was usual in previous winters.

On the evidence of my records alone, it would appear that the numbers of Shelducks using Seal Sands had been reduced as a result of the loss of South Area and that additionally there was a tendency for some of those birds settling there initially in autumn 1973 and 1974 to emigrate earlier than would normally be the case.

Other evidence, however, is against a conclusion of this sort, in particular the fact that counts of birds using Seal Sands in the 1975/76 winter were higher than in any year since the 1968/69 winter, and high levels have again been recorded in subsequent winters (Evans pers. comm.). This demonstrates that the low levels occurring in 1973/74 and in 1974/75 were not permanent: Seal Sands could support as many Shelducks, both in terms of numbers and period of use, as it had done before reclamation. If this is so, perhaps the reason for the low levels in the 1973/74 and 1974/75 winters might be the result of the mildness of the winter, with birds staying in estuaries further south and on the continent.

Thus, it must be concluded that Shelducks were probably not affected by the loss of South Area for feeding.

Grey Plovers.

For this species I have suggested that a steady overwintering population is

established in late autumn after a peak which coincides with the principal period of migration through the north-east of England. High water counts before reclamation also support the fact that the population remains reasonably steady from late autumn. This fact makes it possible to assume that the numbers of birds using Seal Sands in early spring 1973 (Pienkowski, 1973) and my own records in late autumn 1974 were representative of the respective winters as a whole. On this basis it would seem that the overwintering numbers of this species have declined from around 220 in the 1972/73 winter to nearly 100 in the 1973/74 winter and to 80 in the 1974/75 winter.

Of particular interest is that in both winters of my study the successively lower population levels were established at a very early stage of the winter, when temperatures were still relatively mild and when the invertebrate food resources of the flats and their availability were at their highest.

My counts during the 1973/74 winter show that the number of Grey Plovers was maintained with no indication of a progressive decline despite the fact that feeding was confined temporarily to North Area in December 1973 and January 1974. Nor was there evidence of a decline when South Area was fully reclaimed in February 1974. Numbers remained steady until April when normal departure of birds from Teesmouth occurs.

Furthermore, this steady level of population was maintained despite the fact that the reclamation of South Area provided in several months very attractive feeding during which time North Area was sparsely used. In such a situation, it might have been expected that larger numbers of plovers would have used the North Area or made use of the attractive feeding within South Area, yet this did not happen. Certainly the TBC counts indicate that substantial numbers of Grey Plovers were present elsewhere in the Teesmouth area. My own counts in December 1973 showed that 37 fed on Bran Sands while the TBC counts included 140 birds which must have been feeding on sea beaches and North Gare Sands. None of these, however, appeared to move to Seal Sands.

The determination of overwintering numbers in autumn, with the associated maintenance of a steady population, hints at the assessment by individuals of a carrying capacity for the feeding area available. Clearly, birds could not have predicted the changes occurring in feeding area and feeding time that occurred during reclamation so perhaps the maintenance of a steady population in the 1973/74 winter was the fortunate result of the timing of reclamation, the degree to which it provided feeding of high quality and the mildness of the weather. Nonetheless, in the 1974/75 winter the early adjustment of numbers suggests again an assessment of a definite carrying capacity. In this context, I consider that the carrying capacity of an area is expressible in the number of bird days that it can support, and that birds are capable of assessing the food resources required for overwintering, or approximately so, and disperse over the feeding area accordingly.

Curlews.

At Teesmouth, high water counts of Curlew by the TBC before reclamation indicated an autumn peak followed by a decline to low levels in mid-winter, and a rise again in early spring followed by a general departure of birds for breeding in April. This same pattern was maintained in the TBC counts during and after reclamation, and occurred also in counts of birds feeding on Seal Sands in the 1973/74 and 1974/75 winter. Reclamation did not, therefore, seem to result in any major change in the pattern of use of Seal Sands, although there was a slightly earlier departure of birds in spring 1974, occurring in March rather than in April, possibly in response to the mildness of the weather.

My observations suggested that part of the characteristic decline in numbers during the mid-winter period arose from the movement of birds previously feeding on Seal Sands in autumn to feed almost exclusively on flooded pasture. Some of these birds returned occasionally, conspicuous as a single group which frequently did not feed, returning perhaps more permanently in spring and thereby providing

the usual increase in numbers feeding on Seal Sands. The location of roosts counted at high water by the TBC was such that it included primarily those feeding on intertidal areas; hence the similarity in pattern of high water and low water counts.

Considerable day-to-day variation in the numbers of Curlews visiting Seal Sands in spring 1974 seemed to characterise the gradual increase in their regular use of intertidal areas and corresponding diminishing use of field areas. For this reason comparison is difficult with late spring 1973 counts of birds on Seal Sands by Pienkowski. However, his early spring records correspond with a period when the population feeding there would probably equate with the low mid-winter levels and these, therefore provide a better comparison with my own records. Thus, in early spring 1973, Pienkowski found that approximately 120 Curlews fed throughout the tidal cycle on the North-East Enclosure (the preferred feeding site of this species before reclamation), while a further 120 birds, which initially fed there, moved to North Area when this was exposed, a total using Seal Sands at low water, therefore, of 240 birds. In spring 1974 only 100 Curlews fed on Seal Sands, suggesting that in total there had been a reduction of around 140 birds in the population using the area, that is, approximately the number that had previously used the North-East Enclosure. In the mid-winter period in the 1974/75 winter, there were broadly similar numbers of Curlews using North Area as occurred there in the 1973/74 winter, reaffirming that there had probably been a decline in the numbers present at this time of year compared with the 1972/73 winter. However, to set against this conclusion is the fact that the field areas were providing particularly attractive feeding in both winters, owing to the wetness and mildness of the climate, which resulted in extensive flooded and saturated pasture being available for long periods. Perhaps birds simply preferred to feed in field areas in these two winters, although North Area might have supported them equally as well. This is at least in part the case, since in respective months of the

1975/76 winter rather higher numbers fed on North Area than in the 1973/74 and 1974/75 winters, but not as high as used Seal Sands in the 1972/73 winter.

In conclusion, it must be borne in mind that field feeding is of great importance to this species. Although the numbers of Curlews using Seal Sands at various times during winters after reclamation have been similar to those occurring there before reclamation, it is not certain whether remaining intertidal areas can support regularly the numbers which fed there previously. Reclamation seems to have modified the balance in use of intertidal and field areas, which for this species seem equal in their relative attractiveness for feeding, taken over the winter as a whole, the result being that regularly high levels of use of Seal Sands is unlikely.

Godwits.

In the 1973/74 winter, a reasonably stable population level was established following an early autumn peak, and this was maintained despite the temporary loss of feeding in the West Enclosure (between December 1973 and late January 1974) when birds displaced from there were accommodated on North Area. This is very similar to the situation found for Grey Plovers and it is perhaps relevant that both species feed almost exclusively on intertidal areas and for both the South Area provided a very important feeding site during its reclamation.

In contrast with Grey Plovers, the numbers of Godwits using Seal Sands fell when the South Area was finally reclaimed in February 1974, with between 50 - 60 birds disappearing from Seal Sands. Some of these birds possibly emigrated, but others may have moved to Bran Sands and sea beaches outside the estuary where small numbers fed throughout the winter. High water counts suggest that in spring 1974 about 50 Godwits, other than those on Seal Sands, fed in the Teesmouth area.

There was a further substantial departure from Seal Sands involving 30 - 40 birds during March, the month when major departures occur from other estuaries in

north-east England (Evans and Smith, 1975). Since Pienkowski (1973) found that departure of Godwits occurred in February as well as in March before reclamation, it is possible that the entire decline in spring 1974, although coincident with the final loss of South Area, was a normal feature of the seasonal fluctuation of this species at Teesmouth. Thus, as for Grey Plovers, there is no definite evidence of any progressive loss of birds from Seal Sands which might be associated with the phases of reclamation during the 1973/74 winter.

The number of Godwits using Seal Sands before reclamation in spring 1973 was at least 600 (Pienkowski, 1973). About 500 fed almost throughout the tidal cycle on the North-East and West Enclosures, while just over 100 used North Area at low water. Assuming that this early spring count of 600 birds represented the steady population level which appears to be established in autumn, then over 300 less birds used Seal Sands in the 1973/74 winter.

Although the steady overwintering population was established during the period of reclamation of the West Enclosure - being finally achieved at the end of its reclamation - the initial settlement on Seal Sands was some 200 birds fewer than had remained throughout the previous winters and it seems reasonable to assume that this loss was directly attributable to the absence of the North-East Enclosure.

Despite the maintenance of a reasonably steady population over the mid-winter period of the 1973/74 winter, the stable level of population established on their return in autumn 1974 was further reduced by over 50% to less than 100 individuals.

Redshanks.

The high water counts made by the TBC indicate that before reclamation the numbers of Redshanks at Teesmouth usually fell from a peak of 800 - 1,000 in early autumn to levels of around 500 in spring, this fall being progressive through the winter period.

In early autumn 1973, after reclamation of the North-East Enclosure had been completed, numbers of a similar order began to use Seal Sands, particularly the West Enclosure. A loss of around 140 birds between October and November 1973 was probably part of the normal migration through Teesmouth. When the West Enclosure ceased to be important for feeding, there was a loss of 500 birds from Seal Sands. The immediacy of their decline indicates a direct link with the state of reclamation but it seems probable that many of these birds remained in the locality, feeding almost exclusively on field areas, since some 300 Redshanks quickly returned to Seal Sands when reclamation of the South-East Enclosure recreated favourable feeding. This suggests a real decline in the numbers of Redshanks in the locality (and at least in part dependant on Seal Sands) of perhaps 160 birds. However, a decline of this order would perhaps be expected on the basis of their pre-reclamation pattern of decline through the winter. Indeed, the numbers using Seal Sands when the South-East Enclosure was being reclaimed were similar to, if not rather higher than, those present there before reclamation in February 1973. When active reclamation ceased and the South Area was no longer favoured for feeding, many Redshanks again appeared to resort to field areas and this contrasts with the same period in spring 1973 when numbers using intertidal areas increased.

It is evident that during reclamation the South Area was of special importance for Redshanks. The loss of the North-East Enclosure probably did not result in a great reduction in the numbers using Seal Sands since by way of compensation other portions of South Area provided exceptionally good feeding. When this situation changed, the mildness and wetness of the winter enabled most birds displaced to feed inland with the result that possibly numbers in the general area of Seal Sands were no different from before reclamation.

During reclamation the number of Redshanks using North Area was typically just over 100. Only when active reclamation provided attractive feeding in the Greatham Creek section of the flats did numbers exceed this on a regular basis.

Otherwise large numbers of Redshanks only visited North Area occasionally. On balance, it seems that many Redshanks preferred to feed on flooded fields when they were able to do so. In autumn 1974, after an initial peak in numbers - a peak 50% lower than that in autumn 1973 - numbers fell quickly to around 170, a level of population which was broadly maintained throughout the 1974/75 winter (Evans pers. comm.), a small decline only occurring in mid-winter.

It is clear that, although the number of Redshanks using North Area in autumn 1974 was generally greater than during reclamation, the overall use of Seal Sands was much reduced compared with the level of use before reclamation. During reclamation, the special attractiveness of feeding in the enclosures (which was the direct result of the peculiar reclamation technique), combined with the availability of particularly extensive field feeding, enabled numbers to be retained at pre-reclamation levels.

Dunlins.

High water counts before reclamation suggest that the numbers of this species at Teesmouth remained at stable levels over the mid-winter period, with probably 16,000 - 18,000 birds using Seal Sands (Pienkowski, 1973). The initial settlement of birds in autumn 1973 was substantially less than this and by November (when, on the basis of HW counts, fairly stable levels would be expected to have been established) the population was almost 50% lower, between 8,000 - 9,000 birds. This reduction occurred despite the fact that preferred low water feeding areas before reclamation, namely the North Area and West Enclosure, remained intact. The reduction, therefore, must be attributed to the loss of the North-East Enclosure where, before reclamation, Dunlins had fed while the North Area was covered, since much of its area was at a high tidal level (Pienkowski, 1973).

The loss of the West Enclosure for feeding by this species occurred at the end of October but the 3,000 or so birds which had fed there were accommodated

on North Area with no departures from the estuary. In January 1974, however, there was a decrease of around 4,000 birds, amounting to almost half the overwintering population. There is no evidence from HW counts of similar declines at this date before reclamation, and it seems likely that it resulted from adverse weather conditions at the beginning of January when, for a period of several days, temperatures remained at or below zero centigrade. When mild conditions returned these birds did not re-appear. Presumably, they had migrated away from Teesmouth. Only a slight increase in numbers occurred in April 1974 and this was probably connected with northward migration through the estuary which normally occurred at this time.

In autumn 1974, although Dunlins initially settled in numbers similar to those in early autumn 1973, this level declined steadily, stabilizing by mid-winter at the same level achieved after the cold spell in spring 1974. Between December 1974 and March 1975, there was only a further slight decline. This confirms that overall reclamation has resulted in a reduction of between 12,000 - 14,000 in the numbers of overwintering Dunlins. When considering the changes in numbers of Dunlins, it must be pointed out that the construction of the East/West reclamation wall appeared to be particularly beneficial to this species, owing to the additional feeding time which was created by the delay the wall caused to the tidal cycle in the enclosed South Area. Before the wall's construction, the Birds of Estuaries Enquiry counts show that only around 6,000 - 7,000 Dunlins overwintered at Teesmouth and perhaps this level, rather than the inflated populations immediately before the infilling of South Area, should be considered as the baseline for assessing subsequent changes in numbers.

THE UNDERLYING REASONS FOR THE REDUCTIONS IN OVERWINTERING POPULATIONS OF SHOREBIRDS AT TEESMOUTH.

The reclamation of Seal Sands had two important effects:

- (1) There was a reduction in the time available for feeding on intertidal land.
- (2) There was a reduction in the area of intertidal flats available for feeding.

Using the data I collected in the course of this study, it is possible to examine the relative importance of these factors in determining the overall numerical changes in overwintering populations.

Regarding the change in the time available for feeding by shorebirds.

In 1970, the construction of the East/West reclamation wall divided Seal Sands and retarded the flow of water into the enclosed South Area, such that there was a two-hour delay in the attainment of high water and a decrease in the amplitude of the tide in this section (see p.141). This situation existed until spring 1974 when South Area was finally infilled, although the area subject to this delay decreased progressively from spring 1973 when infilling began. The result of these phenomena was that between 1970 - 1974 at least some portions of Seal Sands were available for feeding throughout the tidal cycle, that is, the potential feeding time was 24 hours per day. The benefit which this aspect of enclosure had for shorebirds and the effect it might have had on shorebird numbers has been considered earlier (see p. 144). The exposure time of North Area is 16 hours per day, thus the restriction of feeding to North Area after reclamation meant that potential feeding time there amounted to only 67% of each tidal cycle.

Since the monthly PFT's which I calculated while the West Enclosure was

available for feeding (e.g. in October 1973) are closely similar to those determined by Pienkowski (1973) before reclamation, for purposes of simplifying discussion those of Pienkowski are not referred to further, and instead my early autumn 1973 values are used as baseline data for assessing subsequent change. They show how long birds fed for when feeding on Seal Sands was possible at all times. From the diagrams of PFT in October 1973, it is possible to identify those species for which the feeding time available on North Area after reclamation might have been a factor limiting the overwintering numbers and for which some compensating adaptation would be necessary. Thus, it is evident from data presented in Tables 4 and 5 that for two species - Dunlins and Redshanks - the daylight exposure time of North Area was simply insufficient to allow most individuals to collect enough food since the PFT exceeded 67% - the exposure period of North Area. On the basis of daytime PFT's in the early part of the 1973/74 winter, it might have been predicted that both Godwits and Grey Plovers would also face a shortage of feeding time on Seal Sands when North Area alone remained, since for these species the PFT was close to the upper limit of 67% and in mid-winter exceeded it. Only for two species, Shelducks and Curlews - the largest shorebirds at Teesmouth - were PFT's substantially below 67% and for these it would, therefore, be expected that the exposure time of North Area would be enough for almost all individuals to collect sufficient food, assuming that no other factors operated to modify the required feeding time.

In fact, it was evident from my calculations of PFT that no species could, in fact, utilize North Area for its full exposure time of 8 hours. As a result, prediction based upon comparison of PFT's before reclamation with the 67% exposure time of North Area underestimated the vulnerability of each species to reduced feeding time. Dunlins fed on North Area for the greatest proportion of the time available, a maximum of 90% of the 8 hours' exposure being recorded. Grey Plovers, Godwits and Redshanks seemed capable of exploiting North Area for

around $6\frac{1}{2}$ hours in each tidal cycle, around 80% of the potential feeding time. This upper limit of exploitation of $6\frac{1}{2}$ hours appeared to be related to the tidal level at which feeding sites were situated and there seemed to be little scope for those species to increase their feeding time by feeding longer when the tide was either just covering or uncovering the flats (i.e. HW+1-2 and HW+10-12). It was particularly conspicuous in Grey Plovers and Godwits that the PFT on North Area was increased only by feeding for longer periods over low water.

Although it seems certain that for Shelducks and Curlews also the exploitable period of North Area's exposure was less than that potentially available, there is no evidence to suggest that they too were feeding there for as long as they could.

PFT in all species increased as mean daily air temperatures decreased and in all species this was accompanied by feeding for longer periods on North Area, and for Dunlins, Grey Plovers and Godwits a maximum PFT on intertidal areas was recorded over the mid-winter period. Whether the same was true for Redshanks is uncertain since (in addition to deficiencies in my data for this species), like Curlews, this species appears well adapted to feeding on wet field areas. Indeed, the use of field areas might have been a more profitable strategy, in terms of achieving an optimum net energy intake per unit time, than attempting to exploit North Area to any greater extent. However, since Redshanks fed on North Area for similar lengths of time as other medium-sized waders (e.g. Grey Plovers and Godwits), that is $6\frac{1}{2}$ hours, it seems reasonable to suppose that this species also was feeding for as long on North Area as it could in mid-winter. In summary, therefore, I consider that Grey Plovers, Godwits, Redshanks and Dunlins did feed on North Area for as long as they could in daylight only in the mid-winter period, when mean daily temperatures were lowest and when day-length was shortest.

For those species for which feeding time on intertidal areas was likely to

be limiting after reclamation was completed, three possible means of adaptation may be examined using data I collected:

- (a) To feed on fields and pools during the high water period.
- (b) To feed more extensively on intertidal areas at night.
- (c) To modify their feeding behaviour so as to increase their feeding rate and thereby compensate for any shortage in feeding time.

These possible adaptations are considered in more detail in the following sub-sections.

(a) Field-feeding over the high water period.

While exclusively field-feeding groups of both Curlews and Redshanks existed in the Teesmouth area probably before (Pienkowski, 1973) and certainly during reclamation, it seems that under most conditions individuals of both species which fed on Seal Sands before and during reclamation obtained the majority of their food requirements from intertidal feeding, with only occasional use of the fields at high water.

After reclamation, however, my data suggest that for Redshanks, although feeding for almost as long as they could on North Area, a large proportion of the population spent an additional period feeding in the fields at high water to satisfy their food requirements even in early autumn. For Redshanks, feeding at high water constituted the greatest proportion of the PFT of any species at Teesmouth.

For Curlews on the other hand, although field-feeding became a regular component of the feeding activity of individuals using North Area at low water after reclamation, the proportion this contributed to the PFT was small. Furthermore, their pattern of use of North Area suggested that the flats were not fully exploited and that the use of fields was undertaken because it was

more profitable, but perhaps only marginally so, than feeding on North Area for longer. For Godwits the field areas, and more specifically the brackish, cut-off channel of Greatham Creek within the Brinefields, came to be used regularly after reclamation in autumn 1974 at a time when it seemed that the feeding time on North Area was almost fully exploited. The proportion of the PFT spent feeding there was, however, small and it seems probable that this creek enabled individuals to top up their reserves. Bearing in mind that the PFT's recorded before and during reclamation were only slightly higher than the exploitable portion of the exposure period of North Area, then for this species only slight adaptations to the reduced feeding time were necessary. Similarly, the feeding time needed by Grey Plovers, as judged by observation before and during reclamation, was very close to the feeding time possible on North Area, and again perhaps only slight compensation might have been necessary to offset any shortage of feeding time. Since only occasional individuals were seen to feed on field areas (like Godwits, Grey Plovers used the cut-off channel of Greatham Creek) over high water and on the mudflats at higher tidal levels within Greatham Creek itself, it must be assumed that either the use of field areas was unnecessary or that it was simply not sufficiently profitable compared with other means of adaptation. The use by Grey Plovers of these alternative feeding sites when North Area was covered by the tide did suggest that, as for Godwits, their use was by individuals topping up their food reserves.

Before and during reclamation, Dunlins had regularly spent a small proportion of their PFT feeding on the field and pool areas over high water. As reclamation progressed, an increasing proportion of the population fed at high water, such that in autumn 1974 a quarter of the PFT was spent on field and pool areas. This species then, along with Redshanks, made most use of the extra feeding time which the field areas provided. However, unlike Redshanks, the areas which they were able to use over high water were more confined,

usually comprising shallow flashes of water, and the conditions under which they were able to make use of these (e.g. when water was freezing) were possibly more limited.

Although occasional groups of Shelducks resorted to freshwater and brackish pools within the area covered by the 'standard walk', the contribution of this level of use to the PFT is insignificant. This is perhaps not surprising bearing in mind the fact that only half the available feeding time on North Area was being used.

(b) Feeding at night on intertidal areas.

Although, before reclamation of South Area, Pienkowski (1973) observed individuals of each species to feed at night on several occasions, quantifying this use was impossible. However, it seems probable that during reclamation many species fed far more extensively than they had done previously and at that time it appeared that this greater use of the flats at night was to be one of the major adaptations to the reclamation of South Area. However, this use in fact coincided with a period when the enclosures were still available, and seemingly providing very attractive feeding for some species. Furthermore, in spring 1974, when only the North Area was available and when night feeding might have been expected to continue at a high level, in fact it diminished and in autumn 1974 remained at low levels, involving only a small proportion of the population of most species - the exceptions to this being Shelducks and Grey Plovers.

It is usual to regard feeding at night as being less profitable than feeding in daylight (Goss-Custard et al., 1977b ; Evans, 1976). The basis for this assumption is that most waders usually use visual cues for at least part of their foraging. Prey must, therefore, be more difficult to detect at night, notwithstanding the possibility that changes in the behaviour of the prey may increase their availability, e.g. if they emerge from burrows on to

the surface. This is given support by research elsewhere (Heppleston, 1971). In the case of Redshanks feeding at night (Goss-Custard, 1969 and 1970), a tactile (swishing) rather than a visual feeding technique (pecking and probing) was found to predominate. With respect to this species at Teesmouth, swishing was used almost exclusively at night and in fact Redshanks fed at night only when this method of feeding (being confined to areas of liquid mud) could be used, that is, during active reclamation. The only other species which I studied which fed primarily by the use of tactile means was the Shelduck and this was one species which fed extensively at night both during and after reclamation.

However, Nereis feeders also fed in large numbers at night in autumn 1973 and from their behaviour it was evident that visual cues were used. The data I collected on Curlews showed that searching rates were rather slower than during the day and, therefore, perhaps not as profitable although in fact the few records I obtained of success rates at night were no different from those collected during the day. For Grey Plovers, however, feeding rates at night in spring 1974 and autumn 1974 (but not in autumn 1973) were lower than feeding rates in daylight, which again hinted at lower profitability.

Unfortunately, my data are not sufficient to indicate why feeding at night occurred to such a great extent in autumn/winter 1973, nor why it should have been generally low in autumn 1974. Some possibilities, however, are considered below.

For Redshanks it seems probable that the cessation of active reclamation, which resulted in areas of liquid mud ceasing to be attractive for feeding by swishing, might explain their diminished use of North Area for feeding at night. Similar explanations for reduced night feeding are not available for species such as Curlews, Godwits and Dunlins. One factor which might be involved is the level of illumination. At Teesmouth, adjacent construction lighting and industrial flares provided a very high intensity of light over some parts of

the flats and, although I did not appreciate or record any change in light intensity, perhaps sufficient light to feed was available only in autumn 1973.

A further possibility, again one which is difficult to explore since my data are insufficient, is that those feeding sites exploited by day and at night by large numbers of birds in autumn 1973 (and these might have been the well-illuminated sites, particularly suitable for feeding at night) might have suffered, as a result of heavy predation, a reduction in prey density to levels which made further use unprofitable. If feeding elsewhere on the flats at night was less attractive, then perhaps individuals might have ceased to feed, preferring to adapt in other ways. Other portions of North Area might have been less attractive because of the prey species involved, the nature of the sediment or perhaps other areas were not as well illuminated. Since the central part of North Area held a large roost of gulls, this might have been an important factor limiting night feeding by some species. On occasions, even Curlews were seen to be attacked by gulls at night and for Dunlins, whose preferred feeding site in daylight, i.e. the tide edge, was occupied by gulls at night, this might have been an important deterrent to night feeding. The diminished use by Curlews of the Greenabella Bank might be evidence of such a change since this formerly popular feeding area, subject to regular use by up to 70 individuals by day and by night in autumn 1973, was used by only a handful of birds during the day in spring 1974. Their alternative daytime feeding site, namely the Central Bank, was frequently occupied by gulls.

Only two species, Shelducks and Grey Plovers, fed at night in similar areas and in similar numbers as during the day in both winters of my study. Regarding Shelducks, it has already been noted that feeding by tactile means on prey which are below the mud and/or water surface is least likely to be affected by darkness, and it is perhaps not surprising, therefore, that pacing rates at night are identical with daytime values. Since their feeding areas did not coincide with the sections containing the gull roost, interference was

unlikely, while their own size and the small size of prey they took would reduce the likelihood of actual attack by gulls. The extent of night feeding is perhaps reflected in the low daylight PFT determined for this species. For Grey Plovers, the situation is rather different since for this species visual cues are essential for prey capture and as a result my results show that intake rates at night were lower than in daylight. That Grey Plovers did feed extensively at night after reclamation while other wader species did not, although they were capable of doing so, must depend on the balance in profitability between night feeding and other means of adaptation.

(c) Changes in foraging behaviour.

Despite the fact that I obtained considerable data relating to the feeding behaviour of each species during the course of my study, this information provides very little insight into the manner in which reclamation affected shorebirds. With regard to the topic being discussed in this section, for example, it was possible that, for those species likely to suffer a shortage of feeding time when only North Area was available, individuals might attempt to search for and capture prey at a faster rate or perhaps select different sizes or different species of prey which, by enabling higher intake rates, might compensate for the reduced feeding time.

In fact, for most species the rates of searching and prey capture remained remarkably constant during my study and were broadly similar to the values determined before reclamation by Pienkowski (1973). Some variations in these parameters did occur, however, during the course of my study. For example, I established that in Shelducks pacing rate (a measure representing a combination of searching and feeding rate) decreased in relation to the time after high water, while in Redshanks and Dunlins pacing rate increased significantly as mean daily temperatures declined. Variation of searching rate and feeding rate was also found to occur in these and other wader species in relation to

the particular portion of North Area where feeding occurred, perhaps because of differences in substrate, (thereby affecting physical mobility) or differences in the sizes of prey which were available, although many other factors may be involved (Evans, 1976). For example, I attributed the finding that Curlews tended to take larger numbers of smaller Nereis and search for them at a faster rate in autumn 1974 than in the previous autumn to a change in their feeding site on the Central Bank rather than on Greenabella Bank. Godwits also took larger numbers of smaller Nereis in autumn 1974 than in autumn 1973, but for this species all records were obtained from one site, the Eastern Channel. There are two possible explanations for this. Firstly, larger Nereis might not have been available in autumn 1974 and Godwits, by taking larger numbers of smaller worms, might simply have been maintaining their rate of food intake at levels similar to those before and during reclamation. Alternatively, smaller Nereis might have been positively selected by individuals if this strategy provided a means of increasing their rate of food intake, and compensating for the shorter feeding time available after reclamation. Unfortunately, I do not have the necessary data to calculate accurately the intake rates of Godwits in terms of biomass and only by doing so could this question be resolved.

Before reclamation, Grey Plovers had fed almost exclusively on large Nereis (Pienkowski, 1973) but during reclamation and increasingly in autumn 1974 some individuals fed almost exclusively on smaller prey which were captured at very high rates. Again, this might represent a change in behaviour enabling higher energy intake rates to be obtained while North Area was available, although, as for Godwits, this cannot be resolved without calculating actual biomass intake. Contrary to this possibility, however, is the finding that when Redshanks change the size of prey they select, their ingestion rate is reduced (Goss-Custard, 1977a). Nonetheless, that this was a novel feeding method at Teesmouth suggests strongly a link with the reclamation story.

Regarding the change in area available for feeding.

The reduction in feeding area inevitably resulted in a massive reduction in the total food resources available to overwintering birds. Calculations presented by Evans et al. (1979) show clearly that the standing crop, for example of Nereis, of the size ranges commonly taken by Curlews, Godwits and Grey Plovers would not have supported the bird populations which had used Seal Sands before reclamation while populations of Hydrobia also would have been insufficient to supply the requirements of Shelducks, Dunlins and Redshanks. (This prey is an important food for these species elsewhere in Britain). Only the standing crop of small annelids, especially oligochaetes, could have satisfied the requirements of Shelducks and Dunlins and at Teesmouth, even before reclamation, it was found that these rather than Hydrobia were the most important component of their food (Evans et al., 1979).

At the beginning of my study, two possibilities were envisaged as arising from this potential shortage of food for the shorebirds which would normally overwinter at Teesmouth.

- (1) That similar numbers of birds to those that had occurred in previous winters would initially settle on Seal Sands but, as increased predation reduced the density of available prey, individuals would have difficulty in satisfying their daily food requirements and would die or be forced to emigrate.
- (2) That the settlement of birds in autumn might be adjusted to the changed area available for feeding.

Arising from the first process, there would probably be a progressive decline in the numbers of each species as birds emigrated and this would be detected by monthly counts. However, a more rapid fall in numbers might occur if the density of available prey dropped rapidly below a threshold, e.g. under severe weather conditions. In situations where the density of available prey is reduced, birds might attempt to increase the time they spent feeding, and

it was anticipated that this would be apparent in the increase of PFT's after reclamation, involving, of necessity for some species, the more extensive use of feeding areas at high water. The foraging behaviour of birds might also have changed in these circumstances, individuals failing to collect preferred foods at their usual rates of intake and being forced to modify (if this were possible) their preferences for prey types and sizes. Linked to this, it was thought that birds might move from their preferred feeding sites as these suffered depletion of prey.

Although it was not envisaged that birds would ignore the fact that Seal Sands was so greatly reduced in size when they returned in autumn 1973 (the North-East Enclosure having been reclaimed in spring), it was considered likely that a large proportion of the birds which traditionally overwintered there would attempt to do so again. As a result, features associated with a heavier than usual depletion of the food resources would be exhibited as the first winter of my study progressed, and this would be exaggerated by the on-going reclamation and reduction in feeding area occurring in the course of the 1973/74 winter.

In fact, it became apparent by the middle of the first winter that most birds had reacted to reclamation in accordance with the less likely possibility, that is, they had adjusted their use of intertidal areas to levels which might approximately be supported throughout that winter with little or no further change. At no time was there a progressive decline in shorebird numbers (see p.180) and rapid changes occurred in only two species, Dunlins and Godwits, and in each case these were related to reclamation during the course of the 1973/74 winter and for which prediction in autumn would not have been possible. The possibility that waders might be capable of assessing the food resources of an estuary is supported by research elsewhere (Goss-Custard, 1977b).

In accordance with the finding that each species, if it needed to adjust its numbers, had done so by reductions in the numbers from autumn, was that

PFT's did not appear to increase progressively during the 1973/74 winter, but followed a pattern of change broadly related to temperature. Additionally, the use of high water feeding areas developed only to an extent sufficient to maintain the PFT and to increase it during the mid-winter period. Within North Area, although the feeding areas of some species changed during and after reclamation, and in some cases clearly closely related to the state of reclamation, for example, the use of areas of liquid mud by Redshanks, the preferred feeding areas identified by Pienkowski (1973) before reclamation and occupied as preferred sites again in early autumn 1973 remained the principal feeding sites for the respective populations after reclamation was complete. The diminishing use of Greenabella Bank by Curlews (previously in spring 1973 it had not been used), the increased tendency of Grey Plovers to disperse quickly over the Central Bank and the increased tenacity of Dunlins to feeding on the tide edge, as the 1973/74 winter progressed, probably do reflect changes in the density of available prey, but these were probably part of a normal pattern of changing feeding strategy in those species in all winters. Certainly, there was no gross change in the feeding areas exploited by each species, no dramatic changes which might suggest extensive and heavy depletion of their food.

In discussing the possible effects of reduced feeding time on the foraging behaviour of shorebirds, it has been noted that throughout both winters individuals appeared to search for and capture prey at approximately similar rates during and after reclamation as they had done before. The finding that Godwits took worms of smaller size after reclamation than they had before reclamation, and that Grey Plovers also took larger numbers of small prey in preference to fewer larger worms seems to suggest, however, a reduced density of the larger Nereis which would normally provide the bulk of their diet (Pienkowski, 1973).

Since a diminished density of larger Nereis might arise naturally and be part of their normal year-to-year variation in breeding success, it is not possible to state definitely that the response of these species was related to

the reclamation story, but this must remain a possibility. It is evident, however, that no individual hardship appeared to arise from the change of diet; in each case the smaller prey were taken in numbers which must have compensated in terms of biomass for the absence of the larger prey from the diet and, in fact, might have been a means by which individuals increased their intake rates.

In Table 25 an attempt is made to relate the use of Seal Sands by each species during its reclamation to the area available at different stages of the programme. The values shown represent the broad mid-winter population levels using Seal Sands and, notwithstanding the many qualifications which may be made with respect to these data, some interesting relationships emerge. Shelducks have not been included here since for this species no change in overwintering numbers occurred. It might be noted, however, that for this species the North Area was always the most important feeding site at Teesmouth, and therefore their principal feeding area was unaffected by reclamation.

From Table 25 it seems that the use of Seal Sands by Grey Plovers, Curlews and Redshanks during the mid-winter period is related to the area of intertidal flats available for feeding and population changes have occurred in accordance with reclamation of the flats. Thus, the number of birds/acre in early spring 1973, when all of South Area was available, is maintained after reclamation when only North Area remained. That a relationship exists between the area of the flats and the numbers of birds supported by them is borne out by the observation made in earlier discussion (p.299), that the numbers using North Area before and after reclamation were similar. This is so even for Godwits which seem to have fallen in numbers more than would be expected with respect to the total area available for feeding, that is, the number of birds/acre has diminished since reclamation. Thus, before reclamation around 100 Godwits fed regularly on North Area (Pienkowski, 1973) and this is similar to the numbers overwintering after reclamation.

The case of Godwits clearly indicates that the numbers of birds using

TABLE 25.

THE RELATIONSHIP BETWEEN AVAILABLE FEEDING
AREAS AND OVERWINTERING NUMBERS OF WADER SPECIES.

	1972/73			1973/74		1974/75	
	Numbers of birds =	Nos. of birds/ acre		Numbers of birds	Numbers of birds =	Nos. of birds/ acre	
Grey Plovers	200	=	0.20	100	80	=	0.23
Curlews	240	=	0.26	100	100	=	0.28
Godwits	600	=	0.99	220	75	=	0.21
Redshanks	300	=	0.35	270	170	=	0.38
Dunlins	16,000	=	17.7	4,390	4,000	=	11.4
Area available							
in acres (ha.)	900 (360)			over 350 (140)		350 (140)	

North Area is not a simple function of the area available, and it is expected on the basis of evidence from elsewhere in Britain (Goss-Custard et al., 1977c) that the density of available food is the ultimate factor determining its use by each species. Thus, for Godwits it must be assumed that South Area provided the preferred feeding ground of this species before reclamation and, of course, this is borne out by Pienkowski's observations of feeding distribution. For those species in which there is apparently a direct relationship between numbers and area, it is probable that the abundance and availability of prey was similar in both the South and North Areas.

For Dunlins, there seems to have been a rather greater reduction in numbers than would be expected on the basis of the reduced area alone, this occurring despite the fact that North Area was the preferred low water feeding area before reclamation. This is also surprising since, as for Shelducks, it has been calculated that North Area held sufficient food resources to sustain the original Seal Sands population.

Relating numbers to feeding areas as presented in Table 25 is not satisfactory for the 1973/74 winter using a single figure as given for the other winters and thus none is given. The changes in available feeding area, for example, the progressive loss of West Enclosure during the course of that winter really requires separation on a monthly basis. This would require the actual area available to be estimated in retrospect and for each species this would be different, since for some species reclamation provided very attractive feeding, for example for Redshanks and Godwits, but for Curlews and Dunlins it provided suitable feeding for only a short period. In fact, the use of the enclosures during reclamation illustrates well the irrelevance of area per se and the importance of abundance and availability of prey.

SUMMARY OF CONCLUSIONS.

From the foregoing discussion, it appears that, of the six species which I studied at Teesmouth, only Shelducks were unaffected by the reduction in feeding area and potential feeding time which accompanied the partial reclamation of the South Area of Seal Sands. Sufficient food was available on North Area to support the usual overwintering numbers of this species and, additionally, it seems probable that the ability of Shelducks to feed efficiently at night as well as by day means that individuals required no additional feeding time away from the estuary. Shelducks feed only for a little over half the time available for feeding in each tidal cycle.

All five wader species I studied did, however, show reductions in the numbers which overwintered on Seal Sands, as judged by their use of the intertidal flats there during the mid-winter period. For all species, higher numbers were supported by the estuary in autumn and spring each year, and for Curlews and Redshanks it seems probable that the birds displaced from Seal Sands, due to its partial reclamation, remained in the Teesmouth area but fed, for part of the year at least, almost exclusively on freshwater marshes and wet pasture in the vicinity of the estuary.

For one species, Curlews, the pattern of use of North Area suggests that the time available to feed there was quite adequate for individuals to collect sufficient food, although, despite this, small numbers did in fact feed at high water on the adjacent fields. It seems probable that this use of field areas was by individuals topping up their food reserves. Most of the Curlews that fed on North Area at low water roosted at high water, although the existence of a field feeding flock of Curlews nearby suggested they were quite capable of feeding on the fields if necessary. It may be concluded, therefore, that the reduced feeding time after reclamation did not affect the numbers of Curlews using North Area, but rather it was the reduced area and, therefore,

the reduced abundance of food which determined the overwintering numbers.

For Godwits and Grey Plovers, the feeding time available on North Area was not quite sufficient for individuals to satisfy their daily energy requirements during the daylight tidal cycle. Therefore, assuming that the density of available food on North Area after reclamation remained similar to that before reclamation - and there is no evidence to suggest any marked decrease in food density occurred - then the adaptations to compensate for the shortage in feeding time need only to have been relatively slight and probably necessary only over mid-winter. In the case of Godwits, additional feeding on one section of the Brinefields appeared to provide the principal means by which feeding time was extended and this was used regularly by over half the Seal Sands population in mid-winter months. Although feeding at night by Godwits was conspicuous only in autumn 1973, Grey Plovers fed extensively at night after reclamation, and it seems probable that, although the PFT at night cannot be quantified, night feeding compensated for the reduction of daylight feeding time. Only occasionally did Grey Plovers feed over high water on field areas, although several individuals fed when the main part of North Area was covered by the tide, in the higher tidal portions of Greatham Creek. For neither Godwits nor Grey Plovers was there definite evidence that the rate of food intake was increased so as to reduce the feeding time necessary to collect their daily food requirements. Although both Godwits and Grey Plovers captured prey at a faster rate after reclamation than they did before, the prey taken were smaller and my data are not sufficient to determine whether these changes enabled individuals to merely maintain their food intake rate or to increase it. Notwithstanding this further possibility, it seems that the adaptations previously referred to were sufficient to compensate for the deficiency in feeding time and it must be concluded that the very definite reductions in the overwintering numbers of both species are attributable directly to the reduction in available feeding area.

For Redshanks and Dunlins, it seems that the feeding time available on Seal Sands in daylight after the reclamation of South Area was most certainly not sufficient to enable individuals to collect their daily food requirements. Both species required considerably longer feeding times than the exposure of North Area provided and both compensated for this by feeding for long periods in the field areas over high water. This was so even in early autumn when weather conditions were mild and the density and availability of food might be expected to be at its highest. For neither species was there any indication that they were capable of, or attempted to, increase their rate of food intake. Although both could increase their searching rate to some extent, it seemed likely that this enabled the maintenance of an optimal food intake rate rather than an increased rate of food intake, although my data are not sufficient to verify this opinion. In autumn 1973, both species were seen to feed at night and in some situations it appeared to be as efficient as feeding by day (e.g. Redshanks feeding in liquid mud), but in fact this adaptation to the shortage of feeding time was not used extensively.

Redshanks appear particularly well adapted to using field areas for feeding and, in a manner similar to Curlews, an exclusively field-feeding flock existed in the Teesmouth area. Redshanks are capable of using a wide variety of different feeding habitats, e.g. ditches and dykes as well as saturated pasture and temporary pools, and can exploit such areas under severe weather conditions. Thus, although those Redshanks which fed on Seal Sands at low water after reclamation needed to spend considerable time feeding in field areas, the area available to them was extensive and would probably be unavailable only rarely and temporarily. Thus, I would conclude that the deficiency in feeding time was not an important determinant in reducing the numbers of Redshanks using Seal Sands. As for Curlews, Godwits and Grey Plovers, the food resources of North Area in terms of larger invertebrates, such as Nereis, or other suitable prey such as Hydrobia, could not have

supported the numbers of Redshanks which had previously used Seal Sands, and it seems probable that the reduction in their numbers after reclamation was related to the reduced feeding area and reduced food stocks.

In contrast to Redshanks, suitable feeding locations at high water for Dunlins were more limited: they seemed confined to areas of very wet pasture and surface water pools. Furthermore, Dunlins seemed not to be able to feed in these locations under severe weather conditions. On the whole, therefore, it seems they were less successful in exploiting field areas than Redshanks, and also were more vulnerable to the temporary loss of suitable feeding in the fields. While the food resources of North Area were sufficient to support the previous populations of Dunlins, the numbers fell considerably and I conclude that this resulted from the loss of feeding time available on the intertidal flats. The field areas could not supply feeding of sufficient quality for a sufficient length of time to compensate for this loss as was possible for Redshanks and to a lesser extent for Godwits.

A point of particular interest which emerges from my study is that the species of shorebirds which had to adapt in some way to reclamation, that is by the adjustment of numbers and/or some aspect of feeding activity, did so with relative ease and without individual hardship. There was, for example, no progressive loss of birds from Seal Sands as its area was reduced; nor, with the exception of Dunlins in January 1974, was there a sudden emigration or death of birds because of food shortages created by too many birds attempting to overwinter.

For two species, Grey Plovers and Godwits, the number settling on Seal Sands in autumn were quickly adjusted to the carrying capacity of the feeding areas available (both intertidal and field areas) and in general this level of population seems to have been maintained with relatively slight change throughout each winter. This suggests that individuals are capable of responding to, and of assessing the food reserves within, the available

feeding area. Evidence from elsewhere (Zwarts, 1976 and 1979 (in press); Goss-Custard, 1976 and 1977b and Goss-Custard et al., 1977c) suggests that the number of shorebirds present in a particular feeding site is determined by competition between individuals and involves two counteracting forces. Firstly, there is the tendency for birds to concentrate their feeding in areas where the density of available and preferred prey are highest and, secondly, the tendency for birds to move away from dense concentrations of birds since in such situations feeding rates decline.

Similarly, at Seal Sands, it seems probable that the number of Grey Plovers and Godwits present at any one time is the product of competition amongst feeding birds for the most profitable feeding sites, and that birds space themselves out in a density which is related to the abundance and availability of food. As a result of this process, individuals unable to obtain sufficient food in feeding sites that they are capable of occupying are forced to move elsewhere. That the numbers of these two species remain stable throughout each winter, however, adds a further element to this behavioural dispersion, namely that the dispersion of birds, which results in some birds being forced to emigrate from the estuary, is such that the food reserves in their feeding sites remain adequate to maintain the same numbers of birds throughout the overwintering period.

At Seal Sands, it seems likely that the overwintering numbers were maximal and it is for this reason I have used the term 'carrying capacity'. Since the abundance of food is the basis for dispersion of birds, it is reasonable to suppose that as a result of natural year-to-year variation in food abundance, so the carrying capacity would be expected to vary. It seems likely that the notion of carrying capacity has greatest relevance during the mid-winter period and that the competitive behaviour, which maintains it, must break down in spring, thereby permitting the influx of migrants.

In the research quoted above, feeding dispersion resulting from

intraspecific competition has attracted most attention, but Zwarts (1979) also briefly examines interspecific competition and considers the extent to which this on-going process determines the segregation of feeding sites which is conspicuous on many estuaries, Seal Sands included. That interspecific as well as intraspecific competition operates in the process of determining carrying capacity is supported by other work at Teesmouth (Evans, 1979) which has shown that Dunlins may compete for feeding space with Shelducks and that individual Redshanks are likely to be displaced from a feeding site by Dunlin flocks.

Without discussing this wide topic in greater detail, it is of interest that in Dunlins also there seemed to be a reasonably steady overwintering population after reclamation, suggesting again that some upper limit of bird density or carrying capacity existed. Since it has been concluded that the principal food resource, that is, the area of feeding on North Area, was not a limiting factor on the overwintering numbers of Dunlins, then the available feeding on field areas must have been the principal determinant of carrying capacity.

Because my study attempted to follow the fate of six species populations at Teesmouth during the reclamation of Seal Sands, my conclusions are inevitably dependent heavily on subjective interpretation of observations and provide a rather simplistic assessment of the effects of reclamation on each species and of their responses to the loss of their feeding area. The time available for fieldwork was simply not sufficient for more detailed information to be obtained, for example, of the type that might be gained from observing a single species throughout a tidal cycle. I have no doubt also that because I was looking at as wide a sample of birds as I could, thereby accumulating information concerning the behaviour of the average bird of each species, I overlooked much of interest with respect to the responses of individuals to the changed circumstances for feeding. Since the selection of

the birds which stayed at Teesmouth would have operated at the level of individual competition, the study of individuals would perhaps have provided a clearer insight into the processes by which the numbers of overwintering waders are related to their feeding area. At the present time, a project involving the individual colour-marking of Curlews, Grey Plovers and Godwits is being undertaken at Seal Sands and hopefully this will contribute to further knowledge of this subject.

B I B L I O G R A P H Y .

- Alexander, W.B.; Southgate, B.A. and Bassindale, R. (1935). Survey of the River Tees, Part 2 - The Estuary - Chemical and Biological. Dept. of Science and Industrial Research, Water Pollution Technical Paper No. 5, pp. 171
- Bryant, D.M. and Leng, J. (1975). Feeding distribution and behaviour of Shelduck in relation to food supply. *Wildfowl*, 26, 20-30.
- Burton, P.J.K. (1966). Food and feeding methods of Curlew, Golden Plover, Grey Plover and Lapwing. *Ibis*, 108, 455.
- Buxton, N.E. (1977). Territorial fidelity and feeding behaviour in the breeding of the common Shelduck, *Tadorna tadorna* (L). International Waterfowl Research Bureau, Feeding Ecology Symposium, Gwatt, Switzerland, Sept. 1977. (Proceedings in press: Ver. Orn. Ges. Bayern, 23).
- Davidson, P.E. (1971). Some foods taken by waders in Morecambe Bay, Lancashire. *Bird Study*, 18, 177-186.
- Evans, P.R. (1973). The effects of stage 1 of reclamation of Seal Sands on the invertebrate and bird populations. A report to the Teesmouth Bird Club.
- Evans, P.R. (1975). The effects of partial reclamation of Seal Sands, Teesmouth, on the bird populations, January - September 1974. A report to the Royal Society for the Protection of Birds.
- Evans, P.R. (1976). Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. *Ardea*, 64, 117-139.
- Evans, P.R.; Herdson, D.M.; Knights, P.J. and Pienkowski, M.W. (1979). Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. 1. Shorebird diets, invertebrate densities and the impact of predation on the invertebrates. *Oecologia* (in press).

- Goss-Custard, J.D. (1969). The winter feeding ecology of the Redshank (Tringa totanus). *Ibis*, 111, 338-356.
- Goss-Custard, J.D. (1970). Feeding dispersion in some overwintering wading birds. In: "Social behaviour in birds and mammals", (Ed. Crook, J.H.) pp. 3-35. Academic Press, London.
- Goss-Custard, J.D. (1972). A Rationale for Seal Sands.
- Goss-Custard, J.D. (1973). Current problems in studying the feeding ecology of estuarine birds. Coastal Ecology Research Paper, 4, 1-33.
- Goss-Custard, J.D. (1976). Variation in the dispersion of Redshanks, Tringa totanus, on their wintering grounds. *Ibis*, 118, 257-263.
- Goss-Custard, J.D. (1977a). Optimal foraging and the size selection of worms by Redshank, Tringa totanus, in the field. *Animal Behaviour*, 25, 10-29.
- Goss-Custard, J.D. (1977b). The ecology of the Wash, III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology*, 14, 721-739.
- Goss-Custard, J.D. and Rothery, P. (1976). A method for measuring some components of foraging of certain birds in the field. *Animal Behaviour*, 24, 545-550.
- Goss-Custard, J.D.; Jones, R.E. and Newbery, P.E. (1977a). The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology*, 14, 681-700.
- Goss-Custard, J.D.; Jenyon, R.A.; Jones, R.E.; Newbery, P.E. and Williams, R. Le B. (1977b). The ecology of the Wash. II. Seasonal variation in the feeding conditions of wading birds (Charadrii). *Journal of Applied Ecology*, 14, 701-719.
- Goss-Custard, J.D.; Kay, D.G. and Blindell, P.M. (1977c). The density of migratory and overwintering Redshank, Tringa totanus, and Curlew, Numenius arquata, in relation to the density of their prey in south-east England. *Estuarine and Coastal Marine Science*, 5, 497-510.
- Gray, J.S. (1976). The fauna of the polluted River Tees estuary. *Estuarine and Coastal Marine Science*, 4, 653-676.
- Heppleston, P.B. (1971). The feeding ecology of Oystercatchers (Haematopus ostralegus) in winter in northern Scotland. *Journal of Animal Ecology*, 40, 651-672.
- Knights, P.J. (1974). The effect of recent reclamation of the Tees estuary on the numbers and feeding activities of overwintering waders and Shelducks. Unpublished report to Coastal Ecology Research Station, Institute of Terrestrial Ecology.
- Knights, P.J. (1975). Post-reclamation changes in the numbers and feeding activities of overwintering waders and Shelducks at Teesmouth. Unpublished report to Coastal Ecology Research Station, Institute of Terrestrial Ecology.

- Murton, R. K.; Westwood, N.J. and Isaacson, A.J. (1964). A preliminary investigation of the factors regulating population size in Woodpigeon, Columba palumbus. *Ibis*, 106, 482-507.
- Nature Conservancy Council (1972). North Tees Planning Study. The scientific significance of plant and animal communities at Teesmouth with reference to conservation requirements and the probable impact of further industrial development.
- Newell, R.C. (1974). Wildlife conservation in Teesmouth, pp. 1-78. A report to the County Borough of Teeside.
- Olney, P.J.S. (1965). The food and feeding habits of Shelduck (Tadorna tadorna). *Ibis*, 107, 527-532.
- Pienkowski, M.W. (1973). Feeding activities of wading birds and Shelducks at Teesmouth and some possible effects of further loss of habitat. Unpublished Report to the Coastal Ecology Research Station, Institute of Terrestrial Ecology.
- Prater, A.J. (1970). Studies of the food and feeding habits of some wader species in Morecambe Bay. Morecambe Bay Barrage Feasibility Study: Biological Aspects. A report to N.E.R.C., pp. 1-60.
- Prater, A.J. (1972). Birds of Estuaries Enquiry. Report for 1971-72. British Trust for Ornithology/Royal Society for the Protection of Birds/Wildfowl Trust.
- Prater, A.J. (1975). Birds of Estuaries Enquiry. Report for 1973-74. British Trust for Ornithology/Royal Society for the Protection of Birds/Wildfowl Trust.
- Prater, A.J. (1976). Birds of Estuaries Enquiry. Report for 1974-75. British Trust for Ornithology/Royal Society for the Protection of Birds/Wildfowl Trust.
- Smith, P.C. (1975). A study of the winter feeding ecology and behaviour of the Bar-tailed Godwit, Limosa lapponica. Unpublished Ph.D. thesis, University of Durham.
- Stead, P.J. (1964). The birds of Teeside. Transactions of the Natural History Society of Northumberland and Durham, 15, 1-58.
- Temperley, G.W. (1951). A history of the birds of Durham. Trans. Nat. Hist. Soc. Northumberland, Durham and Newcastle, 9, 1-296.
- Zwarts, L. (1976). Density-related processes in feeding dispersion and feeding activity of Teal (Anas crecca). *Ardea*, 64, 192-209.
- Zwarts, L. (1979). Intra- and interspecific competition for space in estuarine bird species in a one-prey situation. Proceedings of the 17th International Ornithological Congress (in press).

S U M M A R Y .

This study considers separately two examples of the effect of changes in land use on animal populations. In the first case, the effects of a group of agricultural fungicides on soil fauna are examined, while the second case considers the results of large scale loss of habitat on the numbers and feeding ecology of estuarine birds in winter.

1. The effect of organotin fungicides on soil Acarina.

Although the toxicity of organotin chemicals to a variety of invertebrates from several different phyla has been studied, especially with regard to their potential for controlling insect pests, particularly those of cotton, the insecticidal aspect of their biological activity has not been exploited in Britain.

However, two organotin compounds, triphenyltin acetate and triphenyltin hydroxide, are used extensively as fungicides for the control of potato blight and yellow blight on sugar beet. Despite their wide use as agricultural chemicals, little published information is available concerning their effect on non-target organisms.

In my study, the effect of these organotins on soil Acarina was examined through field experiments. The study area, located in County Durham, comprised a recently established grassland which had previously been subject to arable

cultivation. The mite fauna of the site was probably undergoing transition to one typical of grassland but at the time of study it appeared closely similar to that of an arable soil, since it contained a very high proportion of mites belonging to the Order Prostigmata but very low densities of Cryptostigmata.

Most experimental plots comprised a 4 x 8 Latin Square design involving an arrangement of one control plot and three different treatment plots, duplicated eight times. The size of individual plots was related to the number of samples it was anticipated would be taken: the largest plot measured 90 x 90 cms. Samples comprised soil cores of 2.5 cms. in diameter and 3 cms. in depth. Mites were extracted using a Macfadyen High Gradient apparatus. Collections were identified to the level of family, but only a selection of those which demonstrated changes in abundance during preliminary trials or occurred at high densities were identified to species level. When field trials began, the Order Prostigmata constituted around 80% of the mites collected with a single species, Tarsonemus floricolus, accounting for the majority of these.

Five experimental series were undertaken involving seven different treatments. For both triphenyltin acetate (TPTA) and triphenyltin hydroxide (TPTH), these varied the total amount of organotin administered and the regime of treatment, i.e. whether as one large dose or repeated small doses. Each of the different treatments were undertaken in autumn/winter but two treatments of TPTH were repeated in spring/summer.

In the first trial undertaken, samples were taken at frequent intervals immediately after treatment commenced, but in the absence of significant short-term changes sampling at monthly intervals was adopted. Sampling continued for between 4 - 7 months after treatment.

Both TPTA and TPTH were found to reduce the total numbers of soil Acarina occurring when the chemicals were applied in autumn at levels of dosage recommended by manufacturers. Not all soil mites were affected, however. For example, the numbers of Eupodidae and Tydeidae did not vary, and it emerged that the net

reduction in total mite densities occurred as a result of the decline in numbers of relatively few, but often particularly abundant, species. For example, the decline in numbers of the very abundant mite, Tarsonemus floricolus, was severe and it was absent from some samples following treatment with the agricultural recommended dosages. In the same treatments, numbers of Mesostigmata, largely comprising predacious species, were reduced by more than 60%.

The response of mites to both TPTA and TPTH treatments was broadly similar and it is suspected that hydrolysis of TPTA to form TPTH may occur rapidly in the soil, with the result that treatments were in fact identical.

To both TPTA and TPTH, a dose-related response is evident in the post-treatment fall in numbers of T. floricolus and of Mesostigmata, and in the increase in numbers of a collective group of several unidentified species of Prostigmata (mainly Eupodidae and Tydeidae) designated 'Other' Prostigmata. For example, whereas treatment with the recommended agricultural dose brought about near extinction of T. floricolus in treated plots, after half this dosage numbers, although much reduced, were in excess of 500/m². While the full recommended dose of both chemicals produced no effect on 'Other' Prostigmata, the increase in numbers of this group following treatment with a lower dosage suggests that a balance exists between the benefits of treatment to some species within this group and the toxicity of the triphenyltins to the same or different species of the group. Increases in numbers of soil fauna under low dosages of more usually toxic chemicals have been found in other studies, and reasons why this may occur are considered. A treatment of TPTA amounting to 1½ times the agriculturally recommended dosage resulted in a greater reduction in the numbers of Mesostigmata than at lower levels of treatment.

Two trials, one involving the full recommended dose of TPTH and the other a treatment of half this quantity, were carried out in spring as well as in autumn, and comparison of results enabled the effect of the season of treatment to be assessed. In general, it seemed that the response of mites to a given

dosage in spring was similar to their response to half that dosage in autumn. For example, T. floricolus suffered severe reduction after administration of the full agricultural dose in autumn, but was unaffected by similar treatment in spring. The numbers of 'Other' Prostigmata increased after treatment with the full dose in spring, whereas in autumn their numbers remained unchanged. Data were not available to determine why these differences occurred, although it is noted that differences in environmental conditions might modify the effective toxicity of the chemicals, although equally the sensitivity of the mites themselves might vary.

The recommended agricultural treatments with both TPTA and TPTH involve administration on four separate occasions at between 10-14 day intervals. Administration of the same quantity in the form of a single dose produced responses similar to those of half this quantity when administered on two occasions. For example, there was an increase in the numbers of 'Other' Prostigmata which was not evident under the normal recommended treatment regime.

In none of the trial series was there any recovery in the numbers of those species or groups adversely affected, the duration of the experiments being clearly not sufficient. The increase in numbers of 'Other' Prostigmata after treatment was, however, short-lived, being maintained for no more than three months.

Whereas field trials demonstrate the existence of deleterious or beneficial effects of triphenyltin chemicals, they do not provide information about the mechanisms through which population changes occur. Laboratory trials were proposed to examine the processes involved, but unfortunately time was not available to pursue this work. In particular, it was hoped to resolve whether toxicity was arising directly, that is, from contact with or ingestion of the chemical causing mortality, or indirectly, that is, by the fungicides' effect on the quantity or quality of feeding for fungiferous species, for example, T. floricolus, and thereby inducing emigration or starvation.

A successful means of culturing the particularly susceptible species, T. floricolus, was devised, however. The small size of this mite required modification of standard culturing techniques which have primarily been developed for culturing larger Cryptostigmatid species, and a variety of culture systems were critically examined for their suitability for use with small Prostigmatids and their use in re-creating field trial experiments in the laboratory. A micro-immersion filter system, comprising individual culture cells which could be separately removed and examined, was considered most suitable for the study of behavioural characteristics and other detailed study, since they could be checked rapidly and frequently and enabled easy manipulation of individual mites. A perspex block system was considered more appropriate for culturing the large numbers of mites required for laboratory experiments in which simple counts would be necessary.

T. floricolus was found to survive for periods in excess of one month in these culture systems, when fed on a diet of fungal hyphae which are part of the pleurococcus algal and fungal association.

The densities of mites in the control plots of each field trial, combined with an additional series of samples, obtained between successive trials and for a period of six months after the final trials were completed, provide information over a two-year period on the abundance and seasonal changes in abundance of the major groups and of some species of soil mites in the study area at Durham. (Information over such a long period and with such a high frequency of sampling is scarce in the literature).

During this period, mean densities of total Acarina approached $24,000/m^2$, being higher than recorded in other studies of recent pasture, but less than densities recorded in permanent pasture. The majority of mites belonged to the 'Order' Prostigmata which occurred at a mean density of around $20,000/m^2$. Very low densities of Astigmata and Cryptostigmata were recorded but numbers of Mesostigmata were comparable with records from studies of similar grassland

habitats. Reasons for the differences from and similarities to other studies are discussed.

Maxima in the densities of total Acarina were recorded in November 1972, May 1973 and June 1974 and arose from the change in abundance of relatively few species, all of which belonged to the Prostigmata. The November maxima resulted from high abundance of T. floricolus while the May/June maxima coincided with high abundance of species of Eupodidae (in the group 'Other' Prostigmata) and species of the genus Pygmephorus. In common with other studies, the numbers of Mesostigmata showed little seasonal variation in abundance.

The progressive increase in Scutacarus (Variatipes) montanus and Pygmephorus spp. and an increasing abundance and diversity of the Order Cryptostigmata coincided with a decrease in the abundance of T. floricolus during the study period and it is suspected that the study area was undergoing transition from a previously mown rye-grass sward to a longer vegetation containing a variety of different grasses and herb species.

The implications of the toxicity of triphenyltin fungicides is discussed, with particular reference to the role of soil fauna in the processes involved with soil development and maintaining soil fertility. However, it is concluded that these chemicals are unlikely to contribute significantly to the very great changes in abundance of soil mites which occur as a result of other agricultural practices.

2. The effects of reclamation on the numbers and feeding activity of overwintering waders and Shelducks at Teesmouth.

Before 1972, Seal Sands represented the largest and most important overwintering feeding ground for waders and Shelducks within the Tees estuary, and the concentrations of Shelducks there were of international importance.

Reclamation of intertidal sand and mudflats within the Tees estuary began first for agricultural purposes and later for industrial development. The progressive reclamations that had occurred up to the beginning of this study, and involving a reduction in the area of Seal Sands from 2,430 ha. to 360 ha., are documented, and available information about the concomitant changes in sediments and numbers of birds is discussed.

In 1972, a further major programme of reclamation was initiated which, during the course of this study, reduced the area of Seal Sands to 140 ha. by summer 1974. This reclamation involved the sub-division of the tidal flats by porous slag walls, leaving one section, the North Area, directly open to tidal influence and another section, South Area, completely enclosed. South Area was further sub-divided by slag walls. The North Area alone remained after reclamation. The slag enclosing walls had the effect of retarding tidal influence within South Area and enabled birds to feed for 12 hours in each tidal cycle. On North Area, birds could feed for only 8 hours in each tidal cycle. Thus, reclamation not only reduced the area of feeding but reduced the available time for feeding. It seems likely that, before the current phase of reclamation, the conditions for feeding were more favourable than they would normally be on an open mudflat of similar area and productivity.

The purpose of this part of my study was to identify the means by which shorebirds using Seal Sands adapted to the post-reclamation situation, if in fact they needed to or were capable of doing so, and to determine the relative importance of loss in feeding area and loss in feeding time in determining the overwintering population of shorebirds after reclamation was completed.

The North Area of Seal Sands comprises mainly muddy substrates which are enriched by sewage effluent. Nereis diversicolor is the most abundant large annelid prey, occurring at densities of around 250/m². Macoma balthica is widely distributed, but only in relatively few locations does it reach densities of 200/m², while Hydrobia ulvae occurs at densities in the order of 10-15,000/m².

Small oligochaetes and polychaetes constitute a higher biomass/unit area than the macrofauna and occur at mean densities of $206,000/m^2$ and $30,000/m^2$ respectively.

The effect of reclamation was considered with respect to five shorebird species: Shelduck (Tadorna tadorna), Grey Plover (Pluvialis squatarola), Curlew (Numenius arquata), Bar-tailed Godwit (Limosa lapponica), Redshank (Tringa totanus) and Dunlin (Calidris alpina).

There were two main aspects to my work:

- (1) Monitoring the tidal and seasonal changes in the numbers of birds and areas used.
- (2) Quantifying the means by which each species adapted its previous feeding strategies in terms of (a) the duration of feeding in daylight, at night and in different habitats, and (b) foraging behaviour and diet.

The numbers of each shorebird species using Seal Sands were counted each month. Comparisons of these data with population levels in previous winters enable changes to be stated with reasonable confidence. For Curlew and Redshank, numbers using Seal Sands were lowest in midwinter, many individuals moving to feed on flooded fields in the vicinity at this time. For Godwits, Grey Plovers and Dunlins, numbers declined after an early autumn peak to a steady population level which was maintained until spring. The possibility that this 'stable' level in numbers might represent a 'carrying capacity' is discussed. These stable levels were established after the end of immigration, there being no indication of a progressive fall in numbers in the course of each winter which might arise from an imbalance between bird numbers and their food resources. All counts are tabulated and shown graphically.

For most species the principal feeding areas on Seal Sands were segregated, and only for Godwits and Grey Plovers did feeding areas overlap substantially.

There were no major changes in preferred feeding locations after reclamation.

The proportion of each daylight tidal cycle for which individuals of each species fed was determined by assessing the feeding intensities, that is the proportion of the population feeding on Seal Sands at low water and on the fields at high water. This value, the Percentage Feeding Time (PFT), represents the time needed for an average member of the species to collect its food requirements. Monthly PFT values are presented and changes are related to environmental variables and to the state of reclamation.

Since North Area has an exposure time of 8 hours (about 67% of the tidal cycle), species which before reclamation had a PFT exceeding this necessarily fed elsewhere during high water: for example, in field areas, or adapted in other ways after South Area was lost. Only Shelducks and Curlews had a PFT below this upper limit of feeding time. Dunlins exploited North Area for the longest period, most individuals feeding for 90% of its exposure time. For other species, the time available on North Area for effective feeding was considerably less than 67%. The importance of South Area in providing additional feeding time during reclamation is discussed.

Although individuals of all species were seen to feed on field areas after reclamation, feeding there was particularly important for Redshanks and Dunlins, while for Godwits one partially tidal creek was of special importance in providing additional feeding. Curlews appeared to use field areas for 'topping up' their daily food requirements.

Night feeding was observed in all species and was particularly prevalent during reclamation. Adaptations to night feeding, such as the use of tactile cues to detect prey, and the use of different feeding methods, for example, swishing by Redshanks, is discussed. The profitability of night feeding is commented upon and records of feeding and searching rates at night are given. After reclamation, Shelduck and Grey Plover were found to feed extensively at night and its importance as an adaptation to the reduced feeding time is

assessed, but other species, although capable of feeding at night, did not do so.

Extensive data were collected on searching and feeding rates of each species. For those species taking visible prey, such as Nereis, the diet was determined by direct observation. (For other species, the diet of birds at Teesmouth has been determined by other researchers). It was anticipated that, if feeding time was insufficient for individuals to collect enough food, or if food resources of North Area became depleted, then feeding rates and searching rates might change to compensate for this and also there might be a change in food preferences or the sizes of prey selected. All data are tabulated and are discussed in relation to environmental variables, for example, temperature and the locations of feeding, as well as in relation to the state of reclamation.

Research by other workers indicated that North Area did not hold sufficient food resources in terms of Nereis and Macoma to support the previous overwintering populations. Only the stocks of small oligochaetes and polychaetes could sustain the populations of Shelducks and Dunlins, for which these must have been the major foods. The numbers of Hydrobia alone could not have done so, although Hydrobia has been identified as the chief food of Shelducks in studies elsewhere in Britain.

All five wader species studied showed reductions in the numbers which overwintered on Seal Sands after reclamation, as judged by their use of intertidal flats during the midwinter period. Only numbers of Shelducks seemed to have remained unchanged as a result of reclamation. For Curlews and Redshanks, birds displaced from Seal Sands seemed to remain in the vicinity, but fed exclusively on field areas, though North Area supported high numbers in autumn and spring.

The post-reclamation populations of each species are related to the loss in feeding areas. It is concluded that the reduction in numbers of Curlews, Godwits, Grey Plovers and Redshanks is principally related to the reduced feeding area and total food resources available. For Dunlins, however, the loss in feeding time seems to have been a more important factor in reducing overwintering numbers.

