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THE IMPACT OF OVERWINTERING BIRDS
ON THE PRODUCTION ECOLOGY
OF ESTUARINE BENTHIC INVERTEBRATES

Thesis submitted for the Degree of
Doctor of Philosophy

In the
University of Stirling

by

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All birds collected for gut analysis were shot under licence from the Nature Conservancy Council.

20.12.80

DEDICATION

To my parents

ABSTRACT

The aim of this thesis was to study the impact of several species of overwintering birds on the production ecology of their prey populations. The study was carried out at Skinflats, a large intertidal mudflat on the Firth of Forth, between December 1975 and March 1978.

Aspects of the breeding cycle, growth, mortality and production of *Hydrobia ulvae* are given in Section 3.3. *Hydrobia* was found to live for two years, breed once or twice depending on the size attained in the first year and produce 3.9 g AFDW yr^{-1} from a mean annual biomass of 3.32 g.

The results of population studies of *Macoma balthica*, *Cardium edule*, *Nereis diversicolor*, *Manayunkia aestuarina*, *Pygospio elegans*, *Tubificoides benedeni* and *Corophium volutator* are shown in Section 3.4. *T. benedeni* was the most productive species.

The diets and feeding habits of shorebirds on the estuarine Firth of Forth in winter are described in Section 3.5, with particular reference to the Redshank (*Tringa totanus*), and the factors influencing the low tide feeding distribution and density of Redshank, Knot, Dunlin, and Shelduck are discussed in Section 3.6. In general, the density of each species increased with increasing prey abundance but environmental and behavioural factors influenced this relationship.

The energy balance and winter survival of shorebirds, in particular the Redshank, are discussed in Section 4 together with the impact of Waders and Shelduck on the populations of invertebrates at Skinflats. Should large-scale reclamation plans be implemented on the Forth estuary, it is concluded from this study that Skinflats could not support any large/

large populations of displaced birds. Since the Forth estuary is of national and international importance to several species of shorebirds in winter, it is recommended that the integrity of the major mudflats on the Forth estuary is maintained.

1 GENERAL INTRODUCTION

The British Isles provide refuge for more than one third of all wading birds wintering in Europe, the Mediterranean and North Africa (Prater 1973 - 79, Spitz 1969) and for 52% of the N W European population of Shelduck, Tadorna tadorna (L) (Campbell 1978). Together with a significant proportion of N.W. European populations of other wildfowl, waterbirds and gulls, these birds principally occupy estuarine and coastal habitats throughout the winter.

The definition of an estuary has been a subject for discussion amongst environmentalists and biologists alike (eg Caspers 1967) but the most useful definition is probably that proposed by Pritchard (1967):-

"An estuary is a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage".

Estuaries are usually highly productive habitats compared to those of adjacent marine or fresh-water environments, despite the relatively few species capable of tolerating the rigorous and variable conditions therein. The importance of intertidal estuarine areas to fisheries and shell-fishing is recognised by biologists but the reclamation of such areas for industrial purposes is often still regarded by planners as preferable to a possible alternative loss of adjacent agricultural land. The provision of relatively sheltered access for ocean-going vessels and good communications inland along river valleys has undoubtedly contributed to the growth of many major towns and cities on British estuaries with the result that enrichment of the intertidal areas is not only derived from terrestrial erosion and agricultural drainage but also from the input of organic and inorganic material from urban and industrial effluents. These effluents are not always detrimental to wildlife since organic enrichment often results in higher levels of production of/

of many benthic invertebrates and thus improves the food supply of fish and birds. Nevertheless, the pressure of man's activities on the estuarine habitat has recently become a matter of increasing concern owing to proposals for large-scale reclamation and industrial development in many areas. At the beginning of this century Cadell (1913) summed up the then prevailing attitude towards development by considering the Firth of Forth as one of 'those happy and secluded valleys' having great potential for industrial purposes. At present, it is the extent to which estuaries can receive man-made pollutants whilst remaining productive and providing recreational amenities which is the concern of biologists and industrialists alike.

The responses of estuarine organisms to environmental changes, both natural and man-induced, are poorly understood. The first estuarine studies were surveys of the intertidal fauna such as that on the Exe estuary, Devon, (Allen and Todd 1902). In the late 1920's the Water Pollution Research Board was set up by the Department of Science and since then benthic surveys have been carried out on most British estuaries (see Elliott 1979 for review). Only recently, mainly in the last decade, have quantitative population and production studies been initiated (eg Beukema 1971, Chambers and Milne 1975(a) and (b), Hughes 1970, Warwick and Price 1975, Wolff and de Wolf 1977) to increase the understanding of the dynamics of populations of individual species and the functioning communities. Investigations of the relationships between avian predators and invertebrate prey species in estuaries include, amongst others, studies on the Wash and Morecambe Bay (Goss-Custard 1977(c) , Goss-Custard, Jones and Newbery 1977, Prater 1970, 1972(b)) to evaluate the possible consequences of loss of feeding grounds should plans to construct barrages and bunded reservoirs for fresh-water storage be implemented. On the Tees, in the grossly polluted estuary (Gray 1976), the influence of reclamation on wintering waders and Shelduck was carried out (Evans et al 1979) and the distribution

of /

of waders in relation to the distribution of their invertebrate prey species prior to the damming of part of the Grevelingen estuary, the Netherlands was studied by Wolff (1969). The only long-term investigations of the dynamic relationships between the vertebrate predator and prey species have been made on the unpolluted Ythan estuary, Aberdeen, (Chambers and Milne 1975(a) and (b), Joffe 1978, Milne and Dunnet 1972).

The Firth of Forth is the major industrialised estuary on the east coast of Scotland (Fig 1.1). The portion referred to as "the estuary" lies to the west of the Forth Road Bridge, downstream of which the habitat is entirely marine. Above Kincardine Bridge, the Forth narrows abruptly and the water is progressively diluted until it is fresh, though still under tidal influence, at Stirling.

The major inputs of effluent to the estuary are large volumes of heated waste water from Longannet coal-fired power station, industrial effluent from the B.P. and I.C.I. petro-chemical complex at Grangemouth and distillery waste at Alloa. The rivers Carron and Avon also carry effluent into the Forth at Grangemouth from industrial plants on their shores. Despite these industrial discharges, water quality has improved over the last twenty years (Forth River Purification Board reports 1959 - 79) and Stout (1976) has calculated that effluents from the Grangemouth complex should not reduce the oxygen levels in the water greatly, providing they are "continuously and effectively dispersed in the water body". A far greater threat to wildlife on the estuary are the plans by Fife and Central Regional Councils and the South of Scotland Electricity Board (S.S.E.B.) to reclaim large areas of the intertidal area, both for the dumping of waste fly-ash from Longannet power station and for industrial development. Already 20% of the intertidal area on the north shore of the estuary has been reclaimed for these purposes.

The latest report of the Birds of Estuaries Enquiry (B.O.E.E.), implemented

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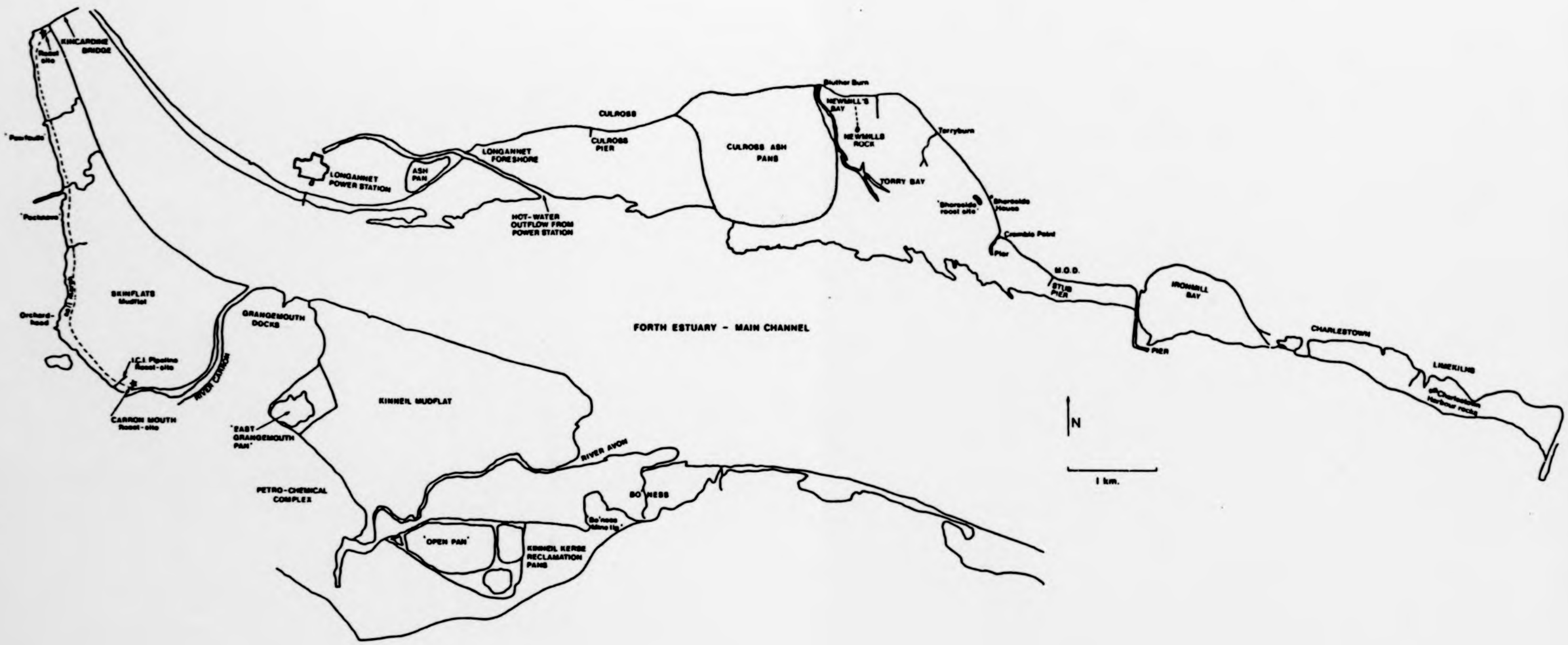

FIGURE 1.1: Map of the study areas of the estuarine Firth of Forth

by the British Trust for Ornithology (BTO) and Royal Society for the Protection of Birds (RSPB), ranks the Firth of Forth seventh in its UK list of important estuaries for wintering wader populations (Prater 1979). In addition, the Firths of Forth and Tay together rank fourth most important in W. Europe for wintering wildfowl (Saeijs and Baptist 1978). Recognition of this importance is reflected in the establishment of five nature reserves (including an RSPB reserve at Skinflats) and nine Sites of Special Scientific Interest (SSSI) on the Forth. It is internationally important for wintering populations of Shelduck, Curlew, Numenius arquata (L), Redshank, Tringa totanus (L), and Knot, Calidris canutus (L) (holding > 1% W European totals) and of national importance for ringed plover, Charadrius hiaticula (L), grey plover, Pluvialis squatarola (L), golden plover, Pluvialis apricaria (L), turnstone, Arenaria interpres (L), bar-tailed godwit, Limmosa lapponica, and dunlin, Calidris alpina (> 1% national totals) (Bryant in : Campbell 1978).

Investigations of the invertebrate distribution and abundance, wintering wading bird and shelduck feeding distributions and densities and the relationships between birds and the invertebrates in the Forth Estuary have been continuing since 1973 (Bryant 1974, 1979, Bryant and Leng 1975, McLusky 1978, McLusky and Brown 1974, 1975, McLusky and Bryant 1975 - 80, McLusky et al 1976, 1978) and studies of the ecology of Macoma balthica (McLusky and Allan 1976) and production ecology of M balthica and other molluscan species at Torry Bay (Elliott 1979) have also been carried out. The intertidal areas of major importance to overwintering waders are located between Kincardine Bridge, Bo'ness on the south shore, and Crombie on the north shore, the area in which industrial development proposals are concentrated (Bryant 1974). Within this area Kinneil, Skinflats and Torry Bay are the most important feeding areas for Shelduck, Redshank, Knot and Dunlin (Bryant 1976) with over 80% of the feeding hours of these "key species" occurring at Skinflats and Kinneil and a further 7% at Torry Bay.

At Skinflats Hydrobia ulvae (Pennant), a small gastropod mollusc , is particularly abundant (McLusky et al 1976) and known to be an important food item for Shelduck (Bryant and Leng 1975, Warnes et al 1980). This, together with the importance of Skinflats as a feeding ground for wading birds and Shelduck in winter, highlighted the need to study, in greater depth, the relationships between the bird predators and invertebrate prey at this site. In the present study quantifying the production ecology of Hydrobia and the mortality due to overwintering Redshank at Skinflats was the principal aim. The term production refers to the organic material accumulated by a population of one or more species in a given area per unit time. The production ecology describes those aspects of a species ecology that are principally associated with this accumulation of material. A further aim was to study, in less detail, the relationship between the winter distribution and density of all four key species of birds (Redshank, Dunlin, Knot and Shelduck) and their prey populations, including an estimate of their impact on the production of these invertebrates over the area. Additionally, a broad study of the diets of several species of wintering waders and Shelduck on the major intertidal areas of the Forth estuary was planned. This was aimed at providing a base for future studies on the importance of all these areas to wintering birds and to link with the studies already carried out (Bryant and McLusky 1975 - 80). In a more general context, predation provides the means by which materials and energy flow between trophic levels within an ecosystem and as such is a building block of community structure. Thus, although the measurement of energy flow through an entire community is often too complex a task to undertake, studies of the ways in which predators utilise their resources and affect their prey populations will increase our understanding of the functioning of the community.

The Redshank is a common shorebird of Europe, breeding in Iceland, the Faeroes, British Isles and Northern Scandinavia (Dementer and Gladkov 1969). Wintering grounds include Iceland, the seaboard of Norway and the Mediterranean

shores/

shores but are centred mainly in N.W. and N.E. Africa. In 1973-4 Britain held 64% of the total West European wintering population (Prater 1976). Three sub-species are generally recognised: *T.t. robusta* (Scholer 1919) breeding in the Faeroes and Iceland; *T.t. britannica* (Matthews 1935) breeding in Britain and *T.t. totanus* (Linneus 1758) which breeds in the remainder of the range. The majority of those breeding in Britain migrate, to winter in the Netherlands, France and Iberian peninsular, those remaining in Britain being joined by Icelandic birds (Hale 1973).

The B.O.E. enquiry has greatly increased knowledge concerning the annual distribution and density patterns of Redshank. In 1972/3 the average winter population in Britain (November - February) was 61,800 increasing through 1973/4 to 76,500 in the winter of 1974/5. Peak numbers occur during the autumn migration with another spring peak as birds move northwards.

Redshank are common shorebirds on British coasts with the exception of the West Highlands of Scotland (Darling and Boyd 1964). Figure 1:2 (Prater in prep.), illustrates the importance of the Wash, Morecambe Bay, Inner Clyde, Forth and Dee estuaries amongst those holding large populations. (B.O.E.E. data). The population in the Forth estuary is probably Icelandic (Davies unpubl.) and annual population fluctuations are consistent with those for the whole country . Greater than 50% of the Firth of Forth population occurs in the estuary and the largest feeding flocks are found at Skinflats (Bryant 1974, 1976).

The Knot also occurs as three sub-species, each characterised by the degree of dark and rufus hues in the plumage colouration. *C.c. canutus* (Linneus 1758) is the darkest and its range extends over Europe and Asia and to Novosibirskie Island in N.E. Greenland (Dement'ev and Gladkov 1969). *C.c. rogersi* (Matthews 1913) is found on Wrangel Island in the East Siberian Sea and has a light colour phase, whilst *C.c. rufus* (Wilson 1813) occurs in America. In Britain, the wintering population consists mainly of *C.c. canutus* and the Wash and/

FIGURE 1.2: Distribution of Redshank in the British Isles (January). (After Prater in prep.)

and Morecambe Bay are the most important areas (Prater 1972-1979). Morecambe Bay supports approximately 16% of the total European and N. African populations, the Wash 12%. In Scotland, the only large wintering populations occur on the Solway Firth and Firth of Forth. Britain as a whole supports 58% of the Western European wintering population (Prater 1976).

In 1974 Bryant estimated that the population of the Forth estuary comprised 85% of the total numbers wintering in the Firth of Forth and 5 - 8% of the national birds. The major feeding areas were Skinflats and Kinneil with smaller numbers at Culross, Torry Bay and Blackness. In subsequent years, numbers have fluctuated reflecting the decreases in wintering populations throughout Britain (Prater 1976) and movements between and within estuaries (Pienkowski pers. comm.).

The Dunlin similarly occurs as three distinct races; *C.a. alpina*, *C.c. arctia*, and *C.c. schinzii*. Those wintering in the British Isles consist almost entirely of *C.a. alpina* from breeding grounds in Arctic Europe and Western Siberia. The autumn peak in Britain is dominated by C.a. *schinzii* from S. Greenland and Iceland, i.e. birds on passage to wintering grounds in lower latitudes.

Prater (1976) estimated that the average population of Dunlin wintering in W. Europe, was 1,200,000, of which 550,000 were found in the British Isles. Of all waders, Dunlin are by far the most numerous in Europe and North Africa and can be found in most estuaries (Prater 1972-75). It is the larger estuaries, notably the Ribble, Dee, Morecambe Bay, the Wash and the Humber which hold the largest populations, although in Scotland, large numbers are recorded on the Solway, Clyde, Forth, Tay and Eden estuaries (Baxter and Rintoul 1953).

In the Forth estuary, Kinneil and Skinflats were found to be of almost equal/

equal importance for feeding Dunlin, the birds following the receding tide over Skinflats and continuing to feed over low water at Kinneil. The reverse movements occurred on flow tides (Bryant 1976-78).

Of the avian species studied, the Shelduck is known to have declined in abundance during the nineteenth century but increased during this century (Sharrock 1976). It is a species of the southern and western Palaearctic breeding principally in the British Isles, Scandinavia and from the Baltic States south to northern France (BOU 1971). The chief moulting ground of Shelduck from much of northwest and west Europe is the Heligoland Bight in the German Waddensea, although amongst other sites around Britain, Grangemouth, on the estuarine Forth, is a refuge for a considerable flock (Bryant 1978). British and Irish wintering flocks number about 65,000 (Prater 1976) resident birds being joined by migratory flocks.

The Curlew and Oystercatcher are both Palaearctic waders which breed and overwinter in Britain. The Curlew breeds in Ireland and western and northern Britain and has extended its range to lowland areas whilst non-breeders remain on coasts during the summer (B.O.U. 1971). The Oystercatcher also breeds around the British and Irish coasts and inland in northern England and Scotland and both species are common in coastal and estuarine habitats in winter. The Bar-tailed Godwit occurs in all coastal areas of Britain in winter, as does the Turnstone, although the latter chiefly inhabits rocky areas (B.O.U. 1971).

The invertebrate species included in this study are:

Hydrobia ulvae (Pennant), the Laver Spire Shell (referred to as Hydrobia throughout this study); a small prosobranch mollusc

Macoma balthica (L), the Baltic Tellin, (referred to as Macoma); a deposit and suspension-feeding bivavle mollusc

Cardium edule (L), the edible cockle (= Cerastoderma edule and referred to as either Cardium or 'the cockle'); principally a suspension feeding bivalve mollusc/

mollusc/

Nereis diversicolor (O F Muller), the ragworm (referred to as Nereis); an errant polychaete capable of exploiting a wide range of foods from the dying young grey mullet to fine particles in suspension in sea-water (Green 1968)

Manayunkia aestuarina (Bourne) (referred to as Manayunkia); a small tube-dwelling sabellid polychaete

Pygospio elegans (Claparede); a spionid polychaete common in estuaries (referred to as Pygospio)

Tubificoides benedeni (= Peloscolex benedeni udekem); a common species of oligochaete in estuarine areas (referred to as T. benedeni)

Corophium volutator (Pallas) (referred to as Corophium); a burrowing amphipod, chiefly a deposit-feeder.

2 MATERIALS AND METHODS

2.1 Invertebrate Sampling and Sorting

Based on data collected during previous studies of the intertidal area of Skinflats (Bryant and Leng 1975, Moffat 1975), three transects, considered to be representative of the area were selected (A, B and C in Fig 2:1). After a preliminary study of the Hydrobia density on each, five sampling stations were located on transect A ($A_1 - A_5$), three on transect B ($B_1 - B_3$) and two on transect C ($C_1 - C_2$). Each station consisted of an area 100 m long by 20 m wide and stations were spaced at 200 m intervals. A_1 was located 200 m from the saltmarsh, B_1 and C_1 adjacent to the saltmarsh. The tidal height (m) of the mid-point of each station was determined from Admiralty Charts (No. 737, 738 : 1976).

Macrofauna deposit-feeders were assumed to be randomly or uniformly distributed (Connell 1963, Lewontin 1972) and sampling proceeded accordingly. Monthly sampling, principally for Hydrobia, but including oligochaetes, small polychaetes and Corophium, involved the collection of four small 5 x 5 x 5 cm cores from each station. The site for each was determined by pacing random co-ordinates parallel and at right angles to the line of the transect. The samples from each station were then pooled and in the laboratory a sub-sample equivalent to 0.25 the area taken for analysis. This sample was sieved over a 300 μ mesh sieve and the fraction retained on the sieve preserved in a 4% saline formalin solution. The animals were sorted under a binocular microscope and stored in 4% saline formalin solution. This method of sampling was devised following discussion with Mr. A. Anderson at the Culterty Field Station, Aberdeen, where Hydrobia populations have been monitored for several years.

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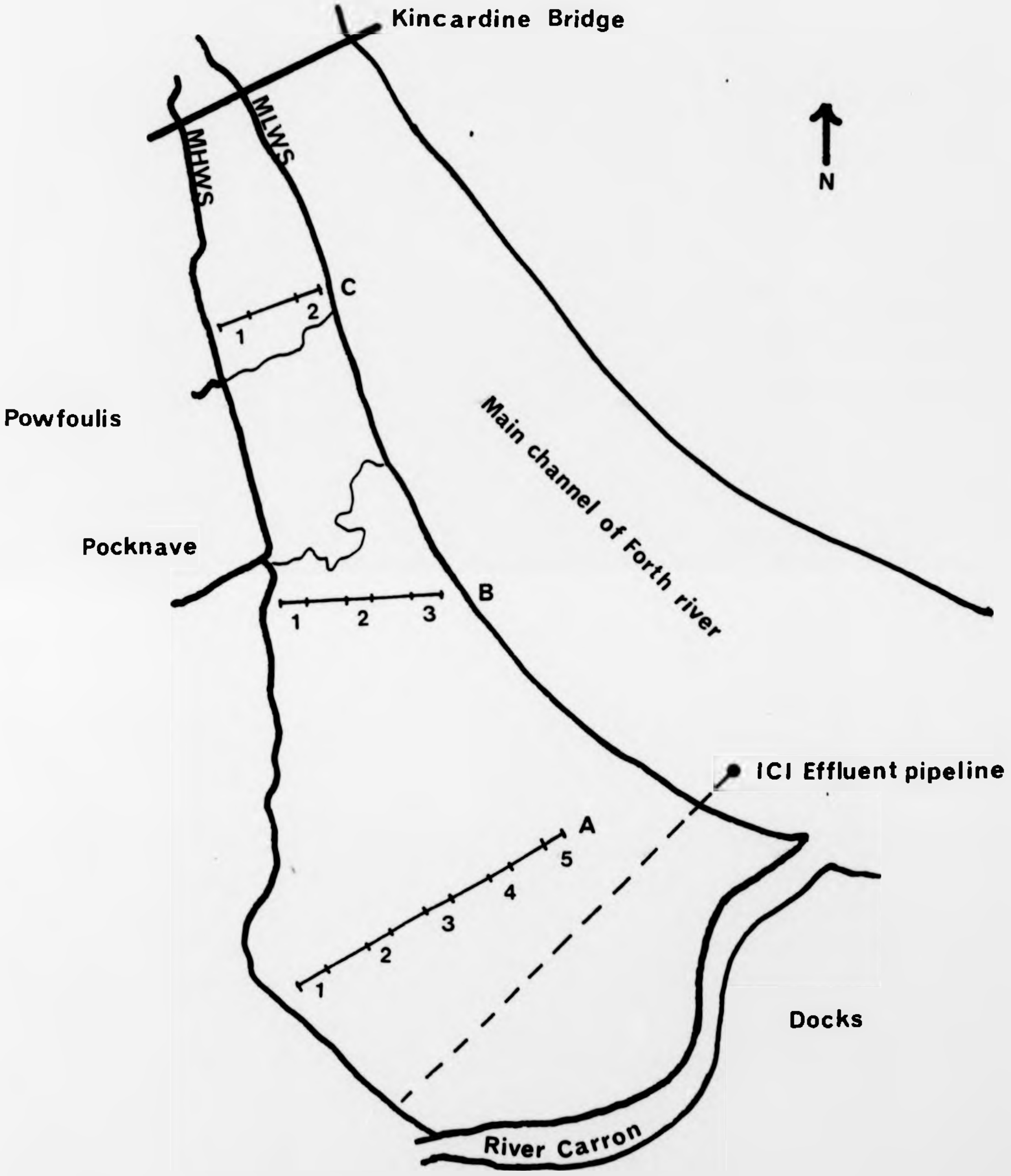


FIGURE 2.1: The study area and sampling sites, Skinflats

In addition to this invertebrate sampling programme, monthly samples of sediment were collected for water content, interstitial salinity and organic carbon and nitrogen analysis. At the mid-point of each station small amounts of surface sediment were scraped into two plastic containers and sealed for water content and carbon and nitrogen analysis. A 5 x 5 x 5 cm core was also taken and sealed in a plastic bag for interstitial salinity determination. In the laboratory, the sample for water content was weighed and then dried to constant weight at 60°C. It was then ground with a mortar and pestle and stored at 60°C for carbon and nitrogen analysis. The sample taken to determine interstitial salinity was centrifuged in a Sorvall Superspeed RC2-B Automatic Refrigerated Centrifuge to extract the interstitial water which was subsequently analysed.

A 5 x 5 x 5 cm sample was taken at each station in March 1976 for particle-size analysis.

A less intensive sampling programme for the study of those invertebrates dwelling deeper than 5 cm in the substrate was also carried out. Three samples 10 x 10 x 10 cm were taken at the mid-point of each sampling station on six occasions during the study period. Since polychaete burrows can extend to 30 cm deep (Goss-Custard 1973, Muus 1967), only that portion of their populations dwelling in the top 10 cm were studied. This was unavoidable owing to the hard nature of the substrate and the practical difficulties associated with dealing with large quantities of mud. It was not possible to sieve samples in the field. However, the sampling method was considered adequate for studying populations of <u>Macoma</u>. The samples were placed in separate plastic bags and then sieved over a 500 μ mesh sieve in the laboratory. The animals sorted were stored in a 4% saline formalin solution as described/

described for the small samples.

Samples were taken in November 1977 and January 1978 to investigate the depth distribution of invertebrates and their availability to wading birds and Shelduck. On each occasion three 10 x 10 x 10 cm samples were taken at station A_2 and each divided into 4 depth zone sections in the field: top 1 cm; 1 - 4 cm; 4 - 7 cm; 7 - 10 cm. In the laboratory these were sieved over a 300 µm sieve and the animals sorted and preserved as described above.

2.2 Monitoring of Environmental Factors

2.2.1 Particle-size analysis

Sediments have often been classified descriptively (eg Boyden and Little 1973, Warwick and Davis 1977) but a more general method, involving a classification based on the frequency distribution of grain sizes in sediments, offers greater precision. Whilst it is acknowledged that, as with all mud sampling, the mechanical analysis of sediment disruptively removes samples from the field and destroys the environment in which invertebrates dwell (Carriker 1967: in Lauff 1967), such analysis enables sediments from different localities to be compared and is thus of value in studies of invertebrate populations.

Samples brought in from the field for analysis were initially placed in distilled water and gently stirred to remove the salt which would interfere with the final weights of the finer sediment fractions. When settled the water was decanted and the procedure repeated. The samples were then wet-sieved over a 63 µm sieve to separate the silt and clay fractions from the larger sand fraction (after Elliott 1979). Each fraction was covered and dried for 2 days at 105°C and then the fraction retained on the 63 µm sieve was transferred to a nest of

Endecott/

Endecott (20 cm) sieves of 5.6 mm, 2 mm, 1 mm, 500 µm, 250 µm, 125 µm, and 63 µm mesh sizes. These were shaken on an Endecott model EFL1 test sieve shaker for 15 minutes, after which no more sediment passed through the sieves. Each fraction was then weighed and any material that had passed through the 63 µm sieve added to that previously collected.

Separation of the silt and clay fraction proceeded by pipette analysis as described by Buchanan (1971), with modifications: instead of standing the columns of suspended sediment in a constant temperature water-bath, settling rates were calculated for ambient temperature (Elliott 1979). The recalculated settling velocities are given in Appendix 1.

The classification of particles given in the above method conform to the Wentworth scale but were also transformed to a Phi (ϕ) scale:

$$\phi = -\log_2 \text{ particle size diameter (mm)}$$

This was devised by Krumbein (1939) and from the transformation cumulative frequency curves of particles can be drawn. Thus the results are amenable to statistical treatment as discussed by Buchanan (1971) and Green (1968).

2.2.2 Carbon and nitrogen analysis of sediment surface

Measurement of either organic carbon or nitrogen content of a sediment gives an indication of the amount of food available to deposit-feeding organisms (eg Elliott 1979, Newell 1965, 1970). Determination of these components can involve lengthy procedures such as loss on ignition (Ball 1964) or wet oxidation methods for carbon (Hughes 1969) and the micro-Kjeldahl method for nitrogen which uses lengthy/

lengthy digestion processes (Longbottom 1970, Newell 1965). More recently, CHN Elemental Analysers have been employed (eg Ansell 1974, Elliott 1979). These enable C, N and H content of sediments to be determined quickly and accurately by detecting and measuring their combustion products (CO_2, N_2 and H_2O). Combustion occurs in pure oxygen and the products of combustion are then analysed automatically in a "self-integrating, steady-state, thermal conductivity analyser". The model available in this study was a Perkin-Elmer 240 model CHN Elemental Analyser and results of the analysis were shown on a chart recorder.

Two samples from each station were analysed monthly for the period January - June 1976.

2.2.3 Water content of the sediment surface

The two sediment samples from each station between January and December 1976 were weighed on collection and dried to constant weight at 60°C.

2.2.4 Interstitial salinity measurement

Interstitial salinity measurements were made by following the procedure given by McLusky (1971). Silver nitrate solution (27.25 gl^{-1}) was titrated against 2 ml subsamples of water from each station every month between January 1976 and June 1977. Potassium dichromate (8% solution) was used as an indicator. Each burette reading was multiplied by an appropriate factor to give salinity in parts per thousand ($^{o}/oo$).

2.3 Body Measurements, Dry Weight Determination and Methods for Estimating the Production of Invertebrates

2.3.1 Body measurements

Linear/

2.3.1 Body Measurements

Linear measurements of all animals have been used throughout this study:-

(a) Hydrobia - Shell height (mm)

(b) Macoma - Shell height and shell length (mm).

Both measurements were used since it is conventional to measure height for growth studies and length for determining the sizes of bivalves taken by wading birds. Thus comparison between studies in both fields was possible.

(c) Cardium - Shell lengths (mm) were measured for comparison with those in the diets of waders.

(d) Nereis - Body contraction, caused by preservation, and body damage resulting from sampling and sieving prevented the determination of the body length of Nereis. Instead body weight was estimated from the regression of body weight (mg) on jaw length (mm) calculated by Chambers and Milne (1975b), the jaws being dissected from the worms and measured as described in Section 2.4.4.

(e) Corophium - The body length (mm) of Corophium, excluding the antennae was measured.

(f) Small worms - The body lengths of small worms were not determined.

2.3.2 Dry Weight and length-weight determination

Hydrobia

Production studies require measurements of biomass to be made and, since only the shell heights of Hydrobia were taken in the monthly samples, it was necessary to establish a length-weight regression equation each month for subsequent biomass and/

and growth determination.

Initially, an experiment to establish the time required for whole animals to reach a constant dry weight in an oven of 60°C was conducted. Five snails of each of the following size-classes were dried to constant weight: 1 - 2 mm, 2.1 - 2.5 mm, 2.6 - 3 mm, 3.1 - 3.5 mm, 3.6 - 4 mm, 4.1 + mm. Every twelve hours the snails were transferred to a dessicator and each class was then weighed. Constant weight for all size-classes was reached at 120 h (Fig 2.2) and thus all subsequent dry weight determinations of Hydrobia involved drying snails for 120 hrs at 60°C.

The units of biomass are in g ash-free dry weight (AFDW) and this refers to organic matter rather than total weight including the shells of molluscs. Snails of known total dry weight were placed in a muffle furnace for 6 h at 450°C to burn off all the organic matter. Subtracting the weight of the remaining ash from the total dry weight gave the AFDW.

This method was chosen in preference to dilute hydrochloric acid and decalcifying agents which dissolve away the shells since the effects of these substances on the flesh is unknown.

Length : ash-free dry weight conversions were established each month by plotting the AFDW of 55 snails (30 from transect A, 15 from transect B and 10 from transect C) against their lengths. The regression equation,

$$W = al^b$$

where w = AFDW
l = shell height
a = a constant
b = exponent

was/

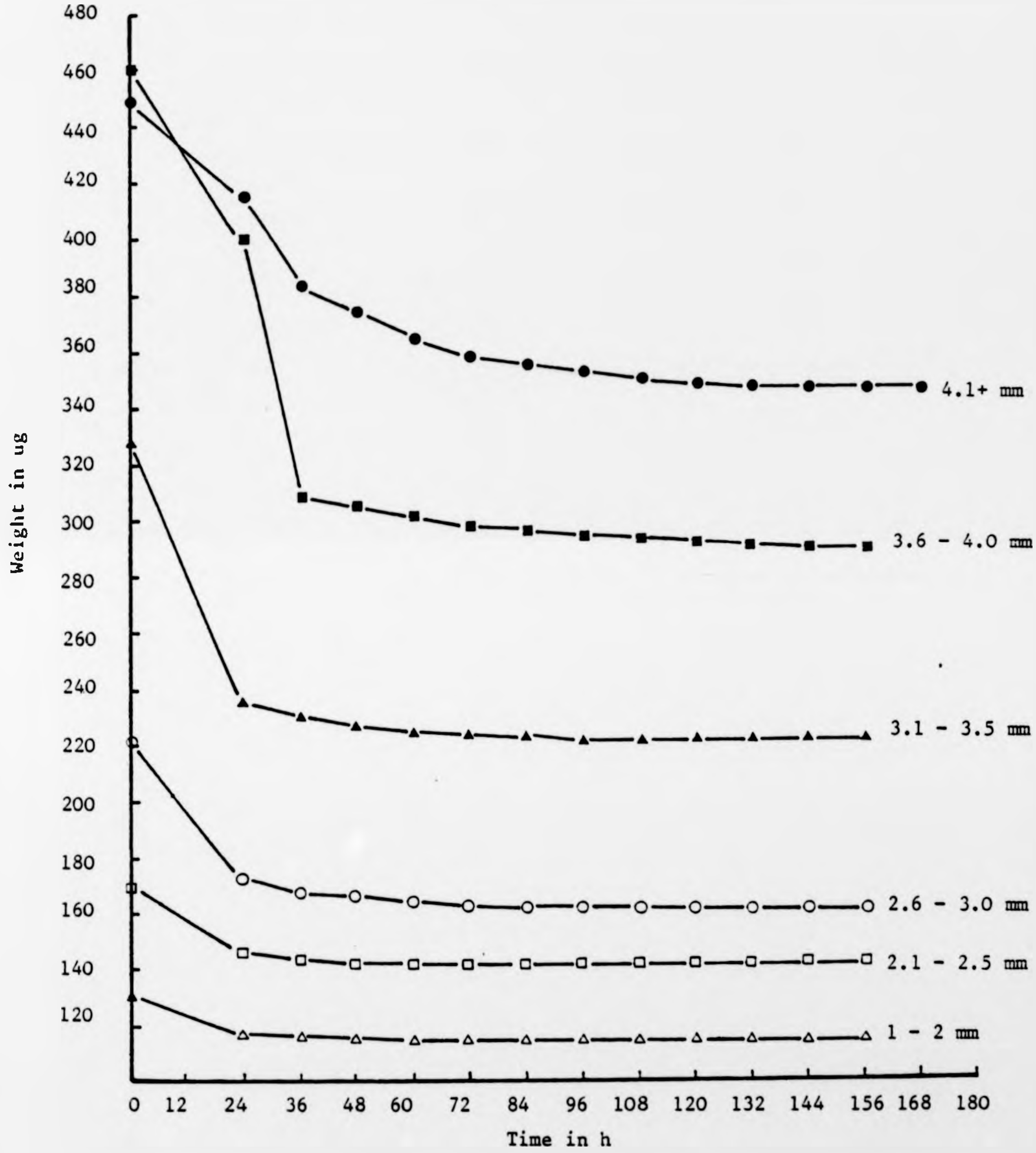


FIGURE 2.2: The time required for each of six size-classes of Hydrobia to reach constant dry weight at 60°C

was then applied to each plot for use in mean weight and biomass determinations.

Macoma and other invertebrates

Dry weights (AFDW) of Macoma of known size were determined by drying the opened shells at 60°C to constant weight to obtain total dry weight and then ashing the animals at 450°C for 6 hours in a muffle furnace and weighing the ash. Subtraction of ash weight from total dry weight gave the AFDW (µg). Length-weight regressions were constructed from these data.

Dry flesh weights of Nereis and Corophium were obtained by drying the animals at 60°C to constant weight. Thus total dry weights (µg) only were obtained for these species. Dry weight determinations of Cardium, oligochaetes and small polychaetes were not made.

2.3.3 Methods for estimating the production of invertebrates

Hydrobia

For a full computation of the production of Hydrobia, growth and mortality estimates were required.

Growth Measurements

Growth was determined in terms of the increase in the mean weight (µg) of each cohort per unit time (months). This method does not refer to an individual's growth but to the growth of the population under study. Thus differential mortality and addition of individuals into the population will influence the mean weight as will variations in the growth rates of individuals constituting the population.

Mortality/

Mortality measurements

The mortality (M) of each cohort of Hydrobia was monitored over one year (July 1976 - June 1977) so that the effects of predation by overwintering birds could be quantified. Mortality included losses from all causes including any emigration which could not be monitored. It was calculated both as (1) change in density between sampling occasions and as (2) the product of mean cohort individual weight ($\bar{w}$) and change in cohort density (N) between each sampling occasion (after Crisp 1971). Thus for (2)

$$M = \sum \bar{w}\Delta N$$

where $\bar{w}$ = mean weight of individuals in the cohort

and ΔN = change in cohort density

Production

In the present study production (P) refers only to that production due to somatic growth (ie the term Pg in Crisp 1971) and does not include production due to reproduction. Estimation of P involves the summation of monthly growth increments of each cohort derived from Allen's (1950) graphical method, as described in Crisp (1971). Crisp's method 2 for calculating production with age classes separable was followed for Hydrobia and Macoma. The methods described in Crisp (1971) were also followed for the other study species but involved the use of published P:B ratios.

For Hydrobia and Macoma the production of each cohort during each sampling period (ΔP) was calculated as the product of the mean cohort density over that period and the change in mean cohort weight ($\Delta\bar{w}$) over the period. Thus:-

ΔP/

$\Delta P = \frac{1}{2}(N_t + N_{t+\Delta t}) . \Delta\bar{\bar{w}}$ (Crisp 1971)

where $\frac{1}{2}(N_t + N_{t+\Delta t})$ = Average value of density (N) of cohort over that period

$\bar{w}$ = mean cohort weight

t = time

The total production was estimated as the summation of all values of ΔP during the study period. Production was expressed in gm^{-2} and, where published data were available, in kcals m^{-2} (kJm^{-2}). Calorific equivalents of Hydrobia flesh weight could not be measured since it could not physically be removed from the shell. The effects of acid treatment and decalcifying agents on calorific values are unknown (Chambers and Milne 1979) and determinations would thus have been subject to unquantifiable error.

2.4 Shorebird Diets

The methods for identifying and quantifying the diet of shorebirds and Shelduck at Skinflats and at other sites on the Forth Estuary included:

(a) Field observations of the prey species taken and feeding rates when possible
(b) Pellet collection and analysis of prey fragments therein
(c) Gut analysis of birds (shot under licence from NCC)
(d) Determination of the size of items in the diet of each species

2.4.1 Field observations

Observations to determine the feeding methods and food items taken by wading birds were made during 1977/8 winter at Skinflats/

Skinflats and between January and March 1980 at other sites on the estuarine Firth of Forth (Fig 1.1). The optical instruments used were Leitz 10 x 40 binoculars and a 25 - 40 magnification telescope. Feeding rates were determined by recording the time (s) for an individual to ingest a known number (5 - 10) of prey items. ~~The size of worms taken by Redshank was estimated by comparing them with the length of the bird's bill. Bill length was derived from Prater et al (1977)~~.

On each occasion air temperature, wind speed and direction, cloud cover and precipitation were recorded.

2.4.2 Pellet analysis

Pellets of Redshank, Knot and Dunlin were collected at species' specific roosting areas at Skinflats during the winter of 1977/78, Oystercatcher and Curlew pellets from roost-sites in other areas of the Forth Estuary early in 1980. Prey fragments were identified under a binocular microscope and the following counted in addition to whole animals present: _H. ulvae_ terminal whorls, the jaws of _Nereis_, _Macoma_ hinge fragments, _Littorina_ and _Buccinum_ operculae and _Cerastoderma_ 'feet'.

2.4.3 Gut analysis

Small samples (max. 5 birds) were shot under licence from the NCC during January - March 1980. In addition, samples of Redshank and Dunlin were shot under licence during 1975/76 winter. When possible, the birds were collected on the feeding grounds and 10 ml of formalim was injected into the oesophagus within three minutes of collection. Within one hour the entire gut was removed, opened and deep frozen for subsequent examination. The oesophagus and gizzard contents were examined/

examined under a binocular microscope and stored in 4% formo-saline solution.

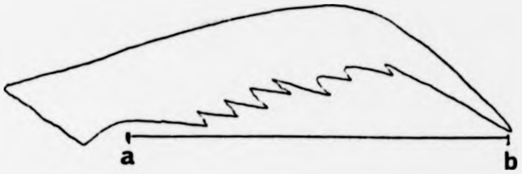
2.4.4 Size of items in the diet

The size of Nereis, Macoma and Carcinus could be determined from the measurements of certain fragments remaining in the guts and pellets:

Nereis:

Body length mm = 48.417 x jaw length $^{1.5674}$ mm

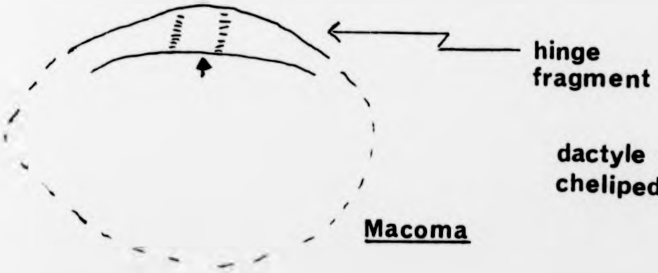
(Chambers and Milne 1975b)

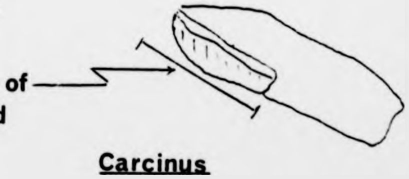


Measurements (a - b) were made taking care to include only those jaws which were unbroken at the tip (b).

Macoma:

Measurements of the thickness of the shell (mm) at the hinge were made, between the arrows. These were related to shell length from data collected on the Ythan (Goss-Custard unpubl.).





Carcinus:

Measurements of dactyle length (mm) were taken although a relationship between this and body length was not established.

The/

The width across the carapace (mm) was also measured if available (a - b).

2.5 Determination of the Factors Influencing the Feeding Density of Redshank, Knot, Dunlin and Shelduck

2.5.1 Field observations

Whenever daylight and visibility permitted observations were carried out to determine the feeding distribution and density of Redshank, Knot, Dunlin and Shelduck at Skinflats between November 1976 and March 1977. Owing to the large size of the area, three consecutive days were required to locate all flocks. Previous studies on feeding intensity (Bryant 1976, Bryant and Leng 1975, Moffat 1975) have shown a consistent daily pattern of feeding ground usage by all four species over a spring or a neap tide period. Thus the three-day observation sequence was considered more accurate than attempts to count and position distant flocks on a single day.

Observations over neap tidal cycles began at the predicted time of high water (HMSO Tide Tables, Rosyth times + 20 mins) and continued until the tide had completely receded from the mudflat, when a stable low-water dispersion pattern and bird density was established (Bryant 1978). On spring tides, observations began at least four hours before the predicted high water time and continued until all birds had ceased feeding which usually coincided with complete submersion of the mudflat. Unfortunately/

Unfortunately, the tidal regime and daylight combinations did not permit observations to be carried out on the ebb-tide of spring tides or the flow-tide of neap tides.

On each day the air temperature was measured and the wind direction and speed (Beaufort Scale) estimated. Cloud cover (in eights of the visible sky) and precipitation were noted together with any frost or snow cover on either the fields or mudflat.

Counts of all species were made every 0.5 h using predicted HT or LT as a reference. The flocks of each species were counted sequentially, Knot and Dunlin to the nearest 50 birds per flock, Redshank individually or to the nearest 10 birds and Shelduck individually. Flocks were accurately positioned by reference to landmarks and mudflat features such as transect marker-posts and drawn on field maps (photocopies of 1:25000 OS Map).

2.5.2 Analysis of field maps

Field maps were overlain by a transparency of a 1:25000 scale OS map divided into 0.2 km squares by reference to the National 1 km Grid System. Each square was identified by a letter and number (Fig 2.3). Data from field maps on the three consecutive days for the same 0.5 h period were pooled. The squares in which a flock occupied at least 0.125 of the area were recorded and the proportion of the flock in each square estimated to the nearest 0.25 bird 0.5 h^{-1}. When flocks of the same species from consecutive days overlapped on the grid maps, a mean value for each square occupied by the flocks was taken.

A map for each species, for each 0.5 hr of the study section of the tide was thus prepared for each three day observation period. Comparisons/

SKINFLATS

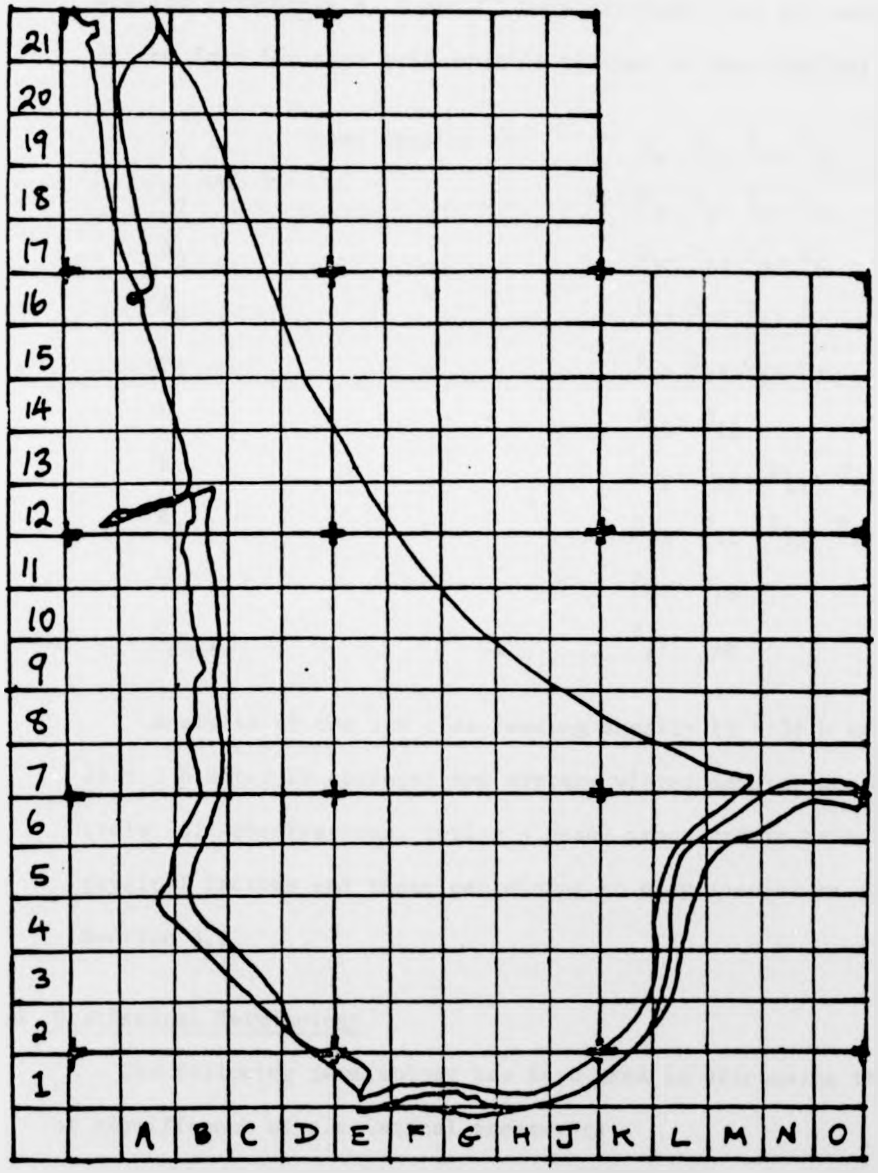


FIGURE 2.3: Grid maps used for recording bird density (Scale 1:25000)

Comparisons of the density of birds between species could be made for a particular stage of the tide and each 0.5 hr summed to give an estimate of the density over a tidal cycle. Extrapolations were required from data over the low water period for this and the ebb and flow dispersion patterns were assumed symmetrical (Bryant 1978a).

The mean value of feeding density of birds at each main sampling station (transects A, B and C) were obtained from the mean density in the four (or two) grid squares closest to the station:

A_1	Mean density of	C_4, C_5, D_4, D_5
A_2		D_4, D_5, E_4, E_5
A_3		D_5, D_6, E_5, E_6
A_4		E_6, E_7, F_6, F_7
A_5		F_6, F_7, G_6, G_7
B_1		B_{11}, B_{12}
B_2		C_{11}, C_{12}, D_{11}, D_{12}
B_3		D_{11}, D_{12}, E_{11}, E_{12}
C_1		A_{17}, A_{18}
C_2		B_{17}, B_{18}

Analysis of the low tide feeding density (3 - 3½ h after HT neaps, 2½ - 3 h after LT springs) and average winter density per 0.5 tide cycle (all observations, spring + neap) proceeded in relation to physical factors and those pertaining to prey species as described in Section 3.6.

2.6 Statistical Terminology

The following terminology has been used in discussing the levels of significance of statistical treatments.

Level/

Level of Significance	Name	Symbol
$> 5\%$	Not significant	ns
$\leqslant 5 > 1\%$	Significant	*
$\leqslant 1 > 0.1\%$	Very significant	**
$< 0.1\%$	Highly significant	***

3 RESULTS

3.1 The Principal Study Area

The 3.82 km^2 area of intertidal mudflat known as Skinflats is bounded to the south by the retraining wall of the River Carron and to the north by Kincardine Bridge (Fig 2.1). The area mainly lies above the mid-tide level, the outer edge dropping steeply to the main channel of the River Forth in the northern section. Two fresh-water outflows meander across the mudflat: at Pocknave and Powfoulis, and the area is dissected by several intertidal creeks. Saltmarsh forms the landward boundary of the mudflat, varying in width according to the position of the sea wall, which protects the low-lying, reclaimed, agricultural land beyond. An I.C.I. Chemicals Division industrial effluent pipeline lies beneath the area, discharging into the main river channel. Disturbance to the mudflat caused by its construction in 1972-3 is still in evidence.

3.2 Monitoring of Environmental Factors

3.2.1 Particle size analysis

The results are shown in Fig 3.2.1 and Table 3.2.1 (data in appendix 2).

In order to classify the sediments according to their median particle diameters (m.p.d.) the following notation was used (after Wolff 1973 with modifications).

m.p.d. between		name
phi units	µm	
0 - 1	500 - 1000	coarse sand
1 - 2	250 - 500	medium sand
2 - 3	125 - 250	fine sand
3 - 4	63 - 125	muddy sand
> 4	< 63	mud

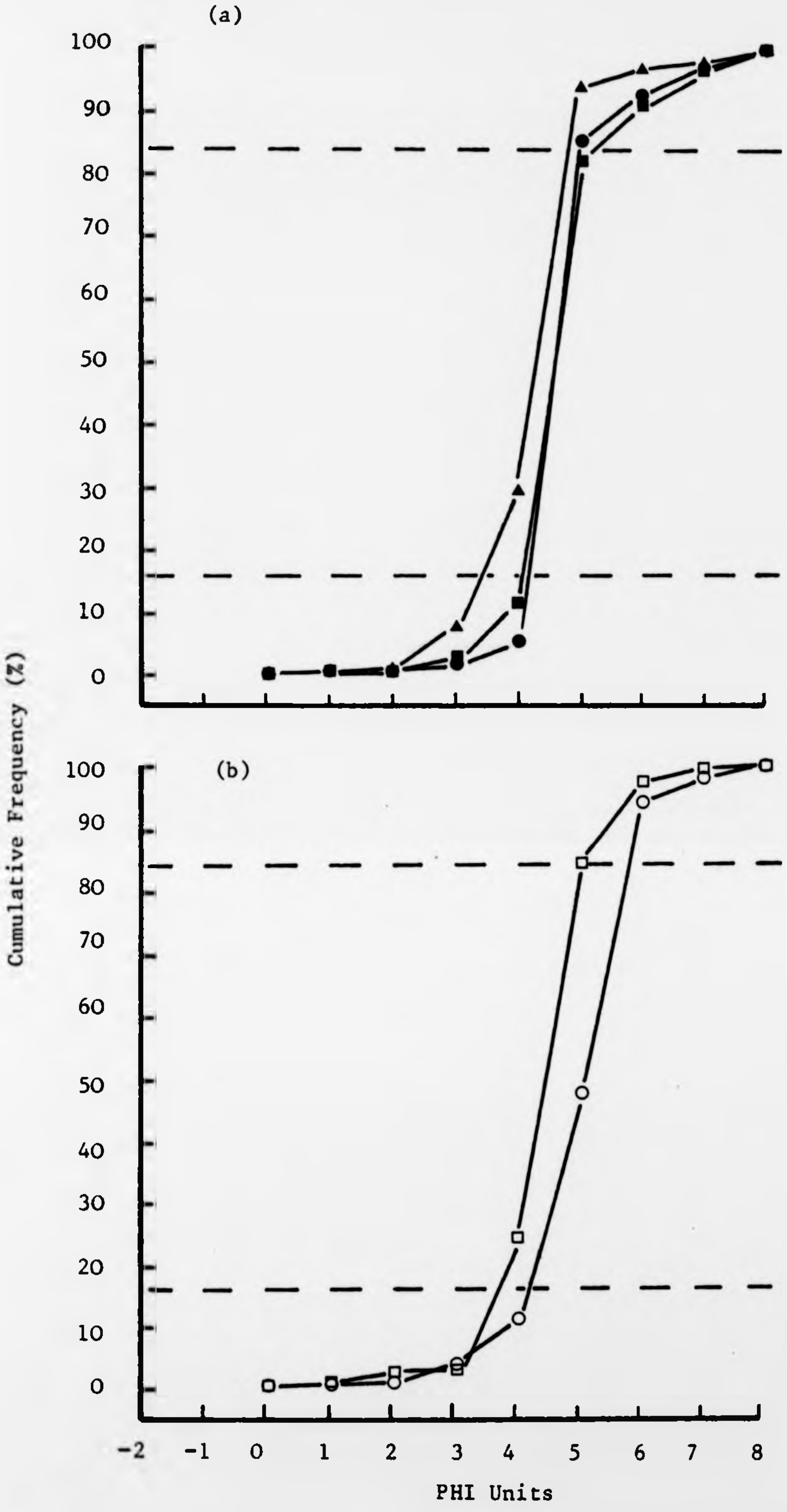


FIGURE 3.2.1: Sediment particle size analysis: Cumulative Phi Curves

(a) $A_1 - A_3$ (b) $A_4 - A_5$. A_1 ● , A_2 ■ , A_3 ▲ , A_4 ○ , A_5 □

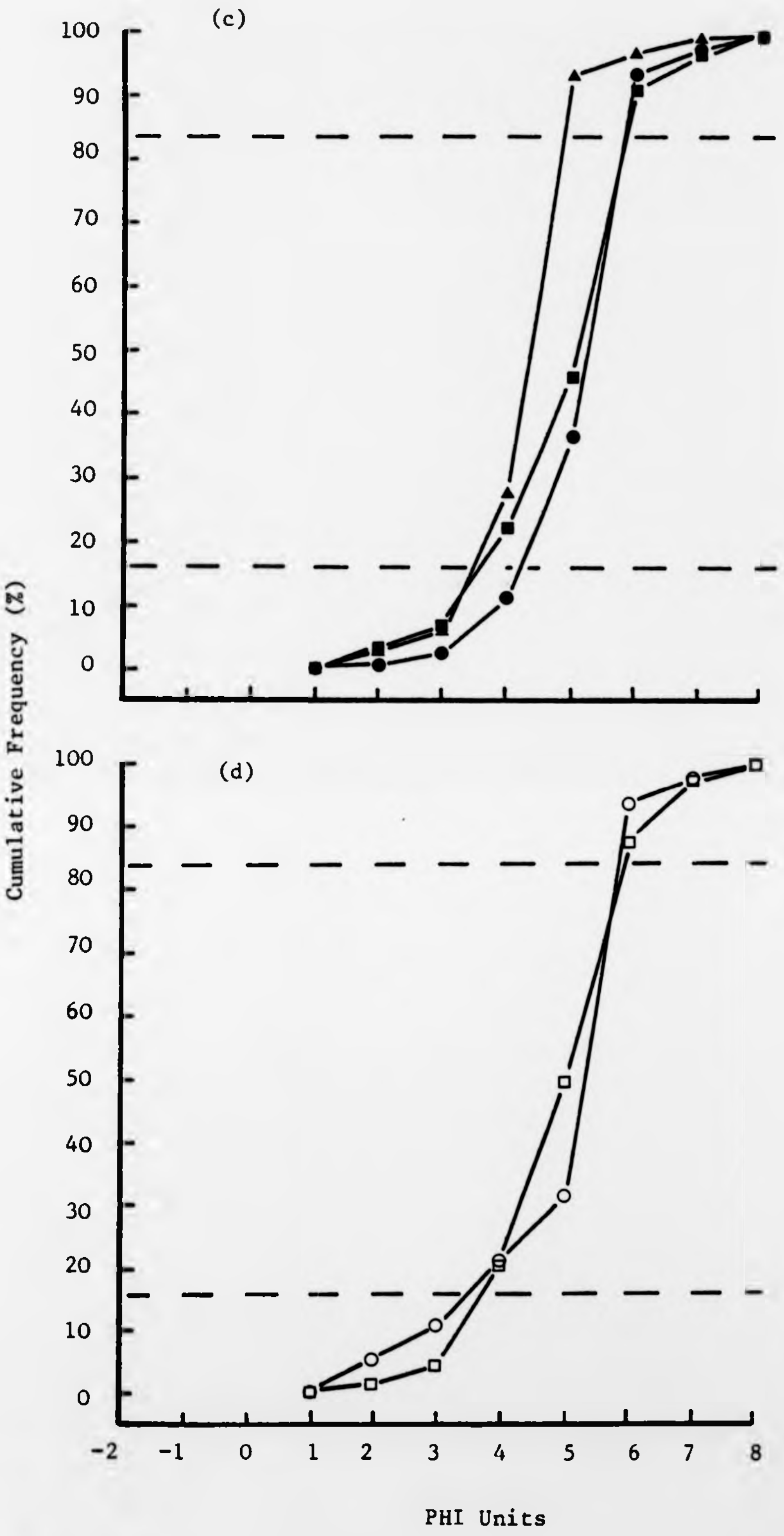


FIGURE 3.2.1 (continued): (c) Transect B; B_1 ●, B_2 ■, B_3 ▲,
(d) Transect C; C1 ○, C2 □

TABLE 3.2.1: Summary of sediment characteristics and tidal height of each sampling station

	A_1	A_2	A_3	A_4	A_5	B_1	B_2	B_3	C_1	C_2
m.p.d. Ø units	4.6	4.7	4.3	5.0	4.5	5.4	5.1	5.5	5.4	5.05
silt & clay fraction (% weight)	94.6	88.0	70.5	88.8	75.5	88.7	77.8	72.1	89.1	79.4
interstitial salinity (cI)	25.7	26.04	27.43	27.3	27.9	24.94	25.61	26.23	25.84	25.21
surface water content (% weight)	48.9	51.3	53.7	53.7	51.5	50.3	63.9	55.5	48.3	54.6
carbon content (%)	3.76	3.93	2.54	2.23	3.39	3.85	3.24	2.73	4.42	3.1
nitrogen content (%)	0.19	0.19	0.16	0.13	0.19	0.24	0.20	0.15	0.25	0.17
C : N ratio	19.79	20.68	15.88	17.15	17.8	16.04	16.2	18.2	17.68	18.24
tidal height (m)	4.5	4.4	4.3	4.0	3.5	4.6	4.0	3.8	4.5	4.2
sorting coefficient	0.40	0.55	0.70	0.85	0.70	0.80	1.12	0.75	1.2	1.1

In addition, the sorting coefficient (G) of the sediments was determined using the terminology of Folk (1966) and Wolff (1973). The sorting coefficient enables the degree of sorting to be estimated and is obtained from the phi-curves, assuming the particles follow a normal size distribution. The distance between the places where the phi-curve crosses the values of 16% and of 84% is approximately equal to twice the standard deviation and thus half this value constitutes a measure for the sorting of a sediment. The nomenclature used is as follows (Folk 1966 in Wolff 1973):-

Sorting coefficient (phi units)	Name
< 0.35	very well sorted
0.35 - 0.50	well sorted
0.50 - 2.00	less well sorted
> 2.00	poorly sorted

The sediments at Skinflats were all classified from the m.p.d. as muds with a high percentage of silt and clay (greater than 70% at all sites) (Table 3.2.1). The degree of sorting ranged from well- to less-well-sorted and the highest values of G were found at B_2 and on transect C. Station A_1 had the only well sorted sediment (0.4 ϕ units).

3.2.2 Carbon and nitrogen analysis

During the six month period of analysis no patterns emerged for the percentage of carbon or of nitrogen present in the sediments. (Data in appendix 3). The mean percentage carbon over this period ranged from 2.23% at A_4 to 3.93% at A_2, that of nitrogen from 0.13% at A_4 to 0.25% at C_1 (Table 3.2.1). The data gave a range of C:N values of 16.04 at B_1 to 20.68 at A_2.

3.2.3 Water content of the sediment

The mean annual sediment water content ranged from 48.9 - 63.9% by weight (Table 3.2..). The seasonal variation (Fig 3.2.2) was greatest at C_1 which remained exposed for the longest periods and was thus most susceptible to drying in the summer months (Fig 3.2.2d). Station A_5 also showed a low water content in the summer months due, not to exposure time, but most likely to the very firm substrate which was covered by only a shallow layer of soft sediment (Fig 3.2.2b). Other stations did not exhibit marked seasonal fluctuations in sediment water content.

3.2.4 Interstitial salinity

There was little variation in interstitial salinity between stations but seasonal trends, with high values in June and low values in February, were detected at all sites (Fig 3.2.3). Salinities were lower in February 1977 than in the previous February.

3.2.5 Spatial interactions between environmental factors

Correlation Analysis was carried out for all environmental variables from the data presented in Table 3.2.1 and the results are shown in Figure 3.2.4.

A significant positive correlation was shown between m.p.d. and the sorting coefficient (r = +0.5658*) and a negative relationship between m.p.d. and interstitial salinity (r = -0.5897*). This indicated that the coarser sediments within the narrow range of muds experienced were better sorted and contained water with a higher interstitial salinity.

Significant/

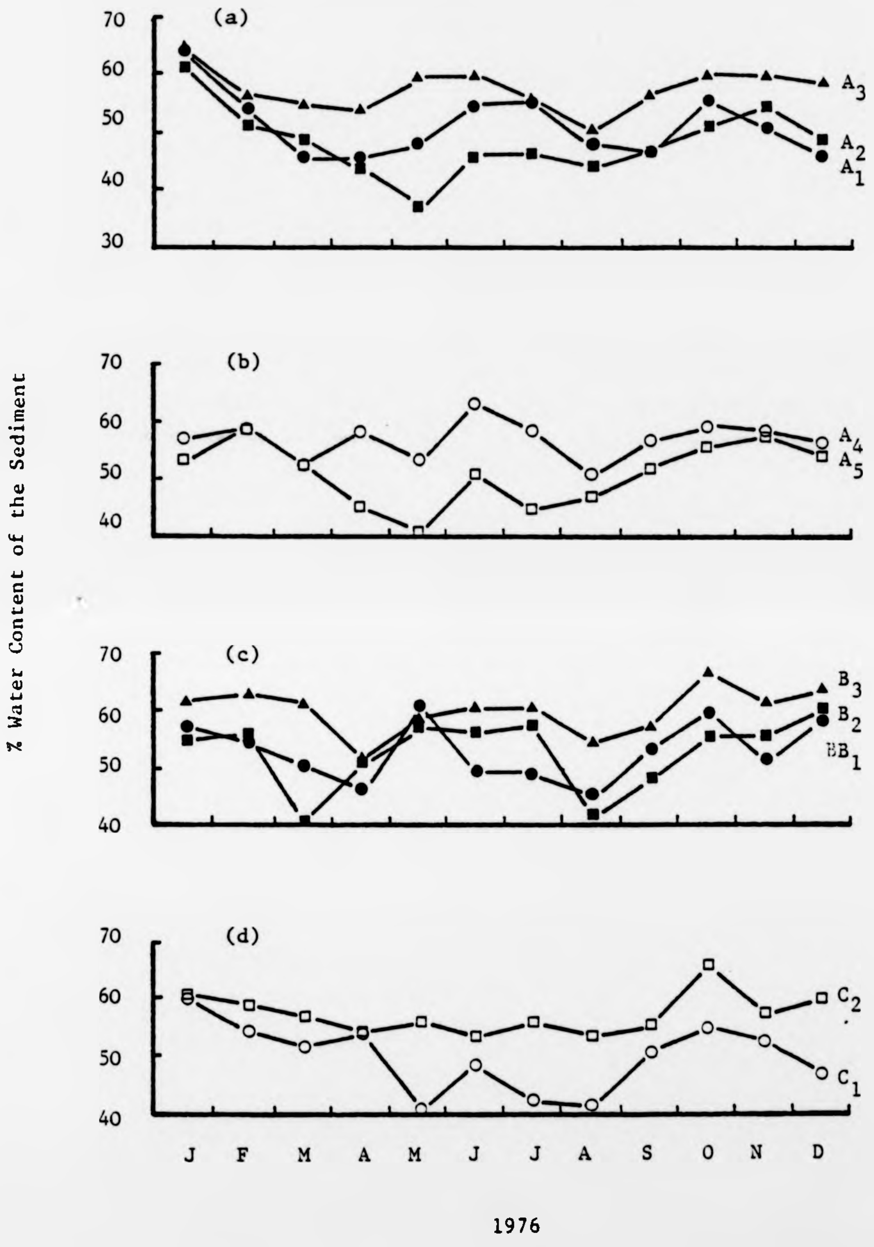


FIGURE 3.2.2: Water content (%) of the surface layer of the sediment at each sampling station.

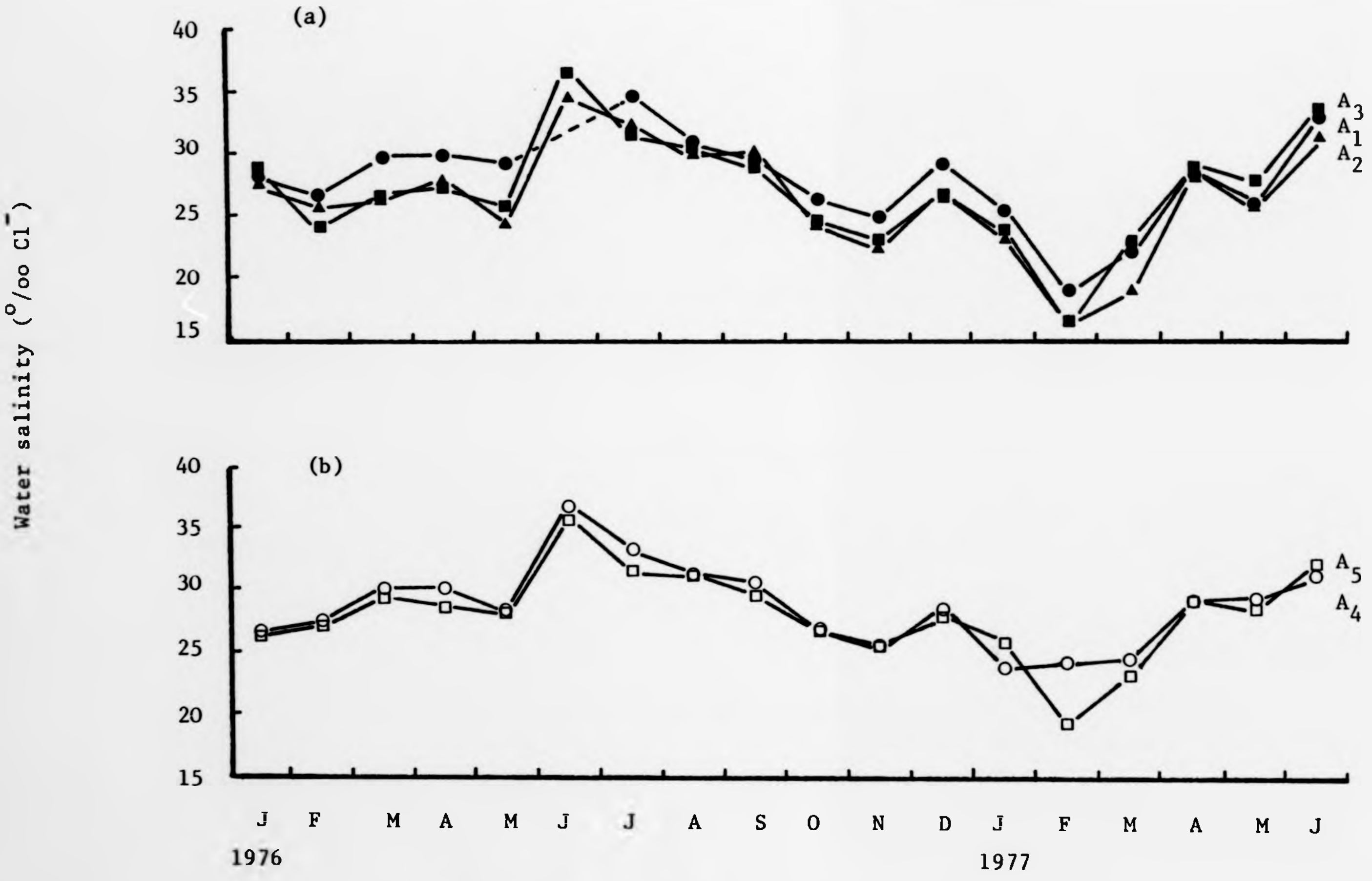


FIGURE 3.2.3: Mean interstitial salinities at each sampling station January 1976 - June 1977 (a) A_1 - A_3 (b) A_4 - A_5

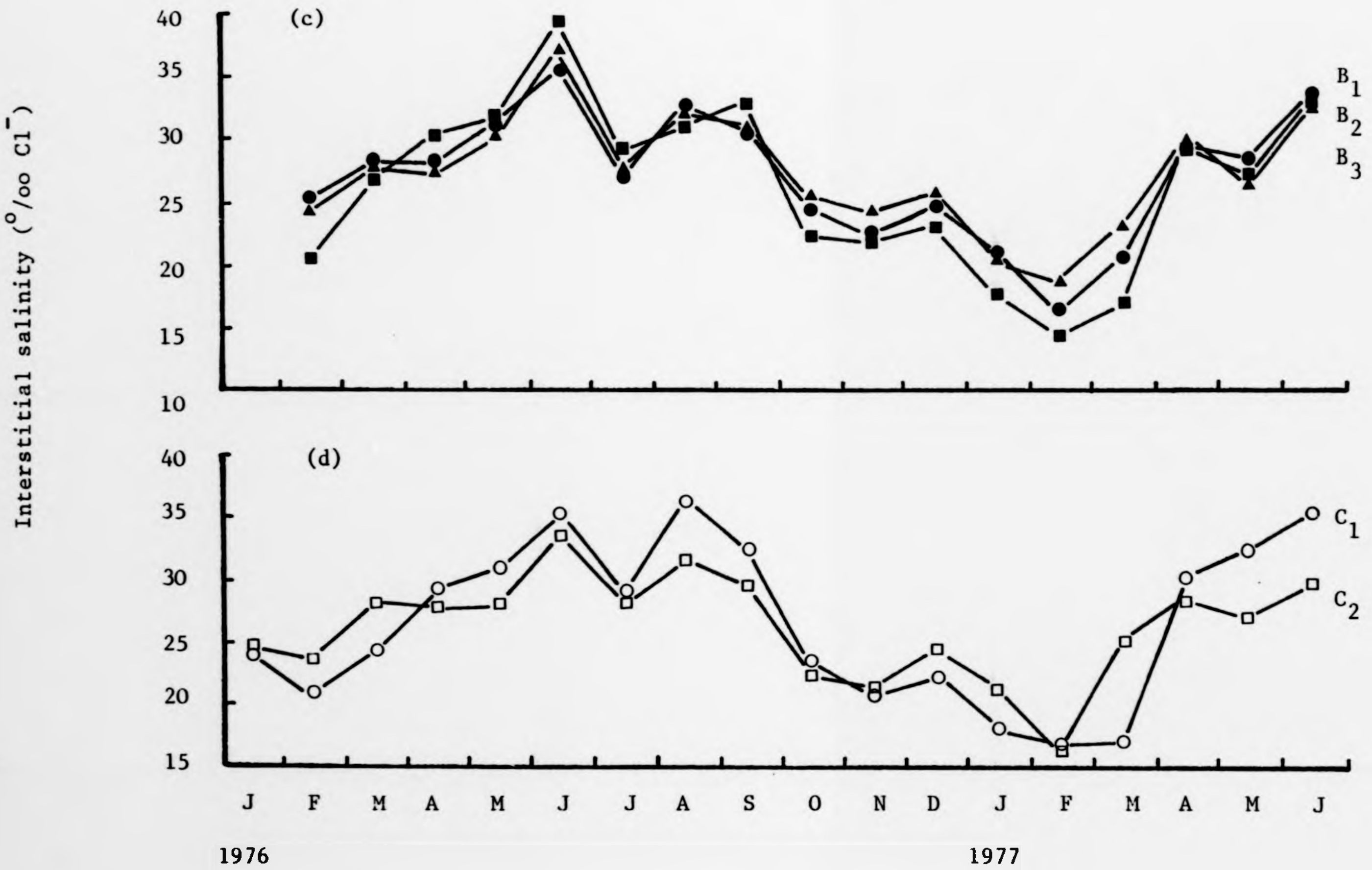


FIGURE 3.2.3 (continued): (c) Transect B (d) Transect C

FIG 3.2.4: Spacial interactions between environmental factors - Pearson correlation matrix

	m.p.d. Ø	sorting coeff. (G)	silt & clay fraction (%)	interstitial salinity	water content of surface (% wt)	carbon content (%)	nitrogen content (%)	C : N ratio	tidal height (m)
m.p.d. Ø		+0.5658 *	+0.1496 NS	-0.5897 *	+0.1166 NS	+0.1904 NS	+0.3120 NS	-0.1733 NS	+0.1147 NS
sorting coefficient (G)			-0.1682 NS	-0.2740 NS	+0.3973 NS	+0.4143 NS	-0.2733 NS	-0.4921 NS	-0.4974 NS
silt and clay fraction (%)			-	-0.4170 NS	-0.5414 NS	+0.5480 *	+0.3961 NS	+0.4135 NS	+0.6300 *
interstitial salinity				-	-0.0369 NS	-0.5146 NS	-0.5191 NS	-0.1234 NS	-0.6243 *
water content of surface (% wt)					-	-0.4899 NS	-0.3308 NS	-0.3977 NS	-0.4307 NS
carbon content (%)						-	+0.8994 ***	+0.3655 NS	+0.5222 NS
nitrogen content (%)							-	-0.0761 NS	+0.5092 NS
C : N ratio								-	+0.1049 NS
tidal height (m)									-

Significant, positive relationships were also found between the proportion of silt and clay in the sediment and both carbon content and tidal height (r = +0.5414*, r = +0.6300*), although carbon content and tidal height were not significantly related to each other. This indicates that sediments at higher beach levels contained higher proportions of silt and clay and that the carbon content was higher in these fine muds.

Tidal height was also negatively correlated with interstitial salinity (r = - 0.6243*) and the relationship between carbon and nitrogen was highly significant.

Further analysis of these relationships was not undertaken.

3.2.6 Discussion

The intertidal area known as Skinflats lies mainly above mid-tide level and the results presented showed that fine sediments, classified as muds (Wolff 1973) occurred at all sampling stations. These fine-grained deposits are characteristic of nearly horizontal tidal flats with low current velocities such as are often found in upper-estuarine areas (Postma 1957 in Wolff 1973). Fine deposits are usually more stable than coarse ones since they have smaller interstitial spaces (Green 1968) and contain a high percentage of water. The amounts of water contained in sediments at Skinflats are high (48.9 - 63.9%) compared with those sandy areas of Torry Bay (Elliott 1979) but are below the threshold level of 70% beyond which the deposit will become fluid and facilitate sediment transportation (Green 1975). They are thus considered stable, a feature of importance for the maintenance of communities of benthic invertebrates.

Sediments/

Sediments containing high levels of fine deposits generally have a high sorting coefficient (G) (Elliott 1979) due to decreasing tidal currents. Compared to the mud and sand areas of Torry Bay, G is high at Skinflats. The occurrence of the finest muds on transect C is most likely the result of oblique currents crossing the area near to high tide, when velocities are least. The accompanying low G values cannot be explained in the limits of this study, nor can the negative correlation between m.p.d. (Ø units) and interstitial salinity which indicates a lower salinity in finer deposits. However, the negative correlation between interstitial salinity and tidal height may result from seepage of fresh water from the salt-marsh drainage.

The percentage silt and clay in the sediment increases with tidal height as does the carbon content of the sediment. Since the percentage carbon and nitrogen content are highly significantly correlated, this indicates that the organic content of fine muds situated upshore is higher than in other sediments in the area. Although fine sediments do contain higher organic content (Zobell & Feltham 1938), enrichment due to the proximity to the saltmarsh may occur.

The C:N ratio indicates the nutritional value of the sediments to consumers (Mann 1972) but on the Forth there are large amounts of coal present in the sediments which will greatly influence the index. In coal-free sediments, C:N of ten or less indicates animal material greater than twenty, plant material (Rullier 1959, in Longbottom 1970) but a range of 15 - 40 is common where coal is present (Buchanan & Longbottom 1970). Values of/

of C:N at Skinflats fall in the lower end of this range, making results difficult to interpret. They are, however, higher than on sandy areas of Torry Bay (Elliott 1979) as expected in finer sediments with a larger area for bacterial attachment (Newell 1965, Zobell & Feltham 1938).

Interstitial salinities were higher than salinities of the water column in the main river channel (Forth River Purification Board annual reports) and levels were fairly constant throughout the year. This contrasts with the seasonal fluctuations in interstitial salinity found in sandy deposits of Torry Bay (Elliott 1979), consistent with the finding by Wolff (1973) that salinity fluctuates less in fine sediments. Thus animals dwelling in muds will be buffered from such fluctuations in sands.

In conclusion, it appears that the fine-grained stable deposits at Skinflats which result from slow water movements over the area largely influence the other physical factors studied as has been found at other localities (Elliott 1979, Pearson 1970, Wildish 1977).

3.3 The production ecology of Hydrobia ulvae

Hydrobia ulvae is common around the coats of Britain and North West Europe (Clay 1960a). It has also been recorded from the Minas Basin in Fundy Bay, Canada, (Tunnicliffe and Risk 1977) and from the White Sea (Kondratenkov 1972), although little detailed information on the extent of its geographical range is available (Clay loc. cit.).

Although found on a variety of substrata on shores around the British Isles, including intertidal muds and sands and saltmarsh,/

saltmarsh, *Hydrobia* appears to prefer muddy sediments, avoiding clean sands (Clay loc. cit.). Distribution on the shore is mainly in mid and upper-tidal levels and early workers have demonstrated a preference for quiet waters (Beanland 1940, Moore 1939, Spooner and Moore 1940, Smidt 1951). This aligns with the preference for fine muds since these are themselves associated with quiet (lentic) biotopes (Wolff 1973). It has further been suggested that *Hydrobia* is most abundant in fine sediments (Fenchel 1975b, Newell 1965), although high densities were found in the field on coarse substrates despite a demonstration of a preference for fine sediments in the laboratory (Barnes and Greenwood 1978). However, Newell (1962) found no preferences for fine sediments in the laboratory and Elliott (1979) concluded that, at Torry Bay, tidal height was more important than particle size in determining mean annual density.

Hydrobia can tolerate muds reduced in oxygen (Raymont 1949) and has been found in foetid muds and intertidal areas polluted by industrial waste (Blegvad 1932, Fraser 1932, Stopford 1951). However, at Kinneil mudflat on the Forth estuary, it is absent from an area 0.5 km radius from the industrial effluent outfall. Here mud temperatures are raised in addition to the effluent loading (McLusky 1979,'80).

The ultimate factor controlling the distribution of *Hydrobia* is salinity. In Danish fjords where there are no tidal influences *Hydrobia* can exist in areas with 10 - > 30‰ Cl$^-$ (Muus 1967). Of the four species of mud snail occurring in the fjords (*H. ulvae*, *H. ventrosa* (Montague), *H. neglecta* (Muus) and *Potamopyrgus jenkinsi* (Smith)), *H. ulvae* prefers the most saline conditions and areas/

areas with most water movement. However, in British intertidal zones tolerance to salinity fluctuations varies with locality (Newell 1964) possibly due to the existence of distinct biological races (McMillan 1948). There is only one record of H. ulvae coexisting with another species of mud snail in Britain (Bishop 1976) and thus the strong influences of competition in determining the distribution of mud snails seen in the Danish fjords (Fenchel 1975, 1976) do not generally apply in British estuaries.

Hydrobia is an abundant intertidal inhabitant of the Forth estuary, found on the south shore between Society Point and Airth and on the north shore between Queensferry and the Black Devon mouth. The highest densities have been recorded at Skinflats and Kinneil (McLusky 1974-80, McLusky, Elliott and Warnes 1978). It has also been recorded in the outer Firth of Forth, notably at Aberlady Bay where it provides food for Shelduck (Nicol 1935, Jenkins et al 1975).

3.3.1 Distribution and density

The results are presented in Fig 3.3.1 and Table 3.3.1.

Hydrobia was widely distributed at Skinflats occurring at all sampling stations during the study period. Only at C_1, in April and June 1977, were Hydrobia absent from the samples.

The mean density ranged from 20320 ± 27567 in July 1976 to 3160 ± 3459 in April 1977 but variation between stations was high as shown in the large standard deviations. There was a pattern in successive years of a high summer density following spatfall and a low winter density (Fig 3.3.1). In general, the densities throughout 1976 were higher than those in 1977 (appendix 4).

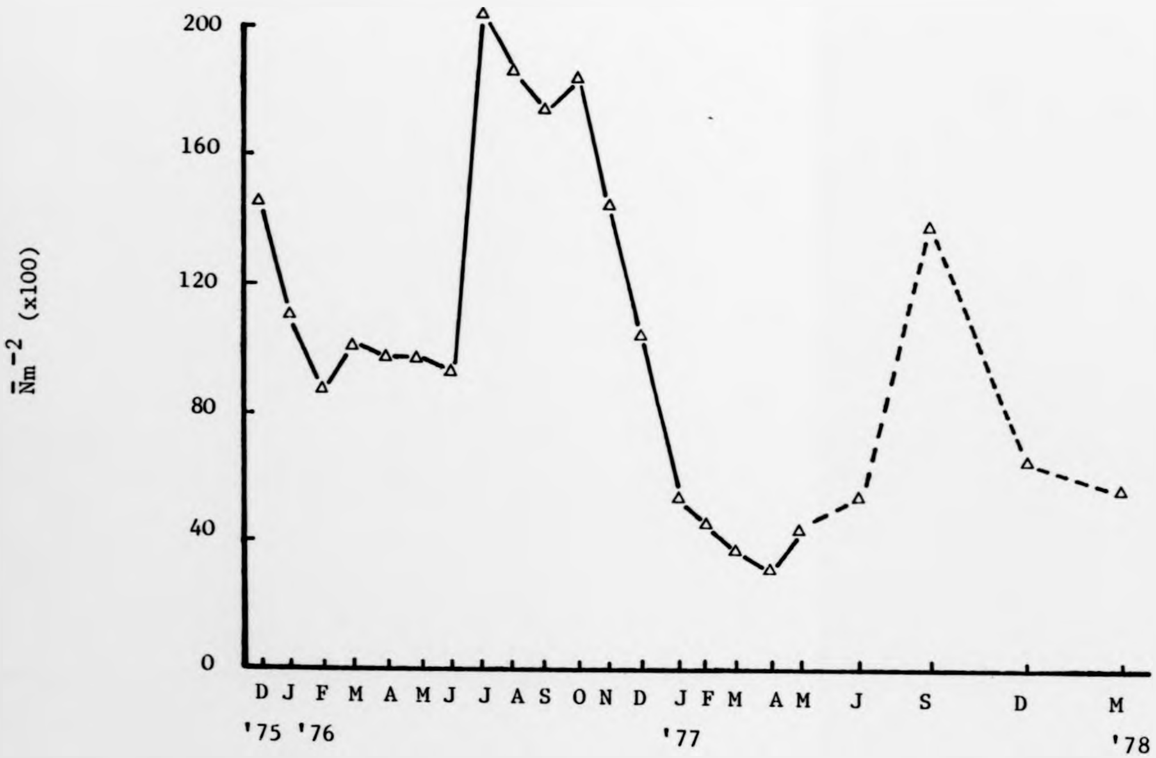


FIGURE 3.3.1: Mean density fluctuations of <u>Hydrobia</u> for the whole area

TABLE 3.3.1: Correlation between mean density of *Hydrobia* (Nm^{-2}) and various environmental factors

	Water content of sediment (%)	Silt and clay fraction (%)	Median particle size diameter (Ø)	Sorting coefficient (G)	Interstitial salinity (^{o}/oo Cl^{-})	Carbon content of sediment (%)	Nitrogen content of sediment (%)	C : N ratio	Tidal height (m above O.D.)
MEAN DENSITY OF *HYDROBIA* (Nm^{-2})	NS	NS	NS	NS	NS	NS	NS	NS	-0.8320 ***

3.3.2 Environmental factors influencing the mean annual density of *Hydrobia*

A correlation analysis was carried out to determine the association between various environmental factors and the mean annual density of *Hydrobia* at the main sampling stations between July 1976 and June 1977.

Included in the correlation analysis were:

(1) mean annual density of *Hydrobia*

(2) percentage of water (by weight) in the surface layer of sediment

(3) percentage silt and clay in the sediment (by weight)

(4) mean particle size diameter (Ø units)

(5) mean interstitial salinity (^{o}/oo Cl^{-})

(6) percentage of carbon in the sediment (by weight))Jan to
)June
(7) percentage of nitrogen in the sediment (by weight))1976

(8) carbon : nitrogen ratio

(9) tidal height (m) above O.D.

The results of this analysis are shown in the correlation matrix, table 3.3.1. The only significant correlation between mean density and any environmental factors was a negative relationship with tidal height (r = -0.8320***) as *Hydrobia* were scarce on the upper flats. The computer plotted "scattergrams" of each pair of factors did not indicate any curvilinear relationships.

3.3.3 Breeding

Hydrobia ulvae is a bisexual species and fertilisation is internal. In the British Isles sexual maturity is reached at the end of the first year in some individuals (Clay 1960a, Fish and Fish 1974) but the majority breed in their second year of life/

life (Anderson 1971, Fish and Fish 1974). On the White Sea, Kondratenkov (1972) has shown that Hydrobia only breed once during a two year life-span and thus reach maturity at the end of the first year. On the Dovey Estuary (Fish and Fish 1974), maturity is reached at a greater shell height on muddy substrates where the snails also grow to a larger size.

The eggs, surrounded by a thin membrane (Fish & Fish 1977, Lebour 1937) are laid on any suitable substrate, although there is a distinct preference for laying them on the shells of live Hydrobia (Fish & Fish 1974, Anderson 1971). The eggs are laid in masses held together and protected by a covering of sand grains or, less frequently, by shell fragments, small stones, plant material and sea-urchin spines (Clay 1960a) Up to 92% of Hydrobia shells may be covered by these egg capsules (Linke 1939) at the peak of the breeding season. Capsules have been found throughout the year (Anderson 1971) but the main breeding season is usually in the spring and early summer (Clay 1960a) with a second peak of egg capsule production occurring at some localities in late summer (Fish & Fish 1974).

The number of eggs within each capsule varies with locality (Table 3.3.2) and the number of egg capsules recorded per shell also varies between study areas ($\bar{x} = 4$ Linke 1939, $\bar{x} = 10$ Smidt 1951).

Within the egg capsules the eggs develop, hatching as veliger larvae (Fish and Fish 1974, Henking 1894, Pilkington 1971, Thorson 1946). Pilkington (1971) suggested that the free-swimming veliger stage wassuppressed, although veligers were found abundantly in the plankton by Thorson (1946) and Fish and Fish (1977)./

TABLE 3.3.2: Variation in the number of *Hydrobia* eggs per capsule between localities

AUTHORITY	LOCALITY	NUMBER OF EGGS/CAPSULE
ANDERSON (1971)	YTHAN, ABERDEENSHIRE	7.8 ± 3.24
FISH AND FISH (1974)	DOVEY ESTUARY, WALES	8.3 (Apr) 8.9 (Aug) 4.0 (Nov)
LEBOUR (1937)	PLYMOUTH, ENGLAND	Range: 3 - 7
MUUS (1967)	DANISH FJORDS	$\bar{x}$ = 15: range 7 - 25
PILKINGTON (1971)	PLYMOUTH, ENGLAND	Max 25
QUICK (1924)	PARKMILL, WALES	Max 25
SMIDT (1951)	DANISH WADDENSEA	$\bar{x}$ = 11: range 5 - 18
THAMDRUP (1935)	DUTCH WADDENSEA	Range: 12 - 70
THIS STUDY	FORTH ESTUARY	x = 15.04 ± 8.34 1976 x = 15.86 ± 7.36 1977

Fish (1977). The larvae hatch between 8 and 31 days depending on locality (Fish and Fish 1974, Linke 1939, Pilkington 1971, Rothschild 1940, Stopford 1951) and veligers are estimated to maintain planktonic existence for three to four weeks before settlement in Cardigan Bay (Fish and Fish 1977).

3.3.3 (i) The occurrence of egg capsules

Determination of the percentage of snails bearing egg capsules did not give an estimate of the reproductive output of *Hydrobia* but enabled the length of the breeding season to be established. In both 1976 and 1977 a single, well-defined breeding period was found, extending from March to August in 1976 and from March to July in 1977 (Table 3.3.3).

The length of the breeding season at each station was negatively correlated with tidal height (1976 $r = -0.6750^*$, 1977 $r = -0.7179^*$) indicating a longer season at lower tidal levels. Additionally in 1976, *Hydrobia* on transect A produced egg capsules in April, one month earlier than on either B or C transects. With the exception of Station B_2, this was also observed in 1977.

(ii) Reproductive output

The mean number of *Hydrobia* eggs per capsule (Appendix 5) did not differ significantly between years (1976 $\bar{x} = 15.04 \pm 8.34$; 1977 $\bar{x} = 15.86 \pm 7.36$ $p > 0.05$) or between sampling stations within each year. Additionally, the mean number of eggs per capsule was similar between adjacent months in each year, with the exception of June and July 1976, the number of eggs being significantly higher/

TABLE 3.3.3: The percentage of *Hydrobia* bearing egg capsules at each sampling station in 1976 and 1977

STATION

		TRANSECT A					TRANSECT B			TRANSECT C	
		1	2	3	4	5	1	2	3	1	2
1976	Mar	6.6	0	7.3	13.6	16.6	0	0	0	0	0
	Apr	33.3	52.38	50.0	61.9	37.5	18.1	39.4	20.0	31.57	14.28
	May	23.08	41.38	50.0	84.85	87.5	0	43.75	28.57	11.76	15.69
	Jun	0	0	28.2	30.76	84.2	0	0	25.0	0	0
	Jul	5.0	0	17.3	16.9	14.7	0	0	0	0	0
	Aug	0	0	0	0	4.7	0	0	0	0	0
1977	Mar	0	16.67	0	12.5	12.5	0	14.29	0	0	0
	Apr	0	0	58	80	57	0	33.3	21	0	0
	May	50	88	100	96	74	35	38	63	50	11
	Jun	43	30	33.3	48.6	65.8	0	0	50	0	30.4
	Jul	0	6	13	0	0	0	11	0	0	0

TABLE 3.3.4: The mean number of *Hydrobia* eggs per capsule at each station during the breeding season (a) 1976 (b) 1977

(a)

1976

	MAR	APR	MAY	JUN	JUL	AUG	TOTALS	n
A_1	17 ± 2.83	16.45 ± 9.09	13.33 ± 10.02	-	5	-	15.29 ± 8.56	17
A_2	-	14.32 ± 6.99	12.09 ± 6.13	-	-	-	13.34 ± 6.66	50
A_3	16 ± 3.6	14.21 ± 6.02	14.91 ± 7.26	12.57 ± 3.98	10.17 ± 4.51	-	14.13 ± 6.26	124
A_4	12.5 ± 9.71	17.48 ± 10.84	15.58 ± 8.43	12.9 ± 6.09	9.45 ± 6.07	-	15.39 ± 8.24	181
A_5	7 ± 7	15 ± 11.07	20.57 ± 11.3	17.52 ± 8.93	19.5 ± 6.36	14 ± 1.4	18.19 ± 10.49	89
B_1	-	19 ± 5.66	-	-	-	-	19 ± 5.66	2
B_2	-	14.1 ± 6.52	14.29 ± 6.05	-	-	-	14.18 ± 6.27	51
B_3	-	6	13.33 ± 4.04	20	-	-	13.2 ± 5.72	5
C_1	-	14.3 ± 9.23	13 ± 14.1	-	-	-	14 ± 9.45	9
C_2	-	12.67 ± 4.16	7.78 ± 4.18	-	-	-	9 ± 4.55	12
TOTALS	12.71 ± 7.7	15.31 ± 6.67	15.37 ± 8.58	15.45 ± 7.8	10.45 ± 6.14	14 ± 1.4		
n	14	204	227	77	20	2		

TABLE 3.3.4 (continued):

(b)

1977

	MAR	APR	MAY	JUN	JUL	AUG	TOTALS	n
A_1	-	-	18.56 ± 9.53	17.33 ± 5.03	-	-	18.25 ± 8.45	12
A_2	10	-	15.71 ± 6.73	10.44 ± 3.13	11	-	13.78 ± 6.12	27
A_3	-	15 ± 8.42	13.59 ± 6.36	16.5 ± 4.95	11.33 ± 2.31	-	14.03 ± 6.76	40
A_4	6.5 ± 0.7	13.45 ± 7.41	17.46 ± 8.13	15.91 ± 8.55	-	-	16.32 ± 8.28	118
A_5	7.5 ± 2.12	10.5 ± 5.26	13.27 ± 7.45	18.65 ± 9.38	-	-	15.68 ± 8.83	123
B_1	-	-	14 ± 6.1	-	-	-	14 ± 6.1	6
B_2	16	14.5 ± 4.95	22	-	9 ± 7.07	-	16.25 ± 9.53	8
B_3	-	14 ± 5.95	18.08 ± 9.64	18	-	-	16.71 ± 8.39	21
C_1	-	-	37.33 ± 8.33	-	-	-	37.33 ± 8.33	3
C_2	-	-	17	14.86 ± 3.53	-	-	15.13 ± 3.36	8
TOTALS	9 ± 3.79	13.3 ± 6.88	16.18 ± 4.46	16.87 ± 8.6	10.5 ± 4.25	-		
n	6	47	179	129	6	-		

TABLE 3.3.5: The reproductive output of *Hydrobia* (a) 1976 (b) 1977

(a)

Station	Total no. egg capsules sampled during breeding season	No. capsules produced m^{-2} during breeding season	Mean no. eggs per capsule m^{-2} during breeding season	No. eggs produced during breeding season m^{-2}	Mean population density during breeding season	Mean no. eggs per individual
A_1	17	6,800	15.29 ± 8.56	103,972	6,560	31.70
A_2	50	20,000	13.34 ± 6.66	266,800	9,200	58.0
A_3	124	49,600	14.13 ± 6.26	698,368	16,880	82.75
A_4	181	72,400	15.39 ± 9.24	1,114,236	18,160	122.71
A_5	89	35,600	18.19 ± 10.49	647,564	4,800	269.82
B_1	2	800	19 ± 5.66	15,200	7,120	4.27
B_2	51	20,400	14.18 ± 6.27	289,272	11,040	52.40
B_3	5	2,000	13.2 ± 5.72	26,400	2,720	19.41
C_1	9	3,600	14 ± 9.45	50,400	7,760	12.99
C_2	12	4,800	9 ± 4.55	43,200	10,720	8.06

TABLE 3.3.5 (continued):

(b)

Station	Total no. egg capsules sampled during breeding season	No. capsules produced m^{-2} during breeding season	Mean no. eggs per capsule m^{-2} during breeding season	No. eggs produced during breeding season m^{-2}	Mean population density during breeding season	Mean no. eggs per individual
A_1	12	4,800	18.25 ± 8.42	87,600	2,480	70.65
A_2	27	10,800	13.78 ± 6.12	148,824	3,120	95.4
A_3	40	16,000	14.03 ± 6.76	224,480	2,560	175.38
A_4	118	47,200	16.32 ± 8.28	770,304	7,920	194.52
A_5	123	49,200	15.68 ± 8.83	771,456	7,360	209.63
B_1	6	2,400	14 ± 6.1	33,600	2,400	28
B_2	8	3,200	16.25 ± 9.53	52,000	2,400	43.33
B_3	21	8,400	16.71 ± 8.39	140,364	4,160	67.48
C_1	3	1,200	37.33 ± 8.33	44,796	720	124.43
C_2	8	3,200	15.13 ± 3.36	48,416	5,120	18.91

higher in June (t = 2.82**) (Table 3.3.4).

Since the mean number of eggs per capsule alone did not indicate the extent of the reproductive output the number of eggs produced per individual at each station during the two breeding seasons was computed (Table 3.3.5). The sex ratio was unknown but assumed to be the same at all stations. Thus a comparison of reproductive output at different stations and between years could be made.

The mean number of eggs per individual ranged from 4.27 to 269.82 in 1976 and 18.91 to 209.63 in 1977, the maxima being produced at A_4 and A_5 in each year (Table 3.3.5). There was no significant difference between years in the number produced per individual ($p > 0.05$).

3.3.3 (iii) Factors influencing the spatial variation in the reproductive output of Hydrobia

During both 1976 and 1977 breeding seasons snails at the end of their first year of life dominated the population at all sites except at B_1 and B_2 in 1977 (Table 3.3.6). An hypothesis that the variation in mean size of these first year individuals (Table 3.3.7) influenced the number of snails attaining sexual maturity and hence influenced the reproductive output at each station was proposed. This was based on the results of an investigation on the Dovey estuary (Fish and Fish 1974). In this it was found that only those first year snails attaining a minimum length during the breeding season became sexually mature and bred. The smaller snails bred at the end of their second year of life./

TABLE 3.3.6: Proportion (%) of <u>Hydrobia</u> at end of first year found in samples during the breeding season

	Breeding season Feb. - June 1976			Breeding season Feb. - June 1977		
	total no. snails sampled	no. 1st yr snails	% contribution of 1st yr snails	total no. snails sampled	no. 1st yr snails	% contribution of 1st yr snails
A_1	81	55	67	40	22	55
A_2	113	77	68	35	24	69
A_3	203	144	71	47	29	62
A_4	219	159	73	137	73	53
A_5	80	67	84	111	86	78
B_1	86	65	76	29	13	45
B_2	136	110	81	36	16	44
B_3	36	35	97	62	58	93
C_1	87	58	67	87	58	67
C_2	156	155	99	59	57	97

TABLE 3.3.7: Mean size (mm) of <u>Hydrobia</u> approaching the end of their first year at each site during the breeding season

	A_1	A_2	A_3	A_4	A_5	B_1	B_2	B_3	C_1	C_2
1976	1.68	2.14	2.3	2.41	2.47	1.57	2.14	1.84	1.57	1.87
1977	2.39	2.48	2.43	2.70	2.58	1.74	1.93	1.80	1.57	2.16

life.

To test this hypothesis, correlation analysis was carried out on data from each breeding season to establish the relationships between the following variables:

mean length of all individuals sampled at each station during each breeding season,

mean length of first year individuals at each station during each breeding season,

tidal height,

total number of eggs produced per individual during the breeding season (March - July)

Tidal height was included in the analysis since there appeared to be an increase in reproductive output towards low shore stations on transect A.

The results are shown in the matrices (Table 3.3.8a and b). In both years there was a positive, significant relationship between the mean number of eggs produced per individual and the mean length of first year snails (1976 r = +0.7980**; 1977 r = +0.6011*). Only in 1976 was the mean number of eggs produced significantly correlated with tidal height (r = -0.7171*). There were no significant correlations with the mean length of all Hydrobia sampled at each station. Thus the hypothesis that the variation in mean size of first year animals influences reproductive output was supported.

The/

TABLE 3.3.8: Summary tables of correlation analysis between mean shell height of population and mean shell height and various factors (a) 1976 (b) 1977

(a)

mean shell height of whole population (mm)	mean shell height of first year individuals (mm)	tidal height (m above OD)	mean no. eggs produced per individual
	-	r = +0.2627 NS	r = +o.2524 NS
		r = -0.6652 *	r = +0.7980 **
			r = -0.7171 *

(b)

mean shell height of whole population (mm)	mean shell height of first year individuals (mm)	tidal height (m above OD)	mean no. eggs produced per individual
	-	r = +0.9268 ***	r = +0.5080 NS
		r = -0.3147 NS	r = +0.6011 *
			r = -0.4256 NS

The size of first year animals was significantly larger at stations on transect A than on transects B and C (d = 10.13*** 1976, d = 228*** 1977) and larger also at lower shore stations (A_4, A_5, B_2, B_3, C_2) compared to upper shore stations (A_1, A_2, A_3, B_1, C_1) (d = 5.602** 1976; d = 11.76*** 1977). According to the proposed hypothesis the occurrence of larger animals accounts for the higher reproductive output in these areas.

3.3.4 Population studies

Basic to an understanding of the ecology of a species and its role in the trophic system is a study of its life history and growth. The condition of an animal throughout its life-history, measured as the change in mean weight of a standard sized animal, indicates weight changes due to emaciation and reproduction and the biomass available at any one period to the next trophic level. The condition of Hydrobia was investigated on the Ythan by Chambers and Milne (1979).

Studies of settlement, growth and mortality increase the understanding of population dynamics of a species. There have been several investigations of the larval stages and settlement of Hydrobia.

On the west coast of Wales veliger larvae hatch at a shell height of 140 - 150 μm. (Fish and Fish 1977). There then follows a pelagic phase which lasts for approximately four weeks during which time the larvae are abundant in the plankton, in particular in May - June and August - September. At Chelston Meadows, Plymouth, however, a complete suppression of the planktonic phase was suggested by Pilkington (1971) since none was found in the plankton. The vela were not considered strong enough to lift Hydrobia/

Hydrobia veligers off the benthos (Fretter and Pilkington 1970) supporting this finding. At other locations in Western Europe (Henking 1894, Lebour 1937, Linke 1939, Smidt 1944, Thorson 1946) differences in the duration of the pelagic phase have in part been attributed to a confusion between the veligers of Hydrobia and Littorina littorea (Fish and Fish 1977), although the possible existence of different races may explain some differences (Bandel 1975, McMillan 1948).

Newly settled spat are found on all substrate types (Stopford 1951) and at all shore levels (Anderson 1971, Smidt 1951), although Elliott (1979) found the highest densities mainly occurred at low-shore sites. The density varies between successive years (Fish and Fish 1974) but as many as 663000 m^{-2} have been estimated in the Danish Waddensea (Smidt 1951).

Although several studies of Hydrobia include descriptions of population growth (Chatfield 1972, Fish and Fish 1974, Muus 1967, Rothschild 1941, Stopford 1951, Smidt 1951) only one quantitative estimate of growth has been made (Wolff and de Wolf 1977). In the present study growth and mortality have been investigated as an integral part of the production computations for Hydrobia.

3.3.4 (i) Dry weight determination and condition of Hydrobia

The components of the regression equations and the correlation coefficient (r) for the dry weight determinations throughout the period January - December 1976 are given in Table 3.3.9. From these the monthly weight changes of 2 mm, 3 mm, and 4 mm animals was determined (Fig 3.3.2). During the period March - June both 3 mm and 4 mm animals lost weight but 2 mm animals maintained an almost constant weight, as they did throughout the year. There was a marked increase in/

TABLE 3.3.9: Parameters of the regression equations for the relationship between length (mm x 10^{-1}) and weight (µg AFDW) of *Hydrobia*

month	$\log_{10}$ a (intercept)	b (regression coefficient)	r correlation coefficient
January	-1.5607	2.8549	0.9851
February	-0.8640	2.4179	0.8879
March	-1.2550	2.6877	0.9537
April	-1.0534	2.5363	0.9735
May	-1.1529	2.6145	0.9851
June	-0.8259	2.3581	0.8466
July	-0.1369	1.9000	0.8100
August	-0.5718	2.2103	0.8950
September	-0.9496	2.4440	0.9074
October	-1.0042	2.4439	0.9614
November	-1.1613	2.5982	0.9626
December	-0.4674	2.1474	0.7993

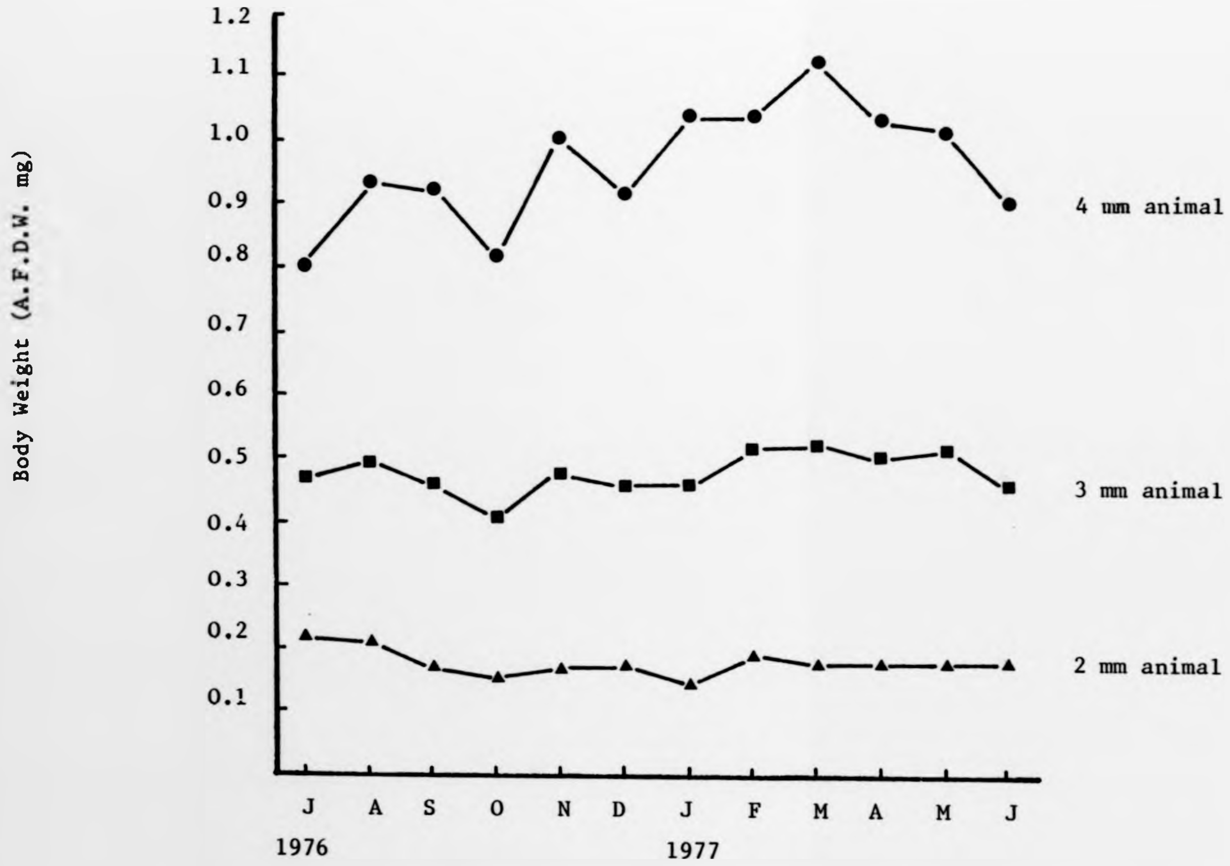


FIGURE 3.3.2: Seasonal variations in A.F.D.W. of selected sizes of <u>Hydrobia</u>

in weight during January - March in 3 mm and 4 mm animals prior to spawning but the increase was less marked in 2 mm animals.

3.3.4 (ii) Population growth and mortality

(a) General description of population structure

The population of Hydrobia throughout the study period December 1975 - March 1978 consisted of two year classes (cohorts). By following the fate of the cohorts, a longevity of approximately two years was indicated (Fig 3.3.3).

Between December 1975 and March 1976 there was little growth of the two cohorts and a substantial decrease in the proportion of second year animals in the population. This decrease continued as growth of both cohorts resumed in April. By June the shell sizes of the 1 + cohort had grown so as to be virtually indistinguishable from the few remaining 2 + individuals.

Spat were first taken in the sieves in July 1976 and growth in shell length of both 0+ and 1+ cohorts continued until December coupled with a decrease in density, particularly of the 0+ cohort.

A similar pattern of growth and recruitment followed in 1977/8 although the population density was lower and recruitment began in June.

(b) Settlement

Spat were first taken in the sieves in July 1976 and in June 1977 when they had a shell height of at least/

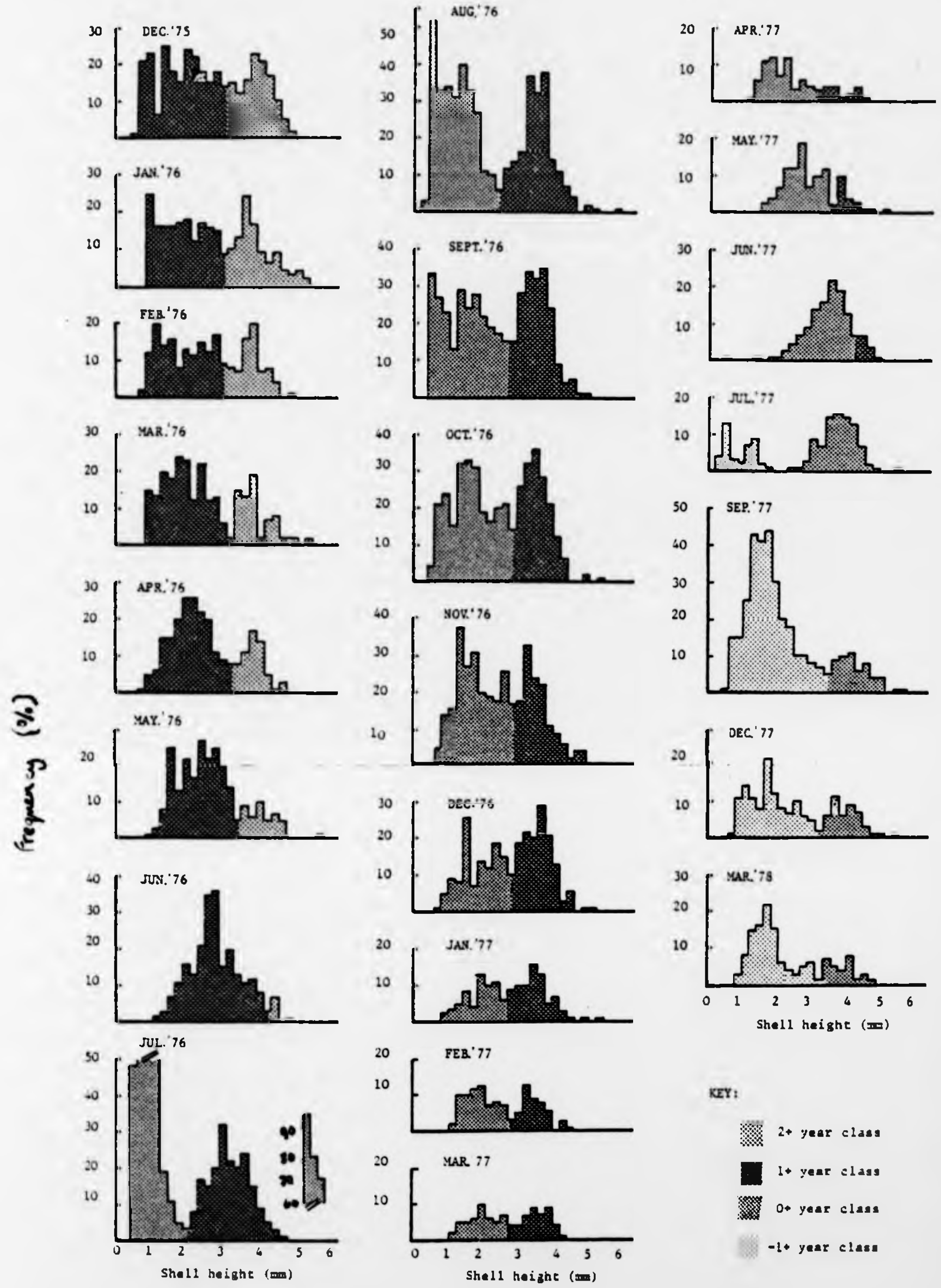


FIGURE 3.3.3: Size-frequency histograms of *Hydrobia* throughout the study period

least 300 μm. They occurred at all stations in each year although in 1977 the spatfall was lower at each station than in 1976 (Table 3.3.10). This reflected the lower population density and egg production in 1977 (Section 3.3.3).

The highest densities of spat occurred at the low shore stations. At B_3 the maximum recorded was 92800 in 1976 (9600 in 1977), at C_2, 27600 (21600 in 1977) and at A_5, 30400 (28400 in 1977). However, high densities were also recorded at B_1 (28400 in 1976) and at C_1 (24800 in 1976), although at A_1, the other up-shore site, a comparatively low spatfall was recorded in each year (max.8000 1976; 11600 1977).

(c) Growth of Hydrobia

Cohort growth, defined as increase in mean individual weight of each year class, was studied from July 1976 to June 1977 for both 0+ and 1+ cohorts.

The mean individual weight ($\overline{w}$) of the 0+ cohort increased rapidly from 43.68 ± 28.06 μg at recruitment in July 1976 to 184.05 ± 98.98 μg in December (Fig 3.3.4). Between December 1976 and January 1977 there was a decline in $\overline{w}$ to 132.51 ±82.14 followed by a period of little growth. Growth resumed in April and was rapid until the end of the cohort's first year of life in June ($\overline{w}$ = 507.68 ± 170.14 μg). The annual increase in $\overline{w}$ of the 0+ cohort was thus 185 μg giving an average monthly increment of 15.42 μg.

Animals/

TABLE 3.3.10: *Hydrobia* spat settlement m^{-2} at each station during 1976 and 1977

		A_1	A_2	A_3	A_4	A_5	B_1	B_2	B_3	C_1	C_2
1976	Jul	0	1200	1200	1200	400	0	0	92800	1600	27600
	Aug.	8000	6800	2400	400	11600	28400	5600	27600	3600	16800
	Sep.	5600	8000	6400	3600	10400	8000	7200	14400	24800	11200
	Oct.	6000	6800	2400	1200	20000	15600	6800	18800	2800	33200
	Nov.	2400	3200	4000	4400	30400	5200	2400	15200	2800	15600
	Mean no. Spat	4400 ± 3175	5200 ± 2870	3280 ± 2008	2160 ± 1734	14560 ± 11259	11440 ± 11029	4400 ± 3098	33760 ± 33416	7120 ± 9909	20880 ± 9154
1977	Jun.	400	0	0	0	400	0	400	0	0	0
	Jul.	6400	400	1200	400	3200	0	1200	800	400	2800
	Sep.	11600	7600	8000	4000	28400	8800	4800	9600	8000	21600
	Dec.	6800	800	7600	6800	4800	4800	4400	2400	4400	4500
	Mean no. Spat	6300 ± 4580	2200 ± 3615	4200 ± 4189	2800 ± 3217	9200 ± 12929	3400 ± 4252	2700 ± 2224	3200 ± 4382	3200 ± 3767	7300 ± 9734

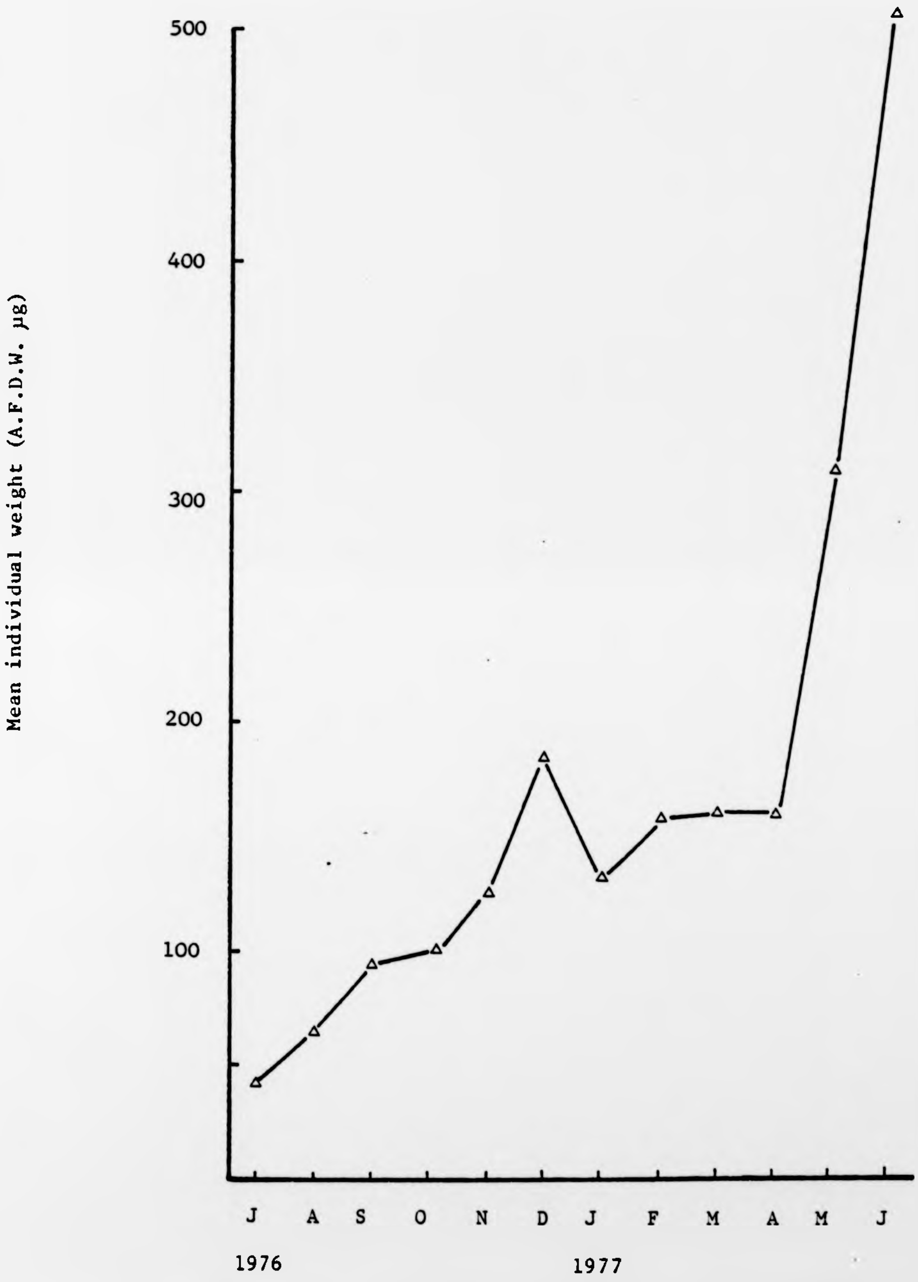


FIGURE 3.3.4: Mean individual weight of 0+ class <u>Hydrobia</u> on each sampling occasion July 1976 - June 1977.

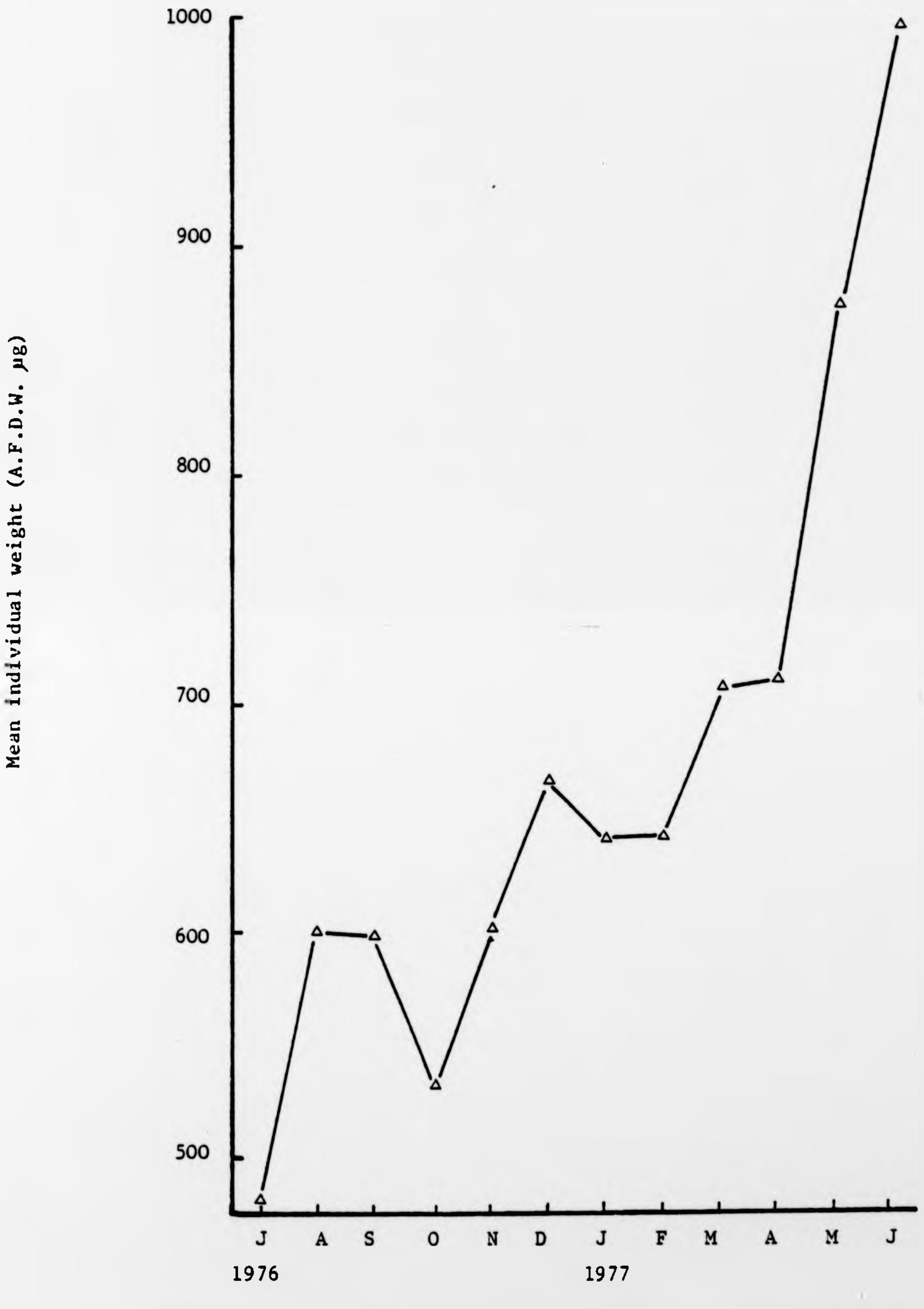


FIGURE 3.3.5: Mean individual weight of 1+ age class Hydrobia on each sampling occasion July 1976 - June 1977

Animals entering their second year of life in July 1976 (1+ cohort) increased in $\overline{w}$ from 478.36 ± 161.7 μg to 598.8 ± 173.9 between July and August (Fig 3.3.5). A decrease in $\overline{w}$ then ensued until October after which there was an increase until December. After a decrease growth resumed between February and March to reach a mean individual weight of 996.0 ± 81.85 μg by June. Growth was most rapid between April and June as for the 0+ cohort. The annual increase in $\overline{w}$ of the 1+ cohort was 487.64 μg giving an average monthly increment of 40.64 μg.

(d) Mortality of Hydrobia

The mortality of the 0+ and 1+ cohorts was referred to in terms of the population as a whole at Skinflats and the fate of the 0+ cohort over the different areas of Skinflats is treated in greater depth.

The recruitment phase of the 0+ cohort took place from July until October 1976 and is referred to as Phase I (Table 3.3.11a). By the end of this an average of 11360 recruits m^{-2} had been added to the population representing the balance between mortality and recruitment. Phase II consisted of a period of winter mortality extending from November until March. At the end of this an average of 9360 0+ cohort individuals m^{-2} had been lost from the population. This is equivalent to an 82.4% decrease from beginning to end of Phase II giving an average monthly mortality of 16.5%. The highest mortality rate (Fig 3.3.6) occurred between January and February.

The/

TABLES 3.3.11 a & b: The mortality of 0+ cohort (a) and 1+ cohort (b) *Hydrobia* from July 1976 until June 1977

(a)

0+ cohort		Mortality increments $-\Delta N$
Phase I	(July '76	+ 12600
	(August	- 1480
	(September	- 960
	(October	+ 1200
Phase II	(November	- 2440
	(December	- 4080
	(January '77	- 2120
	(February	- 0
	(March	- 720
Phase III	(April	+ 480
	(May	+ 1000
	(June	+ 1200

(b)

1+ cohort		Mortality increments $-\Delta N$
	July '76	
	August	- 280
	September	- 120
	October	- 240
	November	- 1520
	December	+ 80
	January '77	- 2680
	February	- 1000
	March	- 200
	April	- 1040
	May	+ 160
	June	- 360

The winter mortality was followed by a period of density increase (Phase III) so that by June 4680 m^{-2} were present in the population. Subsequent mortality proceeded at a slower rate (Fig 3.3.6) until the end of the study period.

The fate of the 1976 spat (0+ cohort) at each station from July until the end of the study period is shown in Figs 3.3.7 a-d. On transect A, with the exception of A_1, where spat were not recorded until August, all stations received the first recruits of Hydrobia in July (Fig 3.3.7 a and b). At the two upshore stations, A_1 and A_2, maximum densities were attained early in Phase I and loss from all causes was high until December (85% at A_1, 80% at A_2). Following this, the population at both sites fluctuated but increased markedly between April and September 1977.

Maximum spat densities at the three lower shore stations of transect A occurred in November 1976 (Fig 3.3.7b), although at each a smaller peak was found in September. Loss from the population was high in Phase II, particularly at A_5 (85%) where the highest spatfall had occurred and at A_4 where 84.2% of the population disappeared between November and February. Densities at A_3 fluctuated less dramatically with only 9.1% being lost in Phase II. At all three stations, there was an increase in density in Phase III. At A_4 and A_5 the increase was 95% and 65% respectively between April and June.

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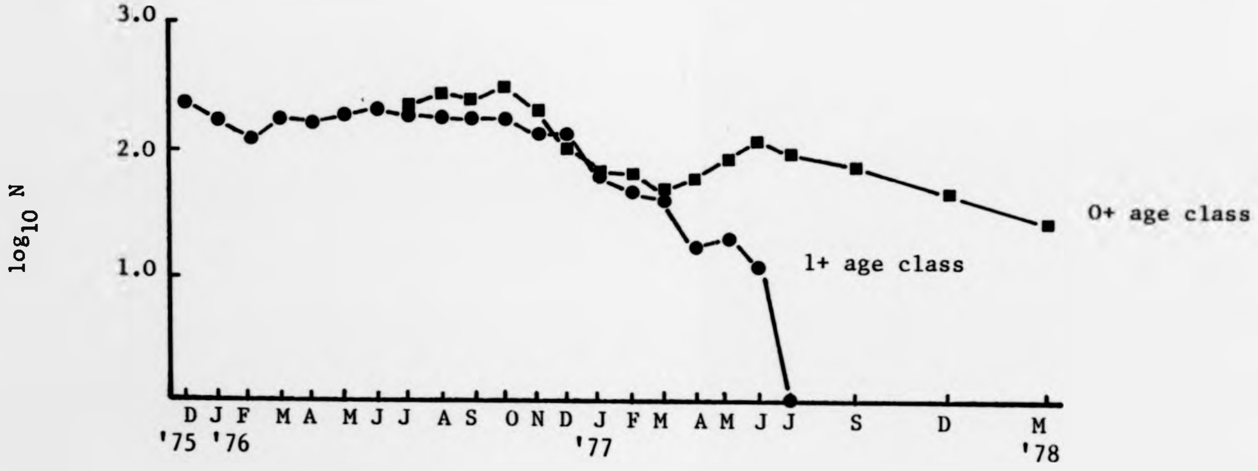

FIGURE 3.3.6: Mortality rates of O+ and 1+ age classes during the study period

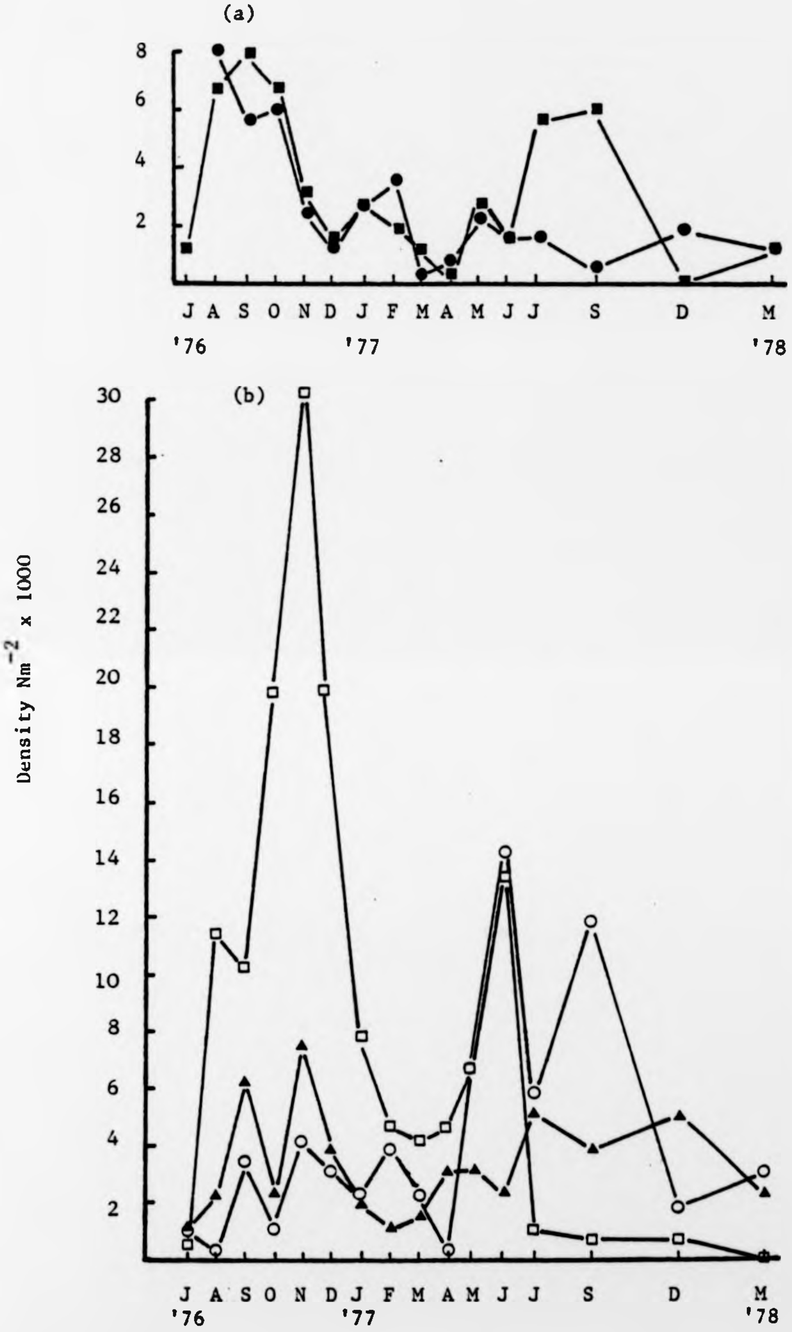

FIGURE 3.3.7 a-d: Density fluctuations of 0+ age class <u>Hydrobia</u> from July 1976 - March 1978 at each station (a) A_1 ■ , A_2 ● (b) ▲ A_3, ○ A_4, □ A_5

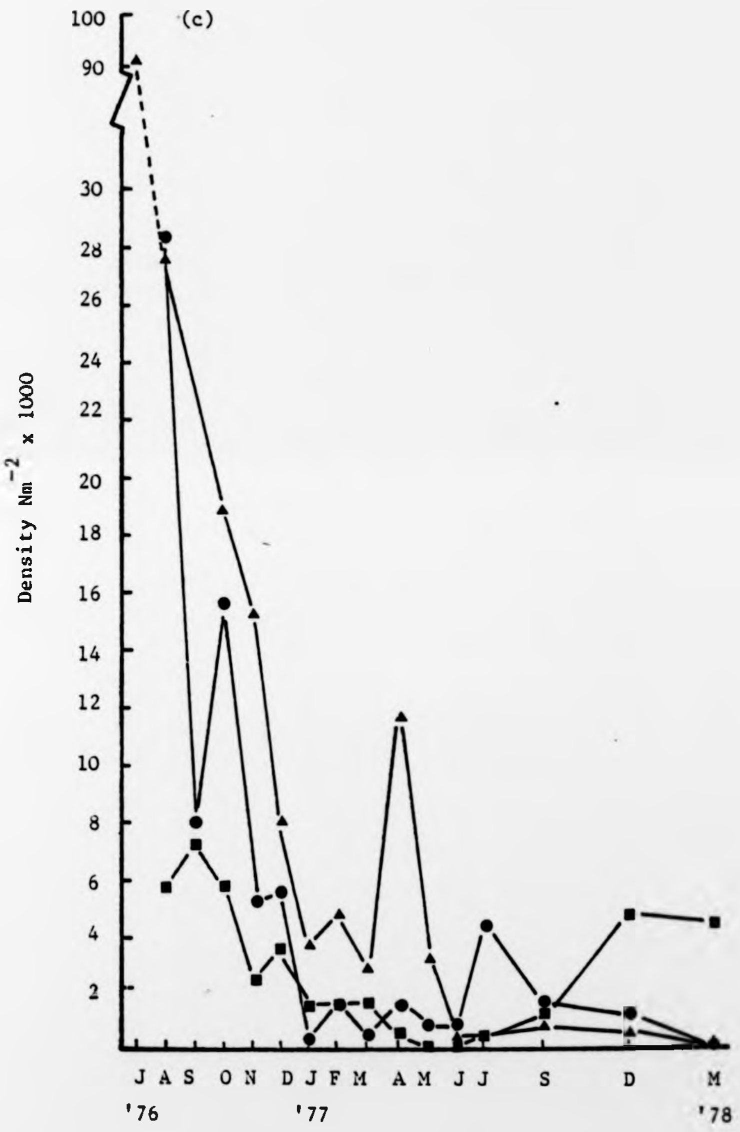

FIGURE 3.3.7 (continued): (c) Transect B ● B_1, ■ B_2, ▲ B_3

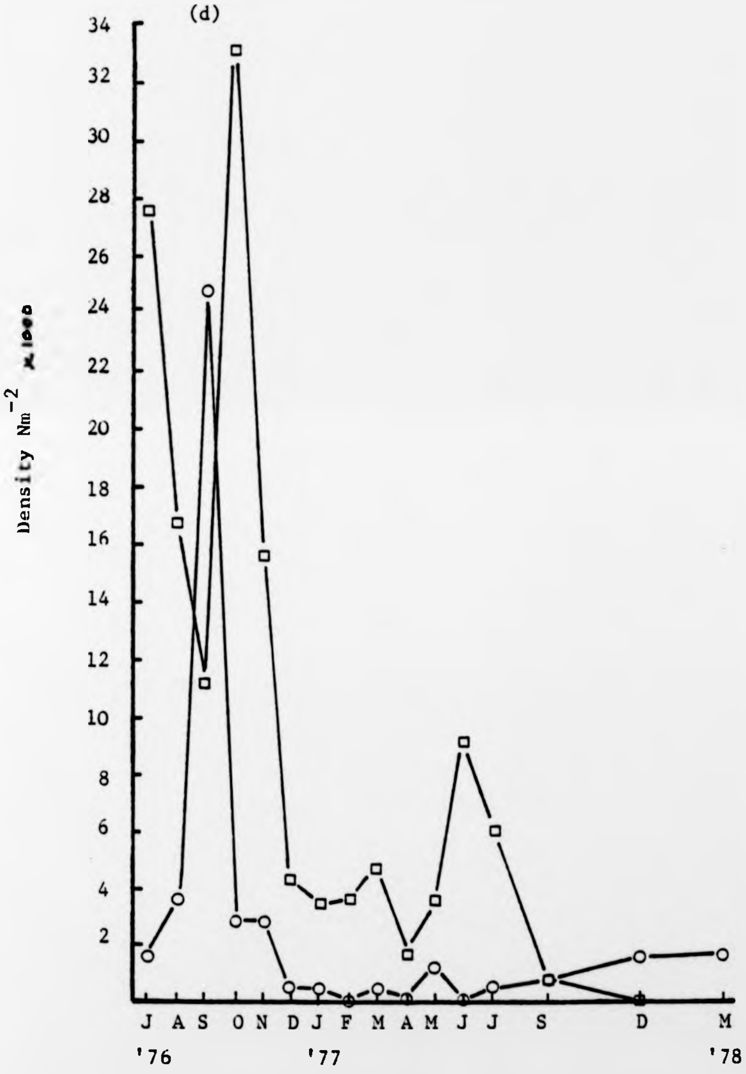

FIGURE 3.3.7 (continued): (d) Transect C, ○ C_1, □ C_2

Similar trends in spatfall and subsequent loss were noted on transects B and C. The large spatfall at B_3 (July 1976) had decreased by 96.1% in January and that at B_1, by 98.6%. At B_2 the losses were less marked (Fig 3.3.7c) and at all sites on transect B there was an increase in the following year. Only at B_3 was the increase confined to Phase III, however, that at B_1 occurring in June and July and at B_2 between July and December.

A double peak in the density of spat at C_2 in July and October was followed in Phase II by a winter loss (Fig 3.3.7d). Between October and January 90.4% were lost but this was followed by an increase of 83% between April and June. At C_1 a single peak of spat was seen in September and by February no 0+ cohort snails were taken in the samples. A gradual recolonisation occurred subsequently until the end of the sampling period.

During the period between July 1976 and June 1977 the 1+ cohort decreased from a mean density of 7680 m^{-2} to 480 m^{-2}, a loss of 94%. Of this, 73% was lost during the winter and the period following reproduction (Fig 3.3.6). On average a monthly mortality of 8.3% occurred during the year of study.

Mortality in terms of biomass is shown in Table 3.3.12. A full computation is given in Appendix 6. Although the highest mortality in terms of density occurred in the first year of life (cohort 0+), the mortality/

TABLE 3.3.12: Mortality ($gAFDWm^{-2}$) of Hydrobia each month (July 1976 - June 1977)

	2+ gm^{-2}	1+ gm^{-2}	0+ gm^{-2}	Total gm^{-2}
July	-	-	-	-
August	-0.122	-0.151	-0.082	-0.354
September	-	-0.071	-0.077	-0.143
October	-	-0.136	+0.117	+0.019
November	-	-0.866	-0.277	-1.142
December	-	+0.506	-0.632	-0.126
January	-	-1.743	-0.336	-2.079
February	-	-0.693	0	-0.639
March	-	-0.135	-0.115	-0.250
April	-	-0.737	+0.077	-0.640
May	-	+0.127	+0.233	+0.360
June	-	-0.331	+0.489	+0.157
Total	-0.122	-4.176	-0.596	-4.837

mortality in g AFDW m^{-2} was highest in the second year of life (4.176 gm^{-2}), accounting for 86% of the total mortality from the population (4.837 gm^{-2}). Loss was highest in the winter months for both cohorts with a maximum of 1.743 gm^{-2} lost from the 1+ cohort between December 1976 and January 1977 and 0.632 gm^{-2} from the 0+ cohort between November and December 1976. The increase in density in the spring is matched by an increase in biomass between April and June which is particularly marked in the 0+ cohort.

3.3.5 The production of *Hydrobia* at Skinflats

Prediction of the immediate and longterm effects of predation on a benthic species involves not only measurements of density and biomass changes but also the rate of incorporation of organic matter (or energy) into the population.

A comparison of production in several localities is required as a basis for examining the causal factors in determining variations. For this the Production:Mean Annual Biomass ratio (P:$\bar{B}$) is a useful tool since populations having similar P:$\bar{B}$ ratios will produce similar amounts of organic matter relative to the mean biomass present. Such comparisons have been made by several workers (eg Hibbert 1976, Peer 1970, Warwick and Price 1975, Waters 1969) and the P:B ratio from one locality has been used to estimate production at another locality if only mean biomass is known. The use of the ratio in this context has been discussed by Robertson (1979).

Calculation of the product of density and mean weight of the total population and of the constituent year classes (N$\bar{w}$) each month/

month gave the mean monthly biomass ($\bar{B}$) of the population and of each cohort, (Fig 3.3.8).

During the whole study period (December 1975 to March 1978) $\bar{B}$ of the total population fluctuated in a similar manner to the mean density (Fig 3.3.8a), consisting of a summer peak and winter trough. The summer biomass peak resulting from spatfall was, however, smaller than the corresponding peak in density since the large number of small individuals contributed little to the population biomass.

The major contributor to $\bar{B}$ between May 1976 and May 1977 was the 1+ age class (Fig 3.3.8b). Concurrent with the elimination after May 1977 of this cohort, the 0+ age class grew rapidly to dominate the population in June 1977. Thus animals in their second year of life dominated the $\bar{B}$ in both years studied.

The production (P) in terms of g. AFDW m^{-2} was calculated for each cohort separately and the results of each were then summed to give the total population production. It was determined for the annual period July 1976 - June 1977 and P for each cohort was calculated from the product of mean density ($\bar{N}$) and change in mean weight ($\Delta\bar{w}$) of the cohort ($\bar{N}\Delta\bar{w}$).

Thus:

$$P_{total} = (\bar{N}_1\Delta\bar{w}_1) + (\bar{N}_2\Delta\bar{w}_2) + (\bar{N}_n\Delta\bar{w})$$

where $(\bar{N}_1\Delta\bar{w}_1) - (\bar{N}_n\Delta\bar{w}_n) =$

P of each constituent cohort

and P_{total} = population production

The full computation is shown in appendix 6, and a summary of $\bar{B}$, P and P:B ratio for each cohort is illustrated in Tables 3.3.13 and/

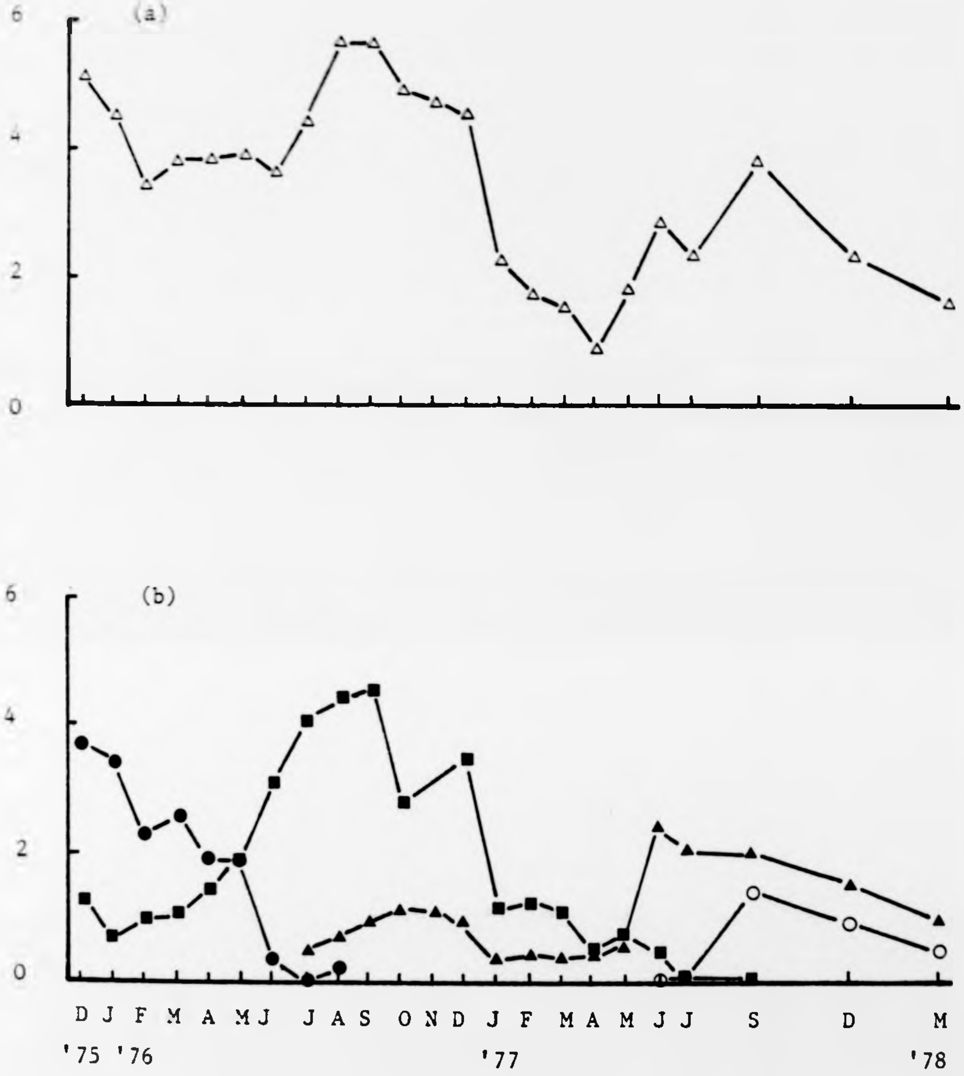

FIGURE 3.3.8 (a) Mean total biomass fluctuations of *Hydrobia* during the sampling period and (b) Biomass fluctuations of each cohort during the same period ● 2+ age class, ■ 1+ age class, ▲ 0+ age class, ○ −1 age class.

and 3.3.14. The 0+ cohort contributed the largest amount to the total production (2.428 g AFDW m^{-2} yr^{-1}) from the smallest mean biomass (0.864 g AFDW m^{-2} yr^{-1}) resulting in a P:B ratio of 2.81:1. The 1+ cohort produced 1.421 g AFDW m^{-2} from a $\bar{B}$ of 2.436 g AFDW m^{-2} yr^{-2}. This gave a P:B ratio of 0.58:1 which was far lower than that of the 0+ cohort.

The 2+ cohort was only present during July and August before being eliminated from the population following reproduction. During this short period it contributed 0.05 g AFDW m^{-2} from a mean biomass of 0.137 g AFDW m^{-2}. The annual P was thus negligible, 0.0042 g AFDW m^{-2} yr^{-1} from a $\bar{B}$ of 0.023 g AFDW m^{-2} yr^{-1} and gave a P:B ratio of 0.18:1. The -1 cohort was only present in June and July 1977 and production was negligible.

The total population of Hydrobia thus produced 3.90 g AFDW m^{-2} yr^{-1} from a $\bar{B}$ of 3.32 g AFDW m^{-2} resulting in a P:B of 1.17:1.

Production each month was not consistently positive (appendix 6). Between December 1976 and January 1977 0+ cohort production m^{-2} was negative, corresponding to a time when growth was minimal and mortality maximal. Similarly between March and April 1977, prior to the resumption of growth production was negative for the 0+ cohort. Between August and September, September and October and December and January production of the 1+ cohort was also negative corresponding to the post-reproductive and minimal growth periods.

3.3.6 Discussion

(a) Distribution and density

Hydrobia was widely distributed at Skinflats occurring at all sampling stations./

TABLE 3.3.13: Biomass (gAFDWm^{-2}) of *Hydrobia* each month (July 1976 - June 1977)

	2+ cohort g AFDW m^{-2}	1+ cohort g AFDW m^{-2}	0+ cohort g AFDW m^{-2}	-1 + cohort g AFDW m^{-2}	Total g AFDW m^{-2}
July 1976	0.039	3.674	0.55	-	4.263
August	0.234	4.431	0.742	-	5.407
September	-	4.314	0.961	-	5.275
October	-	3.788	1.145	-	4.933
November	-	3.317	1.123	-	4.440
December	-	3.718	0.891	-	4.609
January 1977	-	1.859	0.36	-	2.219
February	-	1.231	0.431	-	1.662
March	-	1.216	0.322	-	1.538
April	-	0.483	0.395	-	0.878
May	-	0.735	1.069	-	1.804
June	-	0.464	2.376	0.003	2.843
	$\bar{B} = 0.273$	$\bar{B} = 2.436$	$\bar{B} = 0.864$	Total	3.323

TABLE 3.3.14. Summary of annual production estimates by all cohorts of *Hydrobia*

	2+	1+	0+	-1+	Total gm^{-2}
July 1976	-	-	-	-	-
August	50.1	+ 0.908	+ 0.273	-	+ 1.231
September	-	- 0.045	+ 0.296	-	+ 0.251
October	-	- 0.390	+ 0.067	-	- 0.324
November	-	+ 0.395	+ 0.254	-	+ 0.650
December	-	+ 0.349	+ 0.400	-	+ 0.750
January 1977	-	- 0.115	+ 0.195	-	- 0.310
February	-	+ 0.010	+ 0.070	-	+ 0.081
March	-	+ 0.120	+ 0.006	-	+ 0.126
April	-	+ 0.003	- 0.004	-	- 0.0002
May	-	+ 0.125	+ 0.440	-	+ 0.566
June	-	+ 0.059	+ 0.819	-	+ 0.879
Totals: gm^{-2}	+ 0.051	+ 1.421	+ 2.428	-	+ 3.900
$P:\bar{B}$ ratios	0.19	1.71	2.81	-	1.17

stations. The density fluctuated both temporally and spatially with the widest fluctuations at low-shore stations, resulting from a large settlement and subsequent high mortality there. However, despite these large fluctuations, the negative correlation between mean annual density and tidal height indicated a preference for the lower beach at Skinflats. (NB All stations were above mid-tidal level). This finding was contrary to that at Torry Bay (Elliott 1979) where the presence of _Zostera marina_ at upper-shore levels created a more favourable environment than at lower levels. Thus, although tidal height and hence the exposure period is important at upper reaches of the Forth estuary in determining sites of maximum density, in the presence of _Zostera marina_, it becomes of less importance. _Zostera_ provides additional feeding surfaces and detritus which attract high numbers of _Hydrobia_.

The low density at upshore sites, particularly above MHWN, most probably resulted from the more extreme conditions encountered there. During the summer the mud dried and cracked under neap tide conditions and ice often formed during 1976/77 winter with snow cover common in January and February. It has been found that _Hydrobia_ is only able to survive four days in dry conditions at 15.6 - 29.4°C before mortality increases (Stopford 1951) and, furthermore, mortality was found to be high at upshore areas on the Waddensea during the ice-winter of 1949 (Smidt 1951). This evidence lends support to the idea that conditions will indeed be more extreme at upshore levels and lead to heavier mortality and thus lower population densities.

The lack of significant correlations between mean annual density and any of the other environmental factors measured suggests that the small range of salinity, particle size and organic content encountered has little overall effect on the abundance of Hydrobia at Skinflats. Similarly, the influence of substrate type on abundance was insignificant as found by workers elsewhere in Britain (Barnes and Greenwood 1978, Elliott 1979, Newell 1964). A preference for fine sediments in laboratory conditions (Barnes and Greenwood 1978) but not in field conditions could not be tested since the sediments at Skinflats were all fine muds.

(b) Breeding

The data presented on the occurrence of Hydrobia egg capsules at Skinflats showed a unimodal breeding season in both 1976 and 1977, extending principally from March until July. This was similar to most previously recorded breeding seasons around the British and Danish coasts (Henking 1894, Muus 1967, Smidt 1951, Stopford 1951, Thorson 1946) but differed from that on the Dovey estuary, North Wales, (Fish and Fish 1974). There the breeding season was bimodal with the second peak of spawning activity occurring in August and September. The low percentage of the population carrying egg capsules on the Dovey (maximum 41%) when compared with that at Skinflats (Maxima 100% 1976; 63% 1977) may be a reflection of the extended, bimodal breeding season. On both the Cheshire Dee estuary (Stopford 1951) and the Waddensea (Smidt 1951), the percentage of the population carrying egg capsules was similar to that at Skinflats supporting this suggestion.

It is apparent that environmental conditions at Skinflats do not influence the mean number of eggs per capsule or the mean number of eggs per individual produced in each breeding season since both were similar between years. However, differences between locations in the number of eggs per capsule (Table 3.3.2) would be explained if local races have evolved (McMillan 1948). The number of eggs per capsule for example resembled that found in Danish fjords by Muus (1967) but was far higher than those on either the Ythan or Dovey estuaries. (Anderson 1971, Fish and Fish 1974).

Although the number of eggs produced per capsule and per individual each year were not influenced by environmental factors, these were found to influence the breeding season, which was longer at low shore levels. The causal factors in this were not investigated but may have been related to the shorter emersion period and the consequent amelioration of temperature fluctuations and desiccation. Tidal height and emersion period did not largely affect reproductive output however. This was influenced by the size attained by the first year individuals during the breeding season. It thus appears likely that, as on the Dovey, first year Hydrobia have to reach a certain (although undetermined) size before becoming sexually mature. Since the density of these young snails relative to the population density as a whole was high, their sizes at any station would have a strong influence on the extent of the reproductive output there. Thus on transect A and at low shore stations, where the size of first year Hydrobia was larger, reproductive output was high compared to transects/

transects B and C and to up-shore stations.

Assuming that temperature influences the growing season a mild autumn could enable spat to attain larger sizes than in a cool autumn. This would in turn influence the reproductive output in the following spring and may account for some of the variation in spatfall density between years.

(c) Population studies

The two cohorts present in the *Hydrobia* population at Skinflats revealed an approximate two year life-span similar to that on other muddy substrate localities (eg Anderson 1971, Wolff and de Wolf 1977). As shown in the summary table (Table 3.3.15) longevity on sandy substrates ranges between 1 yr (Wolff and de Wolf 1977) and 1.5 yr (Chatfield 1972), although on the fine sands of the Dovey, the life span was 2.5 yr (Fish and Fish 1974). Under laboratory conditions *Hydrobia* can live for over five years (Quick 1924, Rothschild 1940) in the absence of fluctuating seasonal conditions and predation. An approximate two year life span was also found at Torry Bay on the Forth Estuary (Elliott 1979) where substrate type varied from coarse sand to fluid mud suggesting that substrate alone is not a determining factor in longevity.

Changes in condition of 3 and 4 mm *Hydrobia* throughout the year show an increase in weight prior to spawning and a decrease on release of eggs. The absence of weight changes in 2 mm animals during the same period strongly supports the idea that these small 0+ cohort animals do not reproduce in their first year of life, as suggested in Section 3.3.4 and elsewhere

(Anderson/

TABLE 3.3.15: The longevity of *Hydrobia* in field and laboratory conditions

LOCALITY	LIFE-SPAN	SEDIMENT TYPE	AUTHORITY
YTHAN ESTUARY, ABERDEENSHIRE	2 + yr	Mud, mud-sand	ANDERSON (1971)
WHITSTABLE, KENT	1.25 yr	Sandflats, shingle beach	CHATFIELD (1973)
SEASALTER, KENT	1.5 yr	Sandflats	"
PEGWELL BAY, KENT	nearly 2 yr	Saltmarsh, muddy sand	"
DOVEY ESTUARY, WALES	2.5 yr	Fine sand	FISH AND FISH (1974)
WHITE SEA	+ 2 yr	?	KONDRATENKOV (1972)
LAB. CONDITIONS	+ 5 yr	-	QUICK (1924)
LAB. CONDITIONS	5 yr	-	ROTHSCHILD (1940)
DANISH WADDENSEA	+ 1.5 yr	Mud	SMIDT (1951)
GREVELINGEN ESTUARY	just over 1 yr	Sandy sites	WOLFF AND DE WOLF (1977)
GREVELINGEN ESTUARY	nearly 2 yr	Muddy sites	WOLFF AND DE WOLF (1977)
FORTH ESTUARY	2 yr	Muddy site	This study

(Anderson 1971, Fish and Fish 1974). A similar lack of weight change in 2 mm on the Ythan (Chambers and Milne 1979) also reinforces this. During the winter period there was no marked decline in condition, except in 2 mm animals between December and January, so that predators such as wading birds and shelduck would not suffer from a reduced biomass intake per snail ingested.

In terms of mean weight ($\bar{w}$) both 1+ and 2+ cohorts showed a period of minimal growth in the winter months and a rapid spring growth phase. This conforms to the general pattern of growth in other temperate estuarine benthic invertebrates (eg Chalmers and Milne 1975 a and b, Elliott 1979, Warwick and Price 1975). The growth curves were similar to those on the Grevelingen estuary, the Netherlands, (Wolff and de Wolf 1977) but whereas the 0+ animals reached a mean weight of 185 µg by December, those on the Grevelingen attained 300 µg. This is probably a reflection of lower temperatures and more severe conditions in the higher latitude of the Forth estuary, but studies at other localities are required to substantiate this. Animals in their second year of life at Skinflats only reached 675 µg by December compared with 850 µg on the Grevelingen but by June of the second year of life, the mean weights were similar at the two localities. Growth, therefore, appears to be slower on the Forth over much of the lifespan but may continue for a longer period such that, by the end of the two years, $\bar{w}$ is comparable at the two localities. A similar, slow growth rate was found for Macoma on the Forth (Elliott 1979), although the factors influencing this growth could not be explained.

Recruitment of spat into the Hydrobia population at Skinflats/

Skinflats began in July 1976 and June 1977. Mortality rates of the 1976 spat were high over the winter by comparison to the previous winter's spat mortality, so that coupled with a small 1+ population, only a small breeding population existed in 1977. Consequently spatfall was low in the second breeding season studied. Such differences in spatfall between years have also been recorded on the Dovey (Fish and Fish 1974) and at Torry Bay, Firth of Forth where Elliott (1979) found the 1976 spatfall to be lower than in 1975. Seasonal conditions vary markedly in northern latitudes such that fluctuations in populations are inevitable and resilience to such conditions becomes a feature of estuarine populations of invertebrates.

During the years studied at Skinflats mortality in terms of density of Hydrobia was highest in the first year of life and the period of maximal loss differed between areas. Losses of over 80% at upper shore sites during the recruitment phase (Phase I) occurred prior to the losses of similar magnitude from low shore sites during the winter mortality phase (Phase II). It seems most likely that recruitment at these low shore stations, where the breeding season was longer (Section 3.3.3), continued for a longer period and obscured the effects of mortality seen at up-shore stations. Additionally, risks from desiccation, or dilution by rainfall at upshore stations in the period immediately following spatfall may have increased mortality there relative to low-shore stations. The overall winter mortality was of a similar magnitude to that at Torry Bay (Elliott 1979) and the average monthly mortality was within the 10 - 20% per month found on the Grevelingen estuary (Wolff and de Wolf 1977) suggesting that mortality from all causes was similar at each location. The high/

high mortality following spatfall will result from unsuccessful recruitment and possibly from predation by deposit and suspension feeders (Hancock 1973, Meikilovsky 1974, Thorson 1966).

Mortality in the second year of life in terms of density was lower (mean monthly mortality = 8.3%) than that of 0+ animals but was high after the breeding season indicating that after breeding, they reach senility and die.

Of particular interest was the density and biomass increase during the spring and early summer (Phase II of 0+ cohort life history). It coincided with the onset of floating behaviour (personal observation) but if the proportion of the population engaged in floating is less than 1%, as on the Norfolk coast (Little and Nix 1976), then this cannot be entirely responsible for the immigration. The spring increase in density also featured in the population of *Hydrobia* at Torry Bay (Elliott 1979) but no data are available to offer an explanation.

The occurrence of high spat densities at B_3 and C_2 coincided with areas adjacent to the steep slope to the main river Forth channel, suggesting that passive stranding at the change of slope took place (Newell 1964). Since particle sizes of the sediments were similar over the whole mudflat, it could not follow that settlement was highest in areas where sediments were similar (Wolff 1974). There are two alternative suggestions: firstly, that spat will settle in areas away from the main adult population or predatory species and secondly, that chemical stimulus initiates settlement from the plankton, as occurs in *Nassarius obsoleta* in the USA (Scheltema 1961 in Elliott 1979). However, at Skinflats/

Skinflats spat settled at all stations, including those with high adult density), with occasional high settlement at upshore areas in addition to low shore sites. This indicates that passive settlement, dependent on water movements and tidal conditions, is operating rather than selection of sites in response to particle size, predator avoidance or chemical stimulus. Similarly, there was no evidence for the operation of these stimuli in settlement at Torry Bay (Elliott 1979) where again settlement was heaviest in the outer areas but was occasionally high at upshore sites.

(d) The production of Hydrobia

The mean annual biomass of the Hydrobia population revealed similar fluctuations to that of mean density, the summer peak and winter trough coinciding with spatfall and the period of minimal growth and maximal mortality respectively. This general pattern was also seen during 1975 - 1976 at Torry Bay (Elliott 1979).

Production in terms of g AFDW m^{-2} was highest for animals in their first year of life as found with other estuarine species, particularly bivalve molluscs (eg Chambers and Milne 1975, Elliott 1979, Hibbert 1976) and it declined in succeeding years. This pattern is also reflected in the P:B ratio which was highest in 0+ cohort during the period when energy is channelled more into growth than reproduction. Later, when more energy is diverted into reproduction, somatic production is reduced as in 1+ cohort of Hydrobia.

The mean annual P:B ratio of 1.17 is low in comparison to that at other localities. On the Grevelingen the P:B ranged from

1.24 and 1.36 to 1.78 g dry wt m^{-2} (Wolff and de Wolf 1977) and at Torry Bay the P:B in 1975-6 was 1.675 and in 1976-7, 1.77 (Elliott 1979). The mean biomass 3.32 g AFDW m^{-2} at Skinflats was also lower than that recorded at Torry (4.438 g AFDW m^{-2} 1975-6, 3.057 g AFDW m^{-2} 1976-7) and far below that on the Grevelingen estuary (7.23 - 12.79 g m^{-2} Wolff and de Wolf 1977).

The lower mean biomass and P:B ratio compared with other estimates probably reflects the position of Skinflats in the Forth estuary. Most of the area is above mid-tide height and since it is situated far up the estuary will be subject to wider fluctuations in environmental conditions. These are most likely to influence reproduction and the winter survival of the population and the effects will be more severe than at lower tidal levels further down the estuary. Also the life-span of Hydrobia at Skinflats is longer than on the Grevelingen which may influence the P:B ratio (Robertson 1979). The two factors together probably explain the lower P:B ratio.

3.4 The biomass and production of several benthic invertebrates at Skinflats

3.4.1 Introduction

For practical reasons it was not possible to study the production and ecology of all species of benthic invertebrates occurring at Skinflats. However, estimates of production can be made from mean annual biomass data either using published P:B ratios of the species studied elsewhere (eg Chambers and Milne 1975, Warwick and Price 1975, Wolff and de Wolf 1977) or from a regression equation relating P:B values and lifespans (y) of various marine organisms (Robertson 1979). The species studied at Skinflats included those likely to be preyed upon/

upon by wading birds and Shelduck.

Macoma balthica (Linneus 1758) (=*Tellina inconspicua*)is a deposit-feeding bivalve mollusc which, under certain environmental conditions, suspension-feeds. Its distribution is mainly boreal occurring in the North Atlantic and Arctic seas and extending into the North Pacific as far south as San Francisco Bay (Vassallo 1971). Inhabiting inter-tidal areas and shallow seas within its range, *Macoma* is often one of the most abundant species and the term'*Macoma* community' was coined by Peterson (1913) to describe an assemblage of animals in which *Macoma* dominates.

The density varies with locality from 52 m^{-2} (Cederwall 1977) to 16000 m^{2} in the Danish Waddensea when spat are included (Smidt 1951). *Macoma* thrives best at the relatively low temperatures of 0 - 15^{o}C and intertidally it prefers muddy substrates (Peterson 1913) being more abundant in fine sediments (Newell 1965) at mid-tide levels (Elliott 1979, Spooner and Moore 1941).

In the estuarine Firth of Forth, *Macoma* is widely distributed but particularly abundant in Torry and Culross Bays on the north shore and Bo'ness on the south shore. Here, together with *Hydrobia*, the populations probably support the large numbers of overwintering Knot (Bryant 1979). The ecology and production of *Macoma* at Torry Bay, Firth of Forth, has been studied in detail by Elliott (1979) on the Ythan by Chambers and Milne (1975) and more generally by researchers such as Warwick and Price (1975), Burke and Mann (1974) and Wolff and de Wolf (1977).

Cardium edule (Lineus 1858), the edible cockle (= *Cerastoderma edule*) is a suspension feeding bivalve mollusc. Although tolerant of/

of a wide range of sediments, it avoids areas with large deposits of detritus and prefers muddy sand. (Kristensen 1957). Tebble (1966) and Muus (1967) found that C. edule could tolerate salinities down to 10 - 12 ^{o}/oo Cl^{-} subtidally but in Danish waters, Peterson (1958) did not find it below 20 ^{o}/oo. Intertidally, cockles are infrequent in the upper tidal zones (Wolff 1973) and have highest densities at mid-tide (NERC 1976).

The cockle is one of the principal foods of the oystercatcher (Dare 1966, Hulscher 1964) and is important commercially particularly in the Wash (NERC 1976). Densities range from 64 m^{-2} on Mersey (Fraser 1932) to up to 1000 m^{-2} in muddy areas of Argyll (Raymont 1955). On the estuarine Firth of Forth, its distribution in 1974-5 was confined to Torry Bay and Carriden in densities of up to 200 m^{-2} (McLusky et al 1976) where no individuals older than three years were found. At Torry Bay, C. edule was mainly found in mid - upshore regions particularly in high shore areas of steeply-sloping coarse material. (Elliott 1979).

Production estimates have been made by Elliott (1979) on Firth of Forth, on the Lyhner (Warwick and Price 1975), in the Grevelingen estuary (Wolff and de Wolf 1977) and in Southampton Water (Hibbert 1976).

Nereis diversicolor (O. F. Miller) is a widely-distributed brackish-water polychaete common in European estuaries (Clay 1967a). It is tolerant of a wide range of salinities and temperatures and inhabits a variety of sediment types (Wolff 1973), although not favouring very soft muds (Thamdrup 1935) or very clean sands (Bassindale 1938, Spooner and Moore 1940, Stopford 1951). Its distribution is limited to more estuarine habitats by competition with marine species such as N. virens/

N. virens and *N. succinea* above 22 $^{o}/oo$ Cl^{-} (Wolff 1973) and by reproductive limitations in fresh-water habitats.

Densities of *N. diversicolor* vary from 10 - 200 m^{-2} in the polluted Tees estuary (Gray 1976) to 10000 m^{-2} in the Medway (Wharfe 1977) and 17000 m^{-2} in a brackish pool in Belgium (Heip and Herman 1979).

Nereis is prey to a variety of invertebrates such as *Asterias*, *Buccinum*, *Carcinus* and *Pagurida* (Blegvad 1914), in addition to vertebrates. Fish (Clay 1967) in particular flounders, *Platichthys flesus (L)* (Summers 1974) and both wading birds (eg Goss-Custard 1969, Goss-Custard *et al* 1977) and Shelduck (Buxton 1975) are important predators and *Nereis* are also used by fishermen as bait (Clay 1967).

Since 30 - 50% of *Nereis* population lives in burrows deeper than 5 cm in the substrate (Muus 1967), the behaviour of the worms is important in determining their accessibility to wading birds. They rhythmically irrigate their burrows when inundated by the tide approximately every 20 secs and occasionally extend from the anterior end in seach of food (Trevor 1977, Linke 1939). During irrigation, which lasts for about 40 seconds, the head lies just below the sediment surface and the body oscillates dorso-ventrally. The extent to which this occurs when the mudflats are exposed is not known but there is a vertical migration associated with the tidal ebb and flow (Vader 1964).

Production estimates of *Nereis diversicolor* have been made from the intertidal area of the Ythan estuary (Chambers and Milne 1975b) and from a shallow brackish-water pond in Belgium (Heip and Herman 1979).

Manayunkia aestuarina/

Manayunkia aestuarina (Bourne 1883) is a small tube-dwelling sabellid polychaete recorded from brackish estuarine localities in Britain, Ireland, Holland, Denmark and in the Baltic (eg MacKay et al 1978, Harris 1970, Kendall 1979, Gray 1976, Warwick et al 1979, Bourne 1883, Buchanan 1893, Ekman 1967). It has also been recorded from marine habitats (Harris 1970) but little is known about its ecology or, indeed, any aspects of its biology.

Although occurring in high densities up to 10^4 - 10^5, individuals m^{-2} (Zenkewitsch 1957, Muus 1967), its small size may have led to it becoming overlooked and account for the few records in estuaries. However, in the estuarine Firth of Forth, it has only been recorded in large numbers recently (McLusky 1979a). In January 1979, a mean density of 27562 m^{-2} was found at Kinneil. By August 1979, it had reached a mean density of 51570 m^{-2} at this locality with 103875 recorded at one site (McLusky 1979b). It is absent in areas of gross pollution on Forth and Clyde estuaries but is tolerant of moderate pollution levels (Mackay et al 1978, McLusky 1979 a and b, 1980). It appears therefore to be an opportunistic species.

Oligochaetes and spionids, like Manayunkia which fall, in size, between macrofauna and meiofauna, have generally been disregarded by researchers in both these fields but are very important community members in estuaries (eg Gray 1976, Warwick et al 1978). In Denmark oligochaetes alone contributed 150.3 g AFDW m^{-2} at one locality and 118.3 gm^{-2} at another (Dahl 1960). At Kinneil mudflat (McLusky 1979b), an estimate of 4.17g dry flesh wt m^{-2} was made for August 1979, second in biomass only to Nereis (6.85 g). Annual production was three times that of the macrofauna on the Lyhner estuary, Cornwall (Warwick/

(Warwick et al 1978) and on the inner Forth as a whole a production of 25 g dry wt m^{-2} was estimated by Teare (1979).

Many species of oligochaete are capable of tolerating moderate pollution (McLusky 1979b) and with the reduction of pollution on the Clyde, these opportunistic species have become abundant (MacKay et al 1978). On the Forth they are particularly abundant at Kinneil, Grangemouth docks area and near the mouth of the Grange Burn on the south shore and near the heated water discharge from Longannet power station and Culross Bay on the north shore (McLusky et al 1976).

At Skinflats Teare (1979) found that, of the oligochaetes, Tubificoides benedeni (= Peloscolex benedeni) was the most abundant and of the spionids Pygospio elegans was the only species present.

Important predators on oligochaetes include flatfish and gobiids, which feed mainly on tubificiids (eg Rees 1940, Dahl 1960, Muus 1967, Smidt 1951), large polychaetes (Muus 1967) Crangon crangon and Talitris spp. Reynoldson (1939) mentions bird predators on small worms, mainly enchytraids, but only Evans et al (1979) have suggested that may be an important food source for wading birds and shelduck on polluted estuaries, such as the Tees.

Corophium volutator (Pallas 1766) is a widespread intertidal amphipod found throughout the British Isles and N.W. Europe and on the east coast of N. America (Clay 1960b). Within its range it is patchily distributed with densities varying markedly within even small areas (eg Goss-Custard et al 1977). Densities range from a few hundred to several thousand m^{-2} (Clay 1960b) with a mean density at Benfleet Creek, Essex, of 35000 m^{-2} (Mossman 1977) but only 15 m^{-2} in Amerikahafen (Hagmeier and Kïnne 1951 in Clay 1960b). Watkin (1941/

(1941) recorded 63000 m^{-2} on Thames. Like many other estuarine animals *Corophium* avoids black foetid mud (Hart 1930) but is absent from clean sands (Stopford 1951) preferring muds with a high silt and organic content (Mossman 1977). It can tolerate salinities down to 2^{o}/oo but has a preferred estuarine distribution between 5 and 18 ^{o}/oo (McLusky 1971).

On the Forth estuary *Corophium* is sparsely distributed, present mainly where sediments are coarse (McLusky *et al* 1976) and is not considered to be an important prey item for wading birds. Valleyfield mudflat, the only area where high densities were recorded (McLusky 1976) has now been reclaimed. On other estuaries, *Corophium* is an important food for wading birds (eg Goss-Custard 1969), the flounder (Summers 1974), an insect *Bembidion lateralle* (Green 1954) and *Crangon vulgaris* (Plagman 1939). Its production ecology has been studied at Benfleet Creek, Essex, by Mossman (1977).

Species present in very small numbers and not studied at Skinflats include *Nepthys hombergii*, *Retusa obtusa*, *Eteone longa*, *Mya arenaria*, *Carcinus maenas*, *Littorina saxatilis* and diptera spp. (larvae only). (Appendix 7).

The aim of this section was to study the production ecology and depth distribution of the invertebrate species so that the food of waders and Shelduck and its availability could be quantified.

3.4.2 *Macoma balthica*

3.4.2 (i) *Distribution and density*

Macoma was widely distributed only being absent from Stations/

Stations C_1 from August 1976 - December 1977 and from B_1 in the August and November 1976 samples. The mean density during the sampling period (Fig 3.4.1a) ranged from a maximum of 479.9 $\pm$ 417 m^{-2} (September 1977) to a minimum of 240 $\pm$ 207 m^{-2} (December 1977). (Appendix 8). On transect A, the highest mean density throughout the sampling period occurred at A_1 (739 $\pm$ 338 m^{-2}) decreasing downshore to Station A_4 with 294 $\pm$ 132 m^{-2} and increasing at A_5 to 444 $\pm$ 276 m^{-2} (Fig 3.4.1b). On both B and C transects (Figs 3.4.1 c and d) the mean density increased downshore, the highest mean density being recorded at C_2 (472 $\pm$ 85 m^{-2}).

3.4.2 (ii) Age and growth

The population structure on each sampling occasion is shown by the size-frequency histograms (Fig 3.4.2). The identification of year classes was based on the histograms and winter growth ring analysis. Growth ring analysis was not considered a reliable method alone since interruption rings were common, obscuring the annual rings. The density of each cohort on each sampling occasion is shown in Table 3.4.1.

Six age classes were distinguishable representing the 1977, -76, -75, -74, -73 and 1972+ cohorts. Animals older than six years were grouped with the 1972 cohort since the growth rings were indistinguishable.

The spat was first taken in the sieves in August 1976 and was present in the samples taken in September 1977 (Fig 3.4.2). Numerically, the 1975 and '74 cohorts dominated the population in 1976 and, with a larger spatfall in 1977, the '77 cohort dominated from September onwards.

Growth/

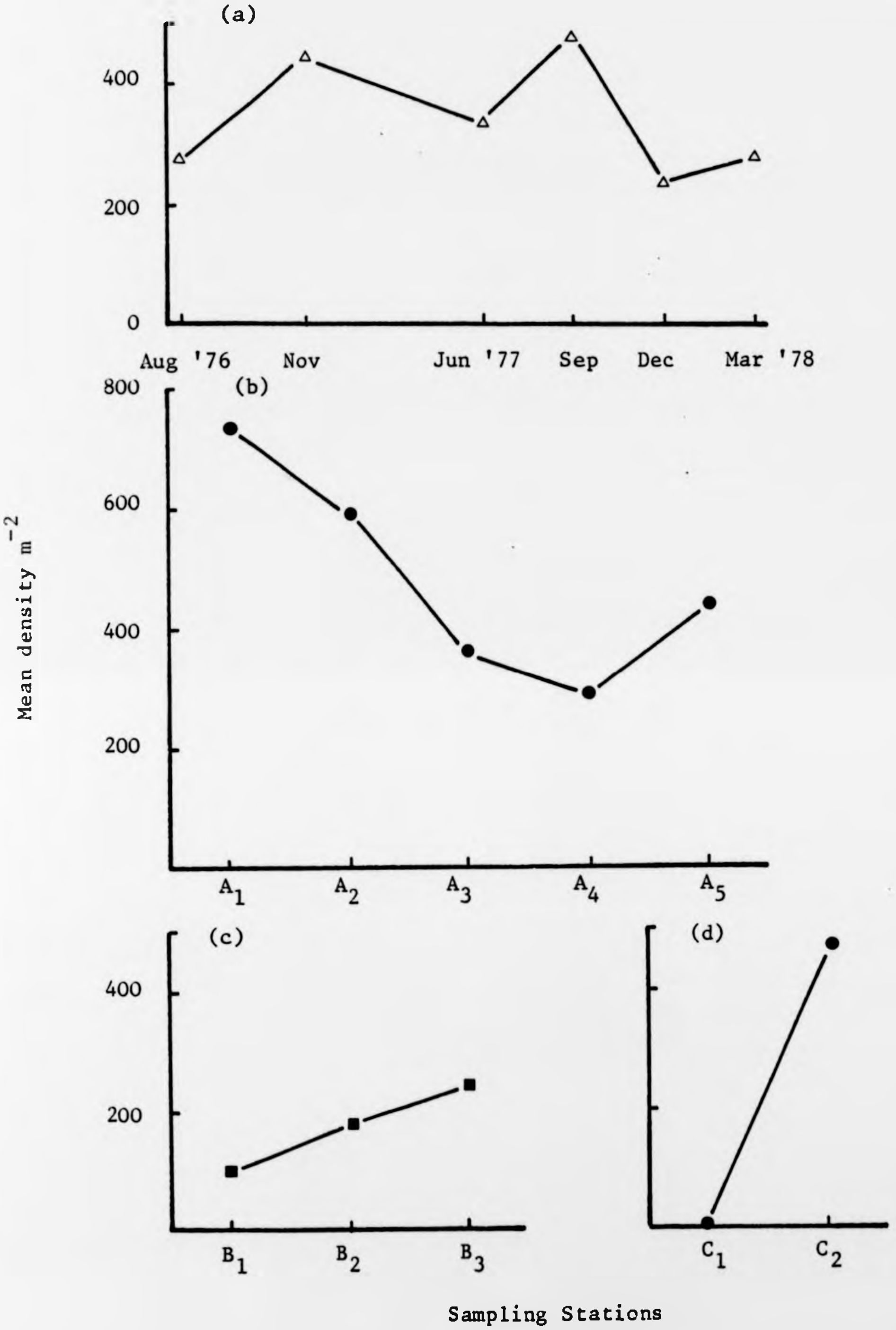

FIGURE 3.4.1: Mean density of <u>Macoma</u> (a) over the whole mudflat on each sampling occasion (b) on transect A (c) on transect B, and (d) on transect C

FIGURE 3.4.2: Size-frequency histograms of *Macoma* on each sampling occasion

⁙ 1972 year class

░ 1973 year class

▓ 1974 year class

▒ 1975 year class

█ 1976 year class

□ 1977 year class

rams
pling

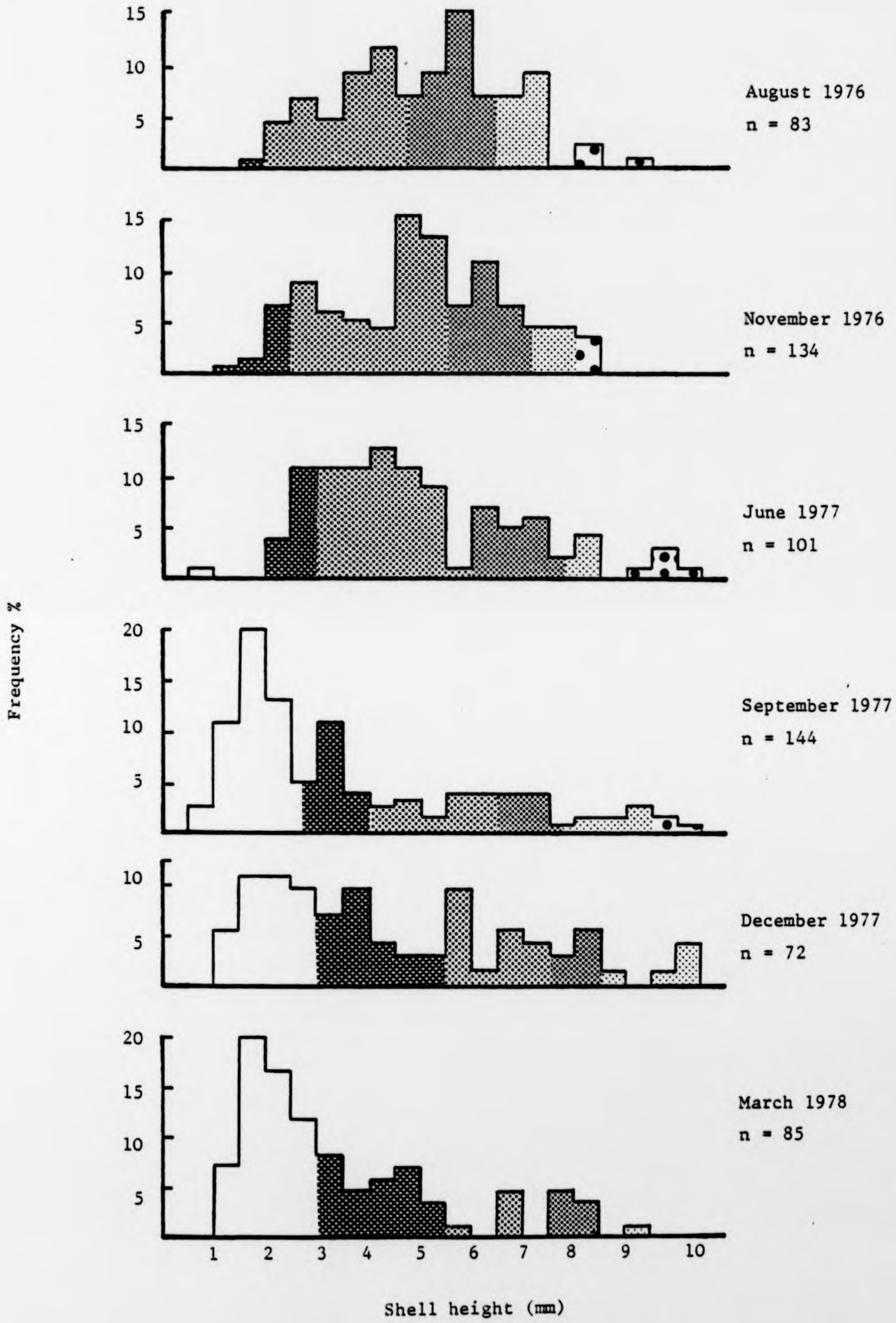
15
10
5
August 1976
n = 83
15
10
5
November 1976
n = 134
15
10
5
June 1977
n = 101
Frequency %
20
15
10
5
September 1977
n = 144
10
5
December 1977
n = 72
20
15
10
5
March 1978
n = 85
1
2
3
4
5
6
7
8
9
10
Shell height (mm)

TABLE 3.4.1: The density ($\bar{n}\ m^{-2}$) of each age class of <u>Macoma</u> on each sampling occasion

Age Class	Aug '76	Nov '76	Jun '77	Sep '77	Dec '77	Mar '78
'72+	10.0	16.7	16.7	10.0	3.3	-
'73	43.3	33.3	20.0	30.0	6.7	3.3
'74	113.2	116.7	59.9	36.7	26.7	23.3
'75	106.7	240	190	76.9	46.7	16.7
'76	3.3	40	46.7	90.0	63.3	83.3
'77	-	-	3.3	236.3	93.3	156.7

TABLE 3.4.2: The mean shell ht. (mm) of each age class of <u>Macoma</u> on each sampling occasion

Age Class	Aug '76	Nov '76	Jun '77	Sep '77	Dec '77	Mar '78
'72+	8.93 ± 0.9	8.32 ± 0.1	9.76 ± 0.4	10.13 ± 0.23	10.3	-
'73	7.08 ± 0.25	7.59 ± 0.23	8.17 ± 0.23	8.71 ± 0.54	9.3 ± 0.99	9.2
'74	5.64 ± 0.5	6.32 ± 0.4	6.75 ± 0.5	7.07 ± 0.32	8.15 ± 0.37	8.06 ± 0.32
'75	3.57 ± 0.79	4.26 ± 0.95	4.28 ± 0.78	5.43 ± 0.77	6.29 ± 0.59	6.58 ± 0.58
'76	2.0 ±	2.18 ± 0.3	2.65 ± 0.3	3.4 ± 0.4	4.13 ± 0.72	4.16 ± 0.7
'77	-	-	0.8	1.79 ± 0.43	2.1 ± 0.5	2.13 ± 0.52

Growth of the cohorts, measured as the increase in mean shell height of each cohort between successive sampling occasion is shown in Table 3.4.2. It is represented graphically in Figure 3.4.3. For all cohorts, growth was maximal between June and December with minimal growth during the winter months (December to March).

3.4.2 (iii) Length-Weight determination

On three occasions length-weight (AFDW) determinations were made. (Table 3.4.3). These were made in preference to height-weight regressions to facilitate the estimation of the weights of Macoma taken by overwintering birds (section 3.6).

Table 3.4.3: Parameters from regression $\log_{10}$ (AFDW) = a + b $\log_{10}$ (shell length (mm))

	N	'a' intercept	'b' regression coefficient	'c' correlatio coefficient
Aug 76	83	-1.9814	2.9153	0.9723
Nov 76	134	-1.847	2.7657	0.9628
Jun 77	101	-1.9251	2.9591	0.9684

A determination of length - height relationship was made so that height - weight relationship could be established.

The regression of length (mm) on height (mm) of shells was:

$$\text{Shell length}_{mm} = 1.2381 \times \text{shell height}_{mm} + 0.1781$$

Estimated from the August 1976 sample. (n = 83) r = 0.9692

Length - weight determinations for September 1977 were made from the August 1976 regression and for December 1977 and March 1978 from the November 1976 regression.

3.4.2 (iv)/

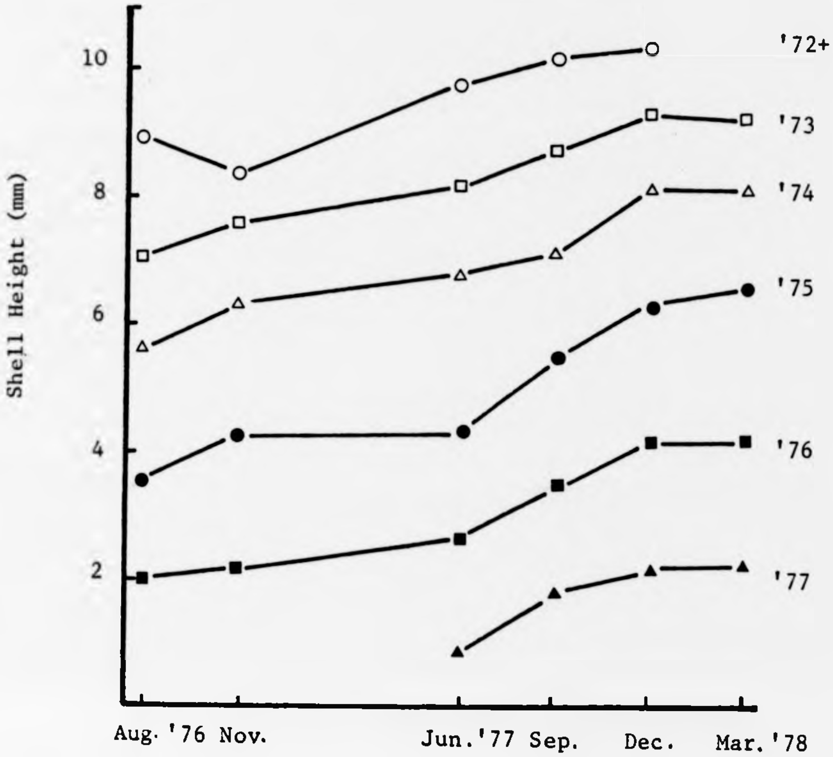

FIGURE 3.4.3: Mean shell height (mm) of each year class of *Macoma* on each sampling occasion

3.4.2 (iv) Biomass and production of Macoma

The biomass (gAFDW m^{-2}) of Macoma was estimated for each sampling occasion from which the production (gm^{-2}) of the whole population and of each constituent cohort was calculated for the period August 1976 - September 1977. The results are summarised in Tables 3.4.4 and 3.4.5 and the full computation of biomass and production are shown in Appendices 9 and 10.

The mean biomass of all cohorts (August 76 - September 77) was 1.29 gAFDW m^{-2} and the total production during this period 0.748 gAFDW m^{-2} giving a P:B ratio of 0.59:1. Assuming a calorific value of 4.77 kcal g^{-1}, production = 3.57 kcals (14.9 kJ) m^{-2}. The 1975 cohort contributed the largest proportion to the total production (317.75 mg AFDW m^{-2} = 44%), the newly settled spat (1977 cohort) the least, (13.18 mg). Production increased from the 1977 cohort through to the 1975 cohort and declined thereafter. The low production of the 1976 cohort was due to the poor spatfall in that year.

3.4.2 (v) Depth distribution of Macoma

The depth distribution of Macoma was determined in November 1977 and again in January 1978. In November 1977 all animals sampled occurred in the top 7 cm and 81% in the top 4 cm. In January 1978, only one animal was found in the 7 - 10 cm zone and 88% occurred in the top 4 cm (Fig 3.4.4).

There were significant differences in the mean size of Macoma from the surface - 1 cm and 1 - 4 cm zones in both November 1976 and January 1977. In November the mean sizes were 2.26 ± 0.68 mm and 6.35 ± 3.3 mm in each depth respectively and in January they were 2.88 ± 0.98 mm and 4.51 ± 2.6 mm

(November/

TABLE 3.4.4: Summary of the Biomass (mg AFDW m^{-2}) of each *Macoma* cohort on each sampling occasion

Cohort Sampling Occasion	1977	1976	1975	1974	1973	1972+	Total
Aug '76	-	0.594	94.874	638.4	268.5	120.6	1123.97
Nov '76	-	10.4	372.0	736.9	244.8	157.6	1520.80
Jun '77	0.06	21.9	345.8	404.3	235.6	330.2	1337.86
Sep '77	30.73	70.2	222.9	258.8	336.9	173.2	1092.73
Dec '77	22.37	90.52	206.0	216.8	84.35	55.7	675.74
Mar '78	39.0	120.79	83.3	187.8	40.95	0.0	471.84
Mean biomass Aug '76 - Sep '77	15.40	25.77	258.89	509.6	271.45	195.4	1268.84

TABLE 3.4.5: Summary of the production by all cohorts of *Macoma* between each sampling occasion

	1977	1976	1975	1974	1973	1972+	Total
Aug '76	-	-	-	-	-	-	-
Nov '76	-	+ 1.73	+114.4	+ 78.13	+ 44.05	- 34.98	203.33
Jun '77	-	+ 9.09	+ 58.05	+ 37.95	+118.28	+172.51	395.88
Sep '77	+13.18	+21.17	+145.3	+ 15.44	- 13.75	- 32.71	148.63
Dec '77	+18.13	+49.82	+93.02	+ 34.13	+ 38.37	- 2.93	230.54
Mar '78	+ 2.5	+ 1.47	+18.04	- 2.24	- 1.83	0	17.94
Total production Aug '76 - Sep '77	+13.18	+31.99	+317.75	+131.52	+148.58	+104.82	747.84
P:B Aug '76 - Sep '77							0.59

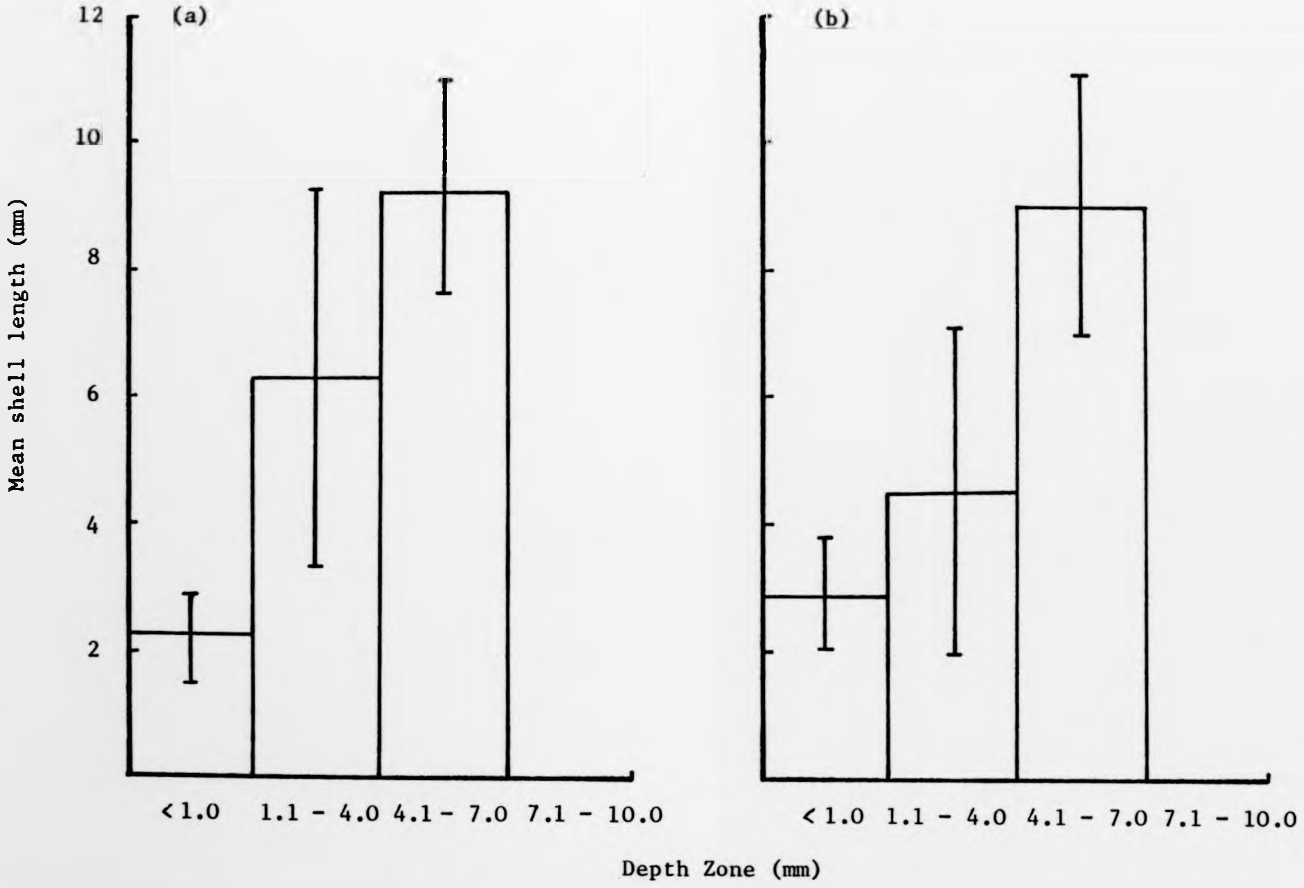

FIGURE 3.4.4: The mean shell length (± 1SD) of Macoma in each sampling depth zone in (a) November 1977 and (b) January 1978

(November t = 3.83 **; January t = 2.4 *). Significant differences in the mean size of Macoma were also found between the 1 - 4 cm and 4 - 7 cm zones in November (t = 2.41 *), although the differences in January were not significant. The mean shell height in the 4 - 7 cm zone was 9.28 ± 1.76 mm in November and 9.0 ± 2.07 mm in January.

To assess the availability of Macoma to wading birds and Shelduck, the bivalves were divided into three classes by length: $\leqslant$ 3 mm, 3 - 8 mm, and 8+ mm, and the proportion occurring at each depth (Fig 3.4.5). Of the $\leqslant$ 3 mm class, 75% dwelt in the top 1 cm in November and 61% in January. None was found deeper than 4 cm.

The 3 - 8 mm class was principally located in the 1 - 4 cm zone in both November and January (84% and 63.6% respectively) but a larger proportion was found in the top 1 cm in January (27.3% compared to 5.2% in November).

Of the 8+ mm class, none was located in the top 1 cm, 45% and 25% in respective months in the 1 - 4 cm and the majority in the 4 - 7 cm zone. Only in January were any Macoma found deeper than 7 cm (n = 1).

3.4.3 Cardium edule

(i) Distribution and density

In the large samples Cardium occurred at very few stations and were confined to the outer areas of the mudflat (Table 3.4.6). It was absent in all areas in June 1977 and March 1978 occurring consistently only at A_4 on the other sampling occasions. Records from other stations included

B_3/

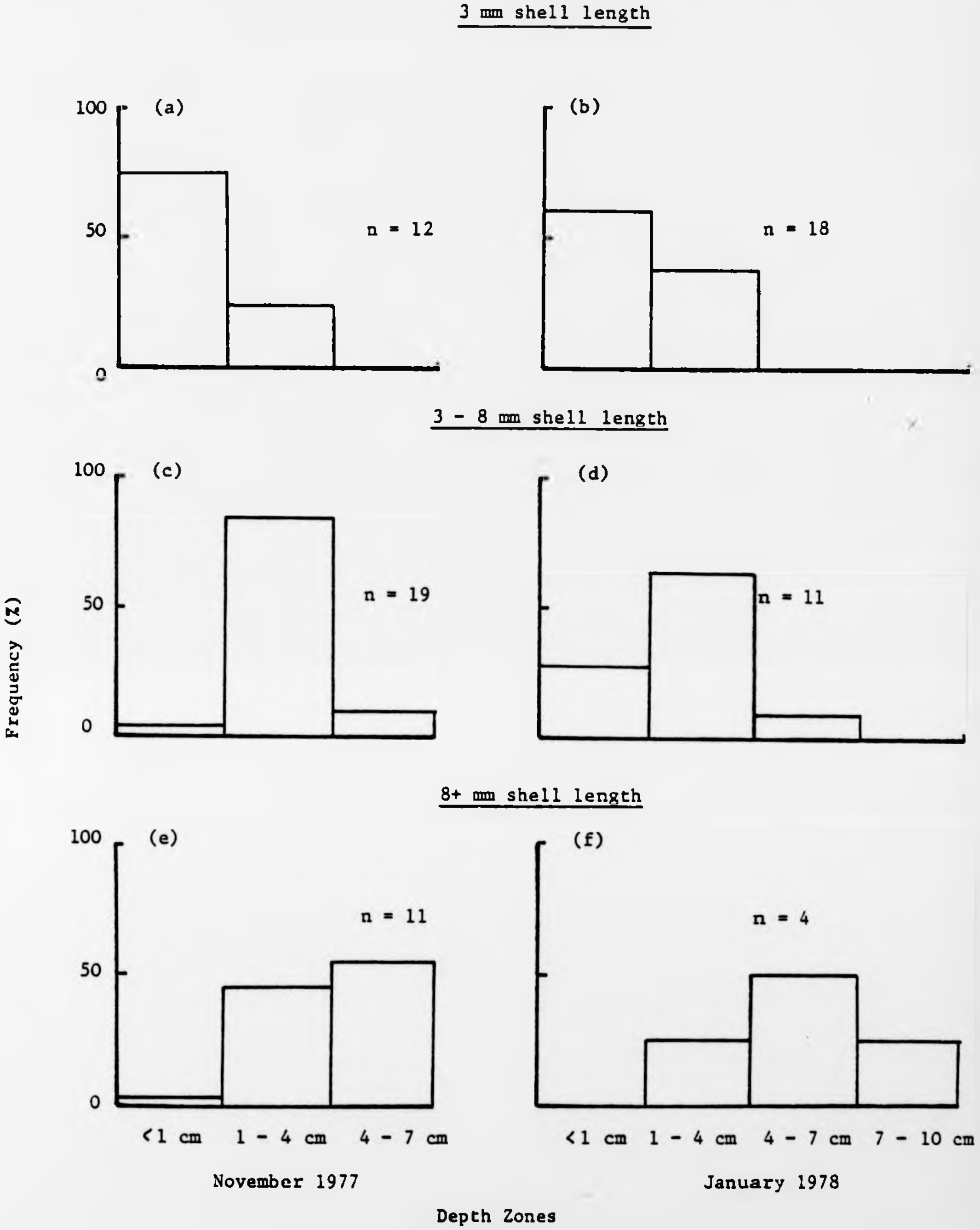

FIGURE 3.4.5: The depth distribution of three size classes of <u>Macoma</u> on two occasions during the winter 1977/78.

B_3 and C_2 in August 1976, B_2 in November 1976, A_3 in September 1977 and at A_5 in both November 1976 and September 1977.

Table 3.4.6: The occurrence of Cardium edule at Skinflats

Month	Station	N m^{-2}
Aug. 1976	A_4 B_3 C_2	367 100 33
Nov. 1976	A_4 A_5 B_2	867 633 33
Sep. 1977	A_3 A_4 A_5	33 233 100
Dec. 1977	A_4	100

The highest numbers were also located at A_4 on all occasions. In the small samples cockles were present in December 1975, July '76 - January '77 and in September '77 at A_3, A_4 and A_5 only.

Over the mudflat as a whole, the density ranged from 10.0 m^{-2} in December '77 to 150 m^{-2} in November '76 (Table 3.4.6).

3.4.3 (ii) Size distribution

The population of Cardium at Skinflats consisted mainly of small individuals with 100% less than 6 mm long in August 1976/

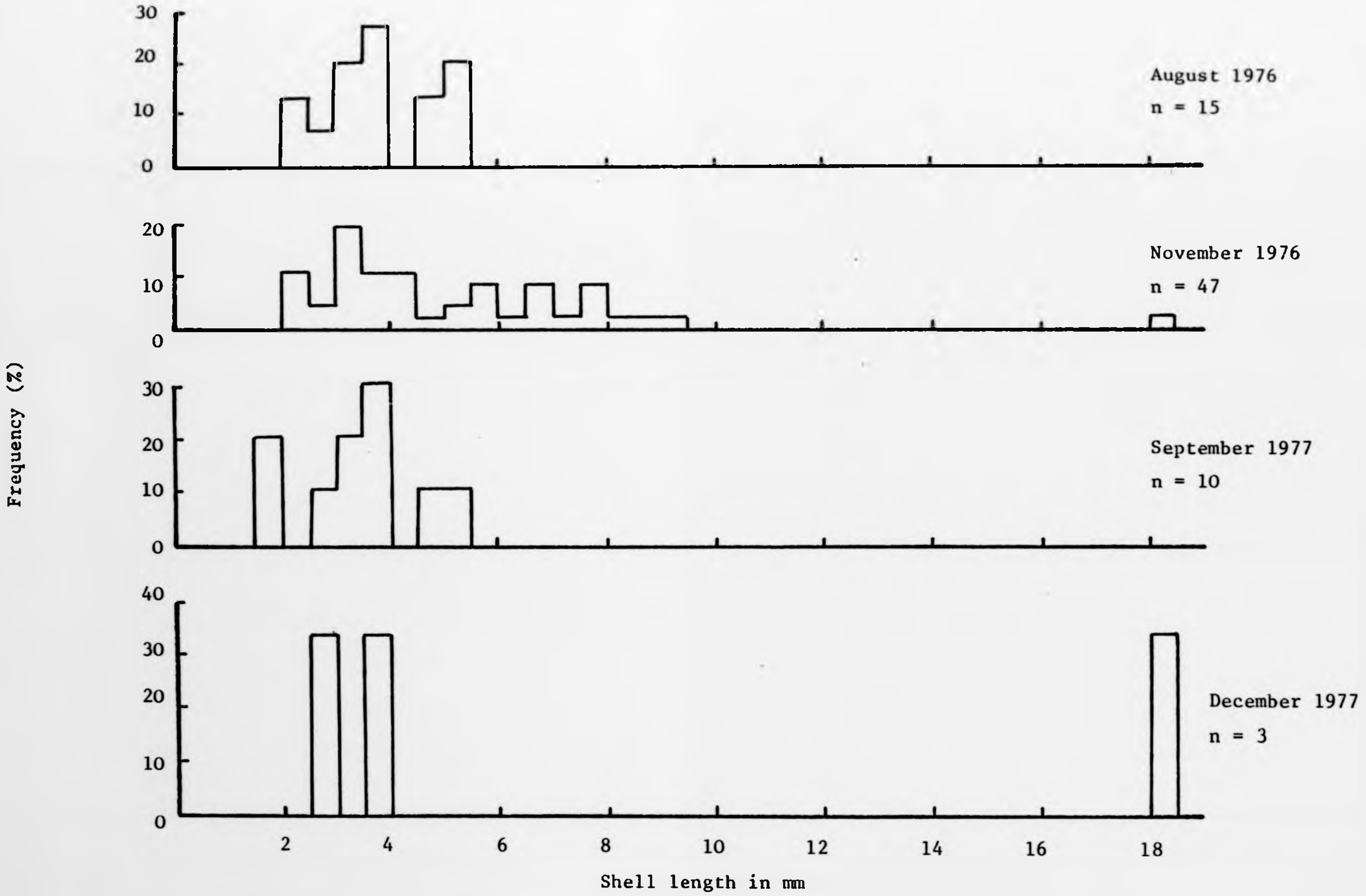

FIGURE 3.4.6: Size-frequency histograms of *Cardium edule* on each sampling occasion

TABLE 3.4.7: Computation of the biomass (g AFDW m^{-2}) of *Cardium edule*

Sampling Month	Density n m^{-2}	Mean Shell Length mm	Mean Shell Height mm	Mean Ind. Wt AFDW mg	Biomass $\overline{B}$ mg
Aug '76	50.0	3.85 ± 1.09	3.34	0.60	30
Nov '76	150.0	5.29 ± 2.9	4.69	1.53	229.5
Jun '77	0	-	-	-	-
Sep '77	36.7	4.19 ± 2.52	3.66	0.77	28.3
Dec '77	10.0	8.8 ± 8.73	8.00	6.77	67.7
Mar '78	0	-	-	-	-

1976 and September 1977 (Fig 3.4.6). In November 26% of the population were between 6 and 10.5 mm and in December, when three individuals were sampled, only 33% were > 6 mm.

3.4.3 (iii) Biomass and production

Biomass estimates for Cardium during the whole sampling period are shown in Table 3.4.7, from which the annual production between June 1977 and March 1978 was computed.

Calculation of biomass required the use of two conversions (after Elliott 1979):

(1) $\text{shell height}_{\text{mm}} = (0.9416 \pm 0.006 \times \text{shell length}) - 0.2892$

(2) $\text{dry flesh wt}_{\text{mg}} = \dfrac{\text{shell height}}{47.86}_{\text{mm}}^{\,2.78 \pm 0.26}$

Total biomass was highest in November 1976 with 229.5 mg m^{-2} following settlement but was low in both August 1976 (30 mg m^{-2}) and September 1977 (28.3 mg m^{-2}).

The mean biomass from August 1976 - September 1977 was 71.95 mg m^{-2} giving a production of 72.74 mg AFDW yr^{-1} calculated from a P:B ratio of 1.011:1 by Elliott (1979) for the Torry Bay populations. Assuming a calorific equivalent of 4.77 kcals (19.97 kJ), g^{-1} AFDW as for Macoma (Chambers and Milne 1975b), the total annual production of Cardium was 0.003 kcals (0.01 kJ) m^{-2} yr^{-1}.

3.4.4 Nereis diversicolor

3.4.4 (i) Distribution and density

Nereis was widely distributed at Skinflats occurring at all/

all stations. The mean density in the top 10 cm ranged from 381.5 ± 364 m^{-2} in August 1976 to 183.2 ± 201 m^{-2} in March 1978, the density declining throughout the study period (Fig 3.4.7). The highest numbers were recorded in August 1976 and September 1977 following spatfall. The spatial differences in mean density throughout the study are shown in Figs 3.4.8 a-c. On both transects A and B, high densities were recorded at upshore sites (A_1 = 522.3 ± 237.3 m^2, B, = 520 ± 254 m^{-2}), decreasing downshore. The mean densities on transect C were low by comparison with A and B transects. The fluctuations about the means at all stations were high as shown by the large standard deviations.

3.4.4 (ii) Population structure and growth

Although small worms of jaw length 0.2 mm were present throughout the year, they were most abundant in August 1976 when they comprised 36% of the population (Fig 4.3.9). Small worms were still present in large numbers in November but by June 1977 had either grown or been predated and larger worms with jaw length 0.4 mm predominated (46% population). Small (0.2 mm jaw length) worms were again present in large numbers in September 1977 suggesting that spat settle between June and September. There is some indication of a secondary spatfall in March. (Fig 3.4.9).

The proportion of large worms of +0.6 mm jaw length in the population fell markedly between August 1976 and June 1977 either through death or growth to sizes dwelling deeper than 10 cm. They were present in large numbers again in September suggesting that rapid growth had ensued. Similarly, in the second/

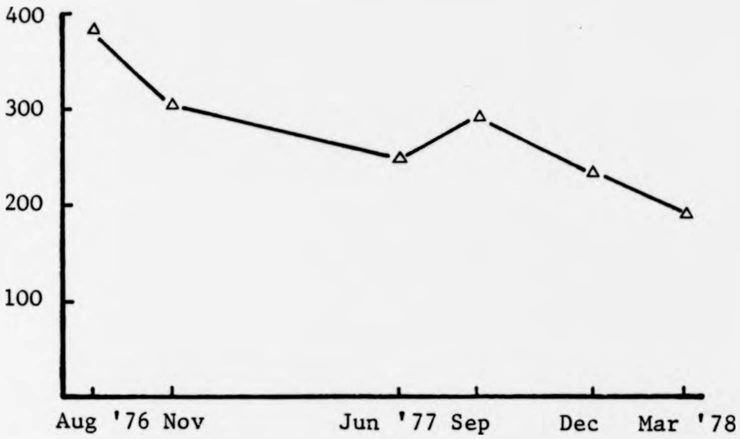

FIGURE 3.4.7: The mean density of Nereis on each sampling occasion

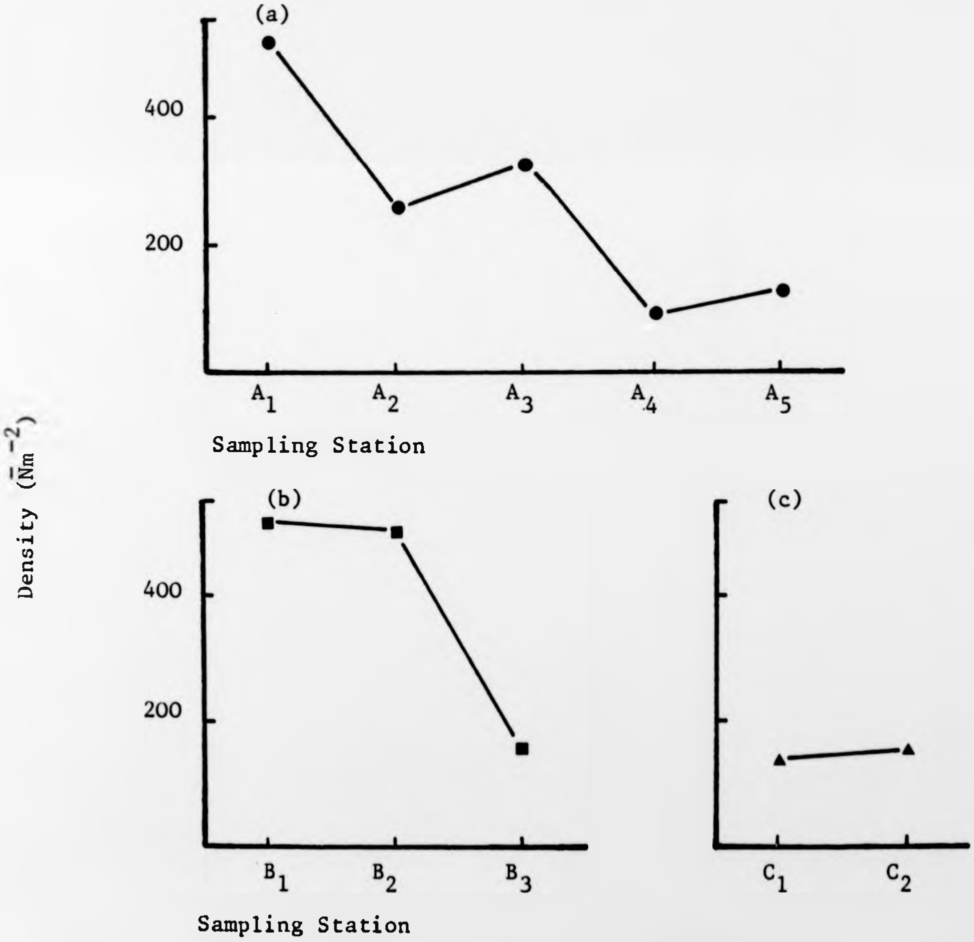

FIGURE 3.4.8: The mean density of Nereis at each sampling station during the study period. (a) Transect A (b) Transect B (c) Transect C

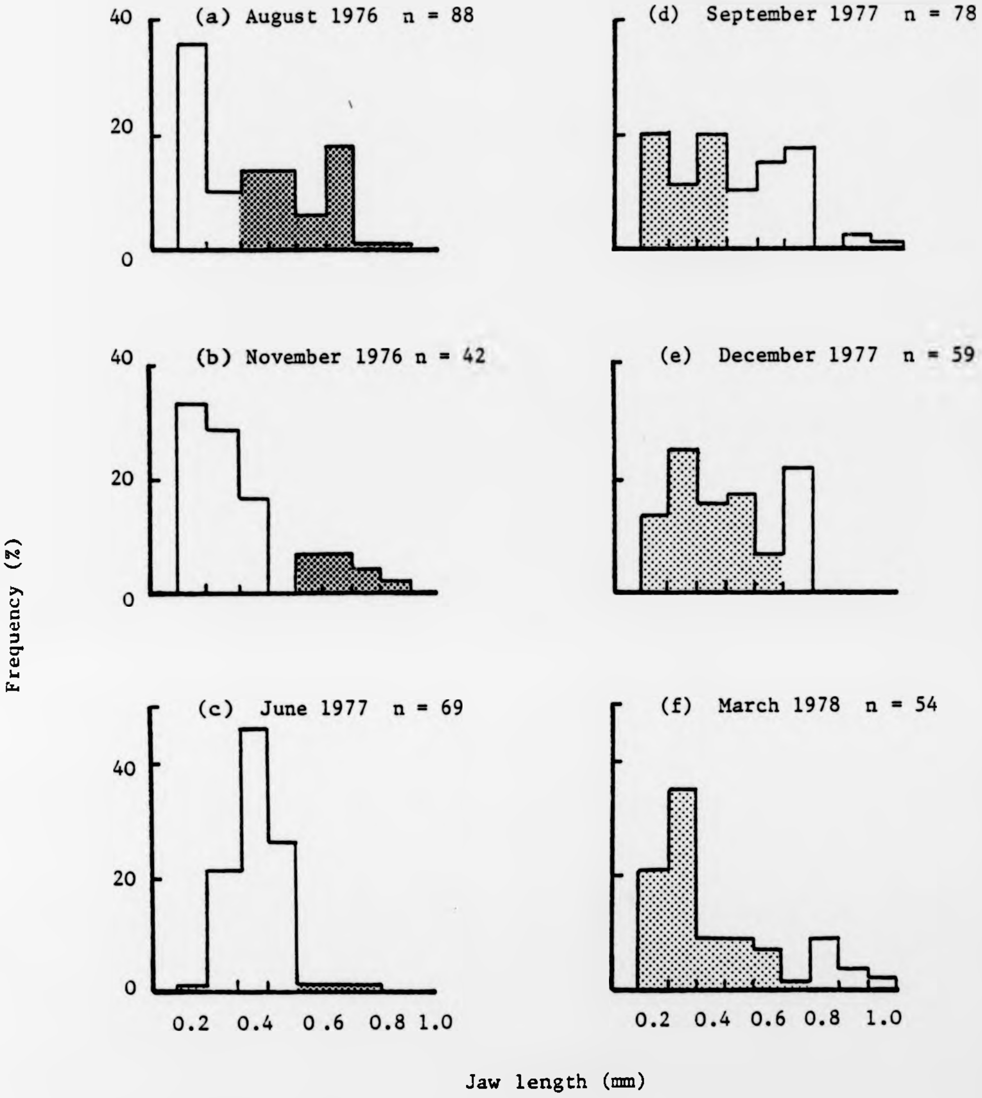

FIGURE 3.4.9: Size-frequency histograms of Nereis jaws on each sampling occasion

▩ 1975 age class

□ 1976 age class

░ 1977 age class

second study year, the proportion of large worms had fallen substantially by March 1978. From the size-frequency histograms, it appears that Nereis lives for approximately two years at Skinflats although it is possible that older individuals dwell deeper than 10 cm and were not sampled.

3.4.4 (iii) Jaw length - body weight regressions

A regression equation of values of jaw length and body weight was computed from the November 1976 sample:

$$\text{body wt}_{\text{mg}} = \text{jaw length}_{\text{mm}}^{\;3.2174}\ (1.3533\ )\quad (n = 22)$$

Jaw length - body weight regressions for the remaining sampling occasions were taken from Chambers and Milne (1975) for Nereis diversicolor occurring in upshore regions.

3.4.4 (iv) Biomass and production of N diversicolor

Mean Biomass ($\bar{B}$) estimates for Nereis derived from the mean monthly density and an estimation of the mean individual weights ($\bar{w}$ mg) (Chambers and Milne 1975b) are shown in Table 3.4.8. Assuming a P:B ratio of 3:1 (Chambers and Milne 1975b) production in the top 10 cm of sediment for the period August 1976 to September 1977 was 1.07 gAFDW m^{-2} from a mean biomass of 0.355 gAFDW m^{-2}. Assuming a calorific value of 4.36 kcals (18.25 kJ) g^{-1}, (Chambers and Milne 1975), this is equivalent to 4.67 cals (19.55 kJ) m^{-2}. Mortality (mg d wt m^{-2}) increased between successive sampling occasions (Table 3.4.8) with 29.62 mg lost between December and March 1977/78.

3.4.4 (v) Depth distribution of N diversicolor

The depth distribution of Nereis in November'77 is shown in Figure 3.4.10. Assuming that the worms withdraw into their burrows/

TABLE 3.4.8: Computation of the biomass ($\bar{B}$mg) mortality (ΔM) of <u>Nereis</u> during the study period

	Density ($\bar{n}$ m^{-2})	Jaw length $\bar{l}$ (mm)	miw ($\bar{w}$ mg)	Biomass ($\bar{B}$ mg)	-Δ N	$\bar{w}$	Δ M (mg)
Aug '76	381.5 ± 364	0.41 ± 0.20	0.78	298.8			
Nov '76	307.3 ± 290	0.37 ± 0.10	0.92	282.7	-74.2	+0.14	10.388
Jun '77	253.3 ± 228	0.41 ± 0.10	1.20	304.7	-52.0	+0.28	14.56
Sep '77	293.3 ± 206	0.48 ± 0.2	1.83	535.5	+40	+0.63	25.2
Dec '77	233.4 ± 147	0.44 ± 0.18	1.50	349.8	-59.9	-0.33	19.767
Mar '78	183.2 ± 201	0.47 ± 0.22	2.09	383.3	-50.2	+0.59	29.618
Mean biomass Aug '76 - Sep '77				355.4			

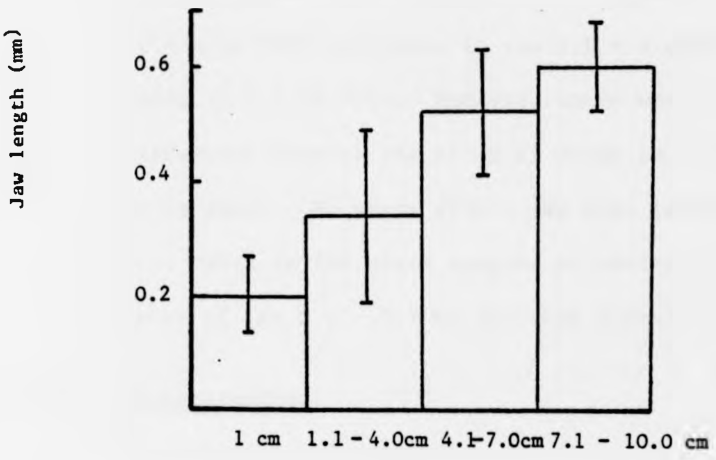

FIGURE 3.4.10: The mean size (Jaw length mm ± 1SD) of Nereis in each depth zone, November 1977

burrows when disturbed, the results indicate that larger individuals are found at greater depths. They occurred at all depths but there was a significant difference between the size of worms inhabiting the top 1 cm and 1.1 - 4 cm zones ($t = 4.44$ ***) and those in the 1.1 - 4 cm and 4.1 - 7 cm zones ($t = 4.66$ ***). However, there was no significant difference between the sizes of worms in the 4.1 - 7 and 7.1 - 10 cm zones. No worms with a jaw size larger than 0.7 mm were taken in the depth samples so that production is assumed to be of the 0.2 - 0.7 mm jaw-size animals only.

3.4.5 Manayunkia aestuarina

3.4.5 (i) Distribution and density

Manayunkia aestuarina was not recorded in either December 1975 or January 1976 and between February and August, the mean density was low (Fig 3.4.11). However, from August 1976 until the end of the sampling period, the mean density rose to a maximum of 53000 ± 43240 in March 1978. The largest increase was between September 1977 and March 1978.

Manayunkia was present on all sampling occasions at A_2 from February 1976 onwards and at B_2 from March of that year until the end of the sampling programme. At A_1 and A_3 it was only absent in one and two months respectively during this period. Occurrence was less consistent at A_4 and A_5 and on B_1, B_3 and transect C.

The mean density at each station over the period (Fig 3.4.12) illustrates the high density at A_2 and B_2 and decreasing numbers at lower tidal levels on these two transects. The mean density at both sites on transect C was low (10522 ± 14370/

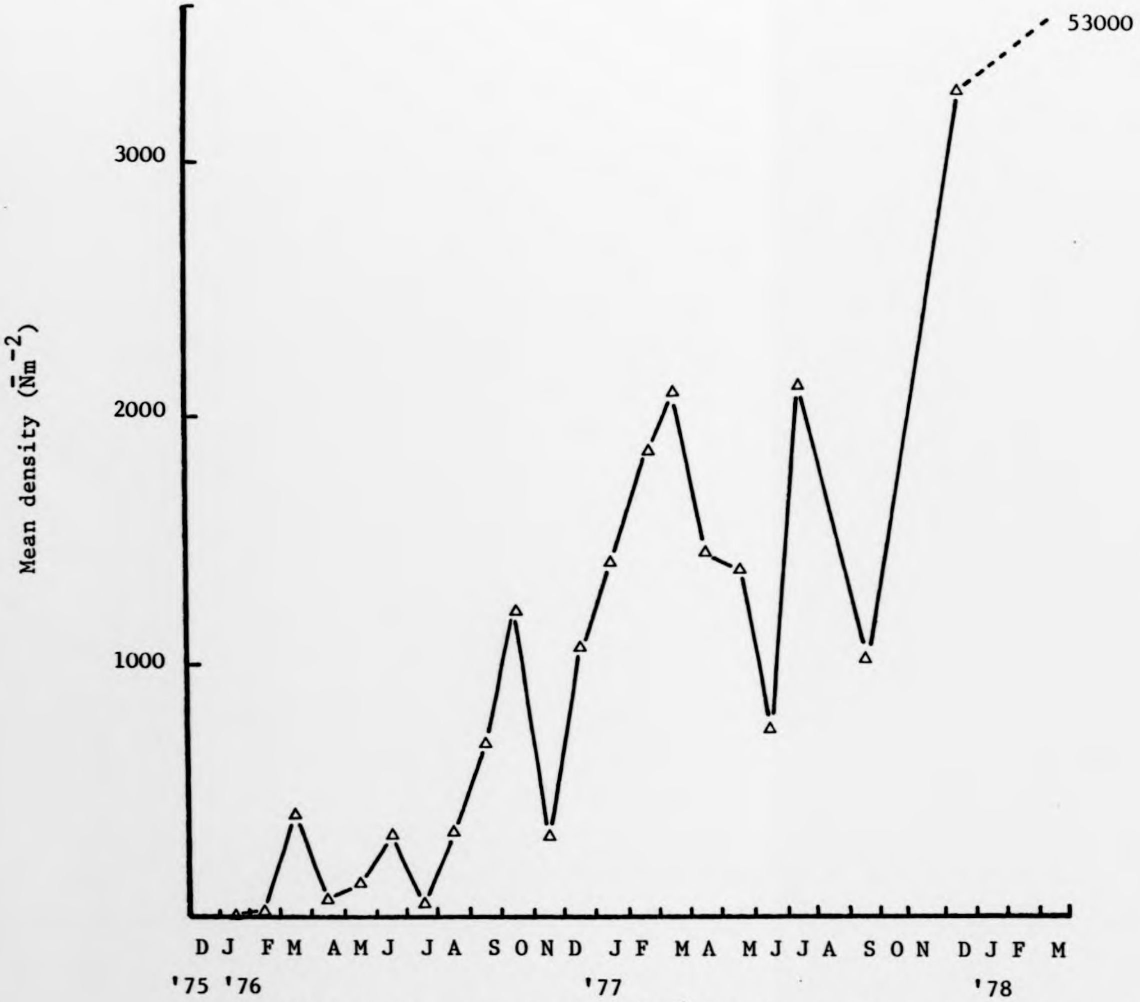

FIGURE 3.4.11: The mean density ($\bar{N}m^{-2}$) of Manayunkia at Skinflats during the sampling period

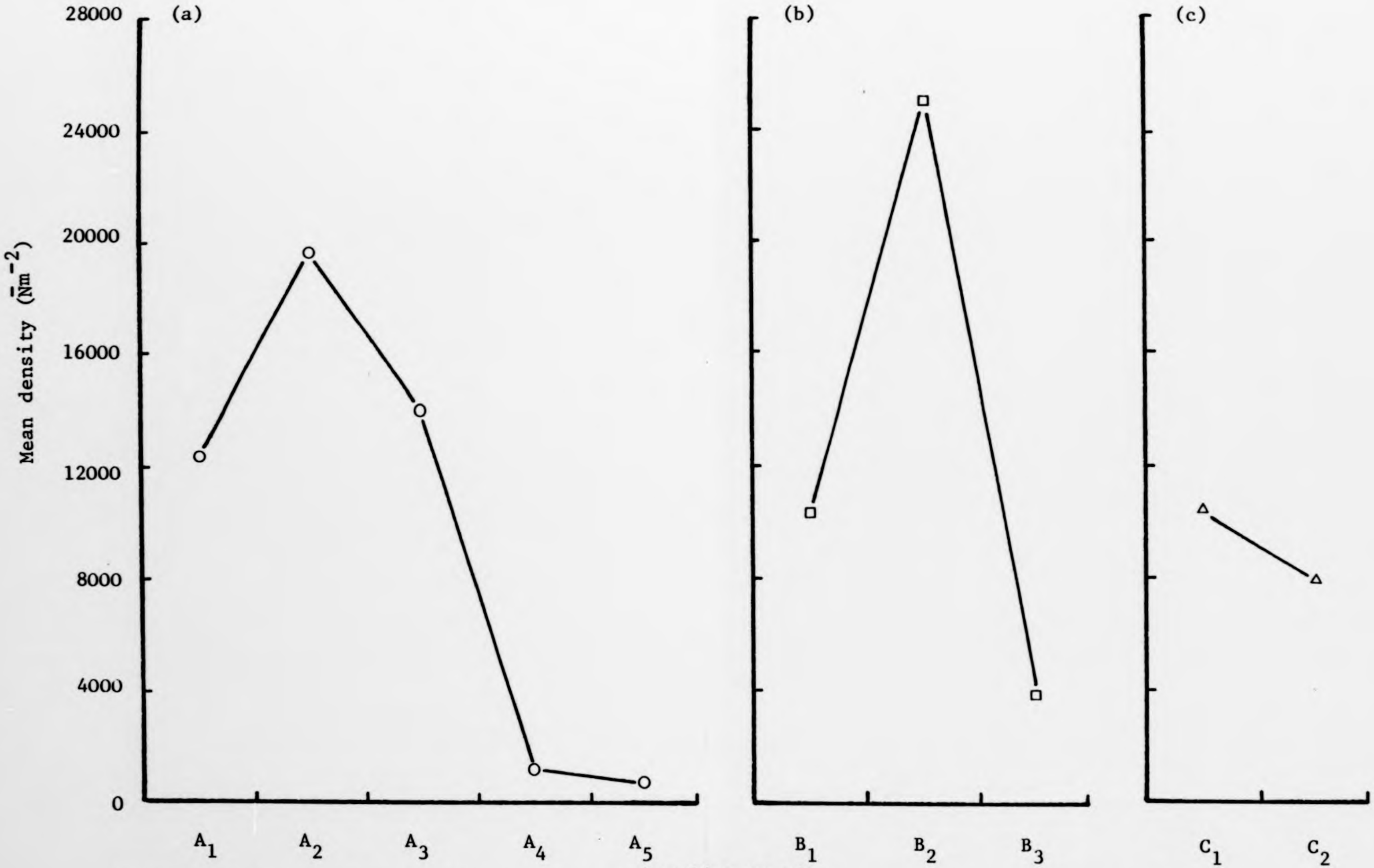

FIGURE 3.4.12: The mean density of Manayunkia at each sampling station during the study period (a) Transect A (b) Transect B (c) Transect C

TABLE 3.4.9: Computation of the mean biomass of *Manayunkia*

	mean density nm^{-2} ± 1SD	mean biomass B mg m^{-2}
July '76	480 ± 860	5.760
August	3480 ± 4462	41.760
September	7000 ± 13320	84.000
October	1240 ± 1313	14.880
November	3360 ± 4200	40.320
December	10640 ± 11040	127.680
January '77	14080 ± 16530	168.960
February	18560 ± 19184	222.720
March	20840 ± 16888	250.080
April	14400 ± 16313	172.800
May	13800 ± 12440	165.600
June	7480 ± 7563	89.760

14370 and 8000 ± 12953 respectively). The high standard deviations reflect the absence of worms on many occasions.

3.4.5 (ii) Population structure

No information is available on the population structure of Manayunkia.

3.4.5 (iii) Biomass and production

Assuming a mean individual weight of 12 μg for Manayunkia at Skinflats (Teare 1979), and a P:B ratio of 5.46:1 as found for Ampharete acutifrons which has a similar life history (Warwick et al 1978), 0.630 g dry wt m^{-2} of flesh was produced annually from a mean biomass (Table 3.4.9) of 0.115 g of dry flesh m^{-2} during the period July 1976 to June 1977.

3.4.6 Spionidae

(i) Distribution and density

Spionids occurred sporadically at all stations but were present most frequently at A_4 and A_5 between December 1975 and August 1976. After this period, the mean density over the mudflat as a whole (Fig 3.4.13) increased to give peaks in December 1976 (2560 ± 2792 m^{-2}) and May 1977 (2240 ± 4874 m^{-2}) but subsequently decreased to the end of the sampling period ($\bar{x}$ = 320 ± 492 m^{-2} March 1978). During the expansion period, occurrence became less sporadic, particularly at B_2 and B_3. The mean density at each station (Figure 3.4.14) was highest at A_4 (1391 ± 2082 m^{-2}) and B_2 (1130 ± 2060 m^{-2}) and lowest on transect C. On transect A, the low level of abundance at A_3 is striking.

(ii)/

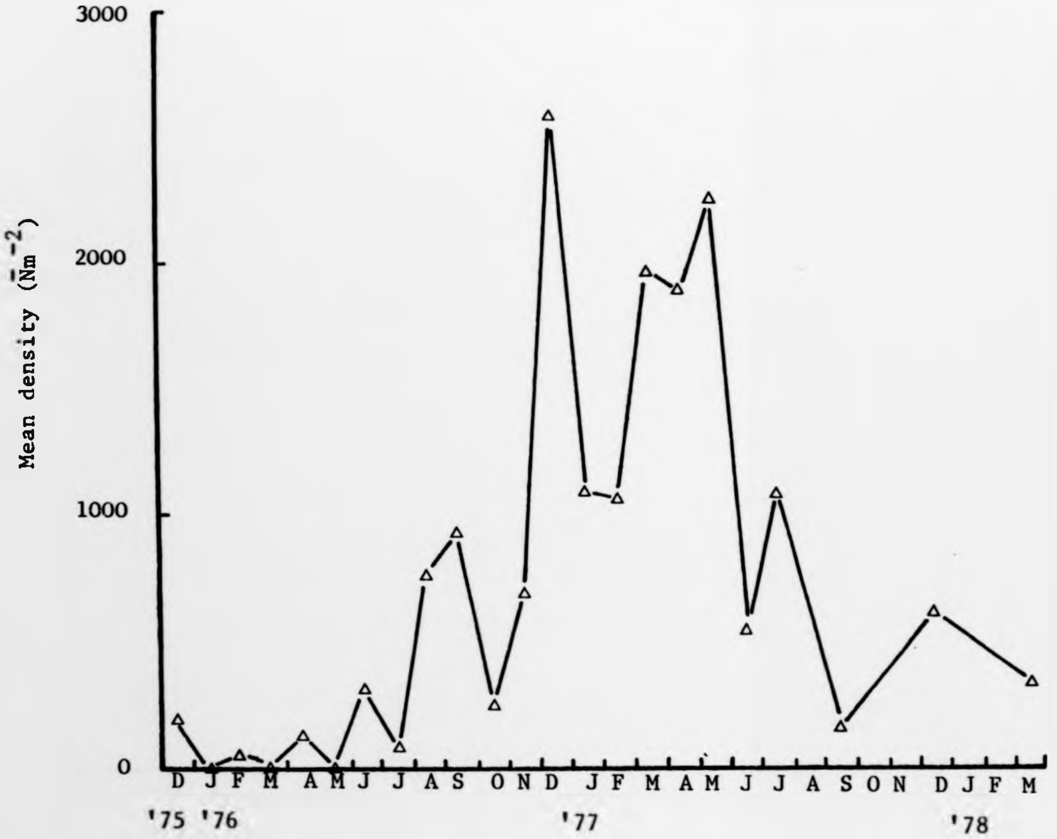

FIGURE 3.4.13: The mean density of <u>Spionid</u> spp. at Skinflats during the study period

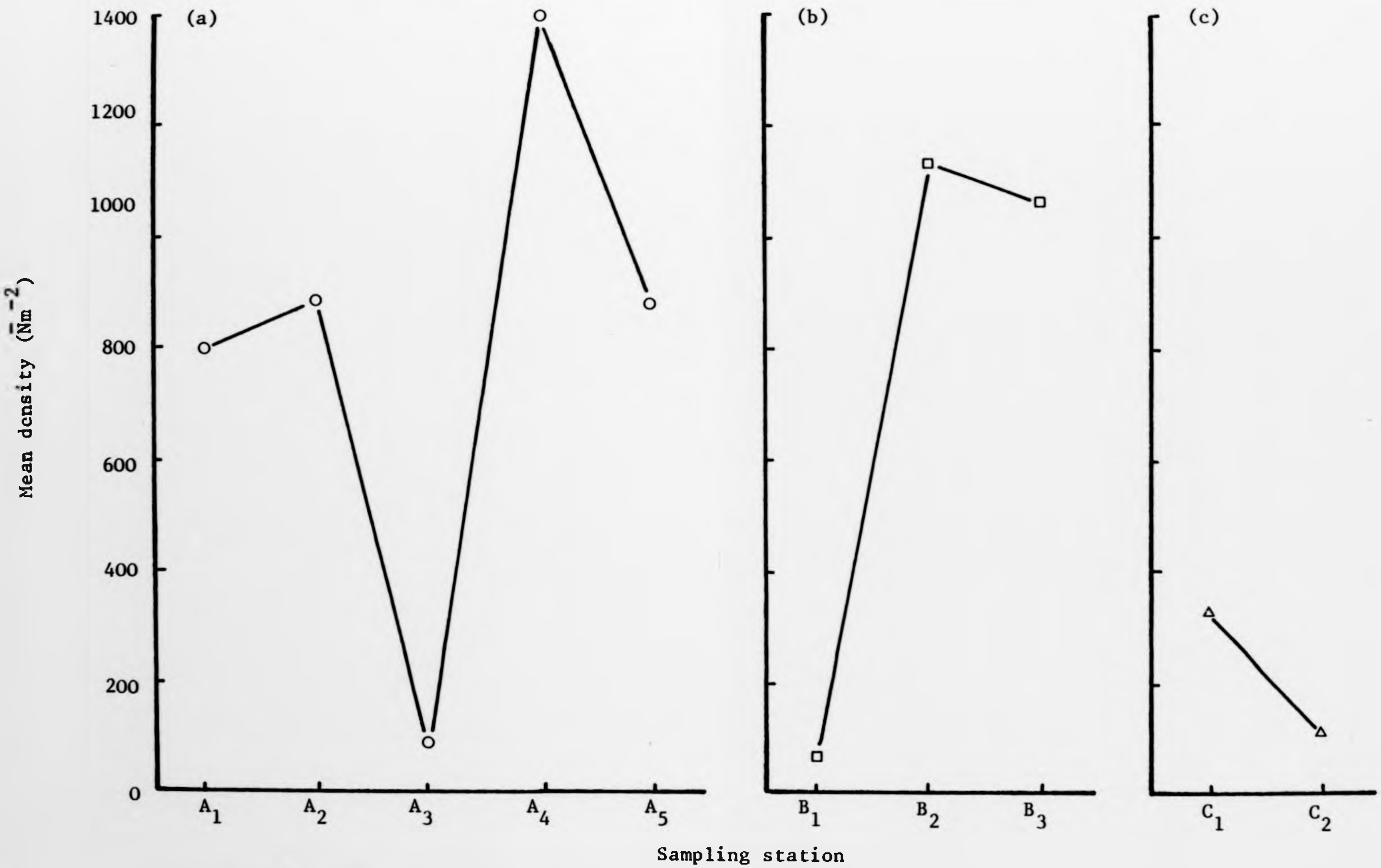

FIGURE 3.4.14: The mean density of <u>Spionid</u> spp. at each sampling station throughout the study period. (a) Transect A (b) Transect B and (c) Transect C

TABLE 3.4.10: Computation of the mean biomass of <u>Pygospio</u>

	Density $n\ m^{-2}$	Biomass $\bar{B}\ mgm^{-2}$
July '76	80 ± 253	9.200
August	760 ± 853	87.400
September	920 ± 1634	105.8
October	240 ± 506	27.6
November	680 ± 1497	78.2
December	2560 ± 2792	294.4
January '77	1040 ± 1070	119.6
February	1040 ± 1897	119.6
March	1960 ± 2129	225.4
April	1880 ± 2083	216.2
May	2240 ± 4874	257.6
June	520 ± 535	59.8

$\bar{B}$ 133.4 ± 92.9

3.4.6 (ii) Population structure

No information on the population structure of spionid worms was available.

(iii) Biomass and production

Since Pygospio elegans was the only spionid species recorded at Skinflats by Teare (1979), biomass and production estimates were based on data for this species. Assuming a mean individual weight of 115 µg dry wt (Teare 1979) and a P:B of 5.46:1. as for Manayunkia, the annual production of Pygospio was 0.734 g dry wt m^{-2} from a mean annual biomass of 0.133 g dry wt m^{-2} during the period July 1976 - June 1977. (Table 3.4.10).

3.4.7 Oligochaeta

3.4.7 (i) Distribution and density

Oligochaetes were present at all the main sampling stations, with the exception of A_3 in January 1976 throughout the study period. The mean density fluctuated between a minimum of 9200 ± 11440 m^{-2} in January 1976 and a maximum of 25000 ± 13000 m^{-2} in September 1977 (Fig 3.4.15). The mean densities were highest at A_1 - A_3 and decreased downshore (Fig 3.4.16). These were also high at B_2 and C_2 but low at C_1 and B_1, particularly compared with A_1.

(ii) Population structure

No information on the population structure of oligochaetes was available.

(iii) Biomass and production

The dominant species of oligochaetes at Skinflats was Tubificoides benedeni/

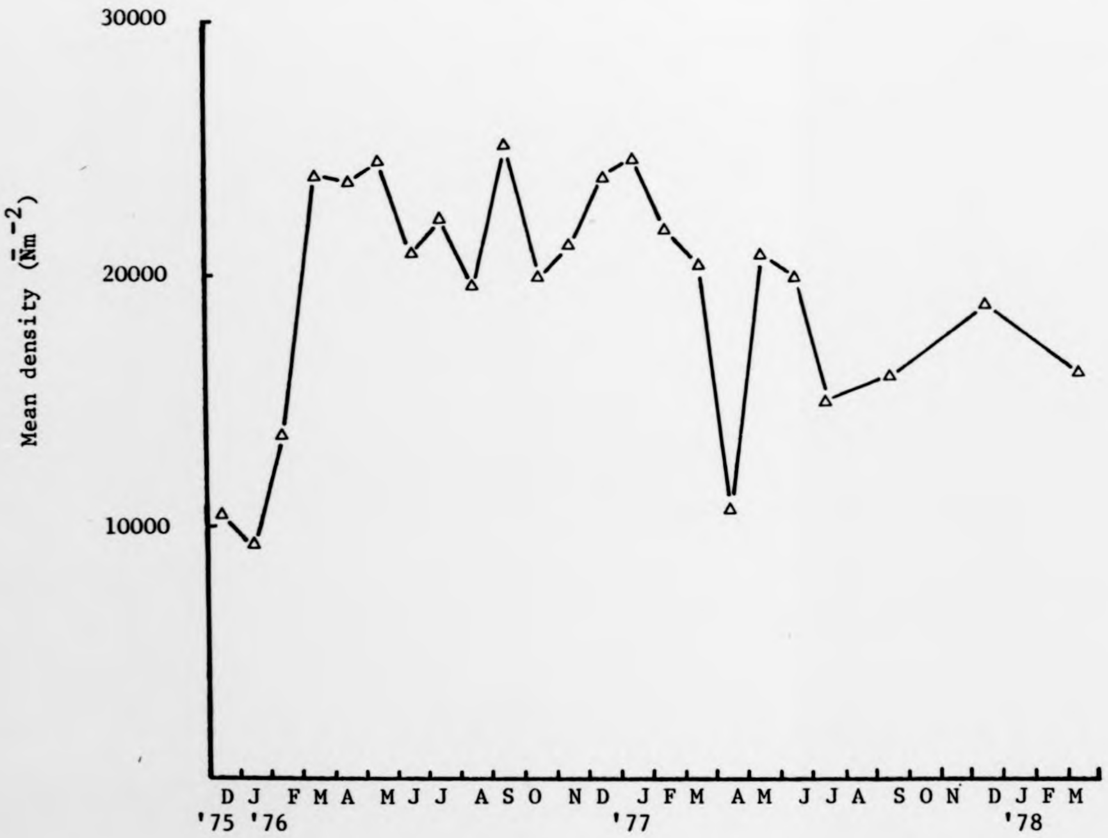

FIGURE 3.4.15: The mean density of oligochaete spp at Skinflats during the study period

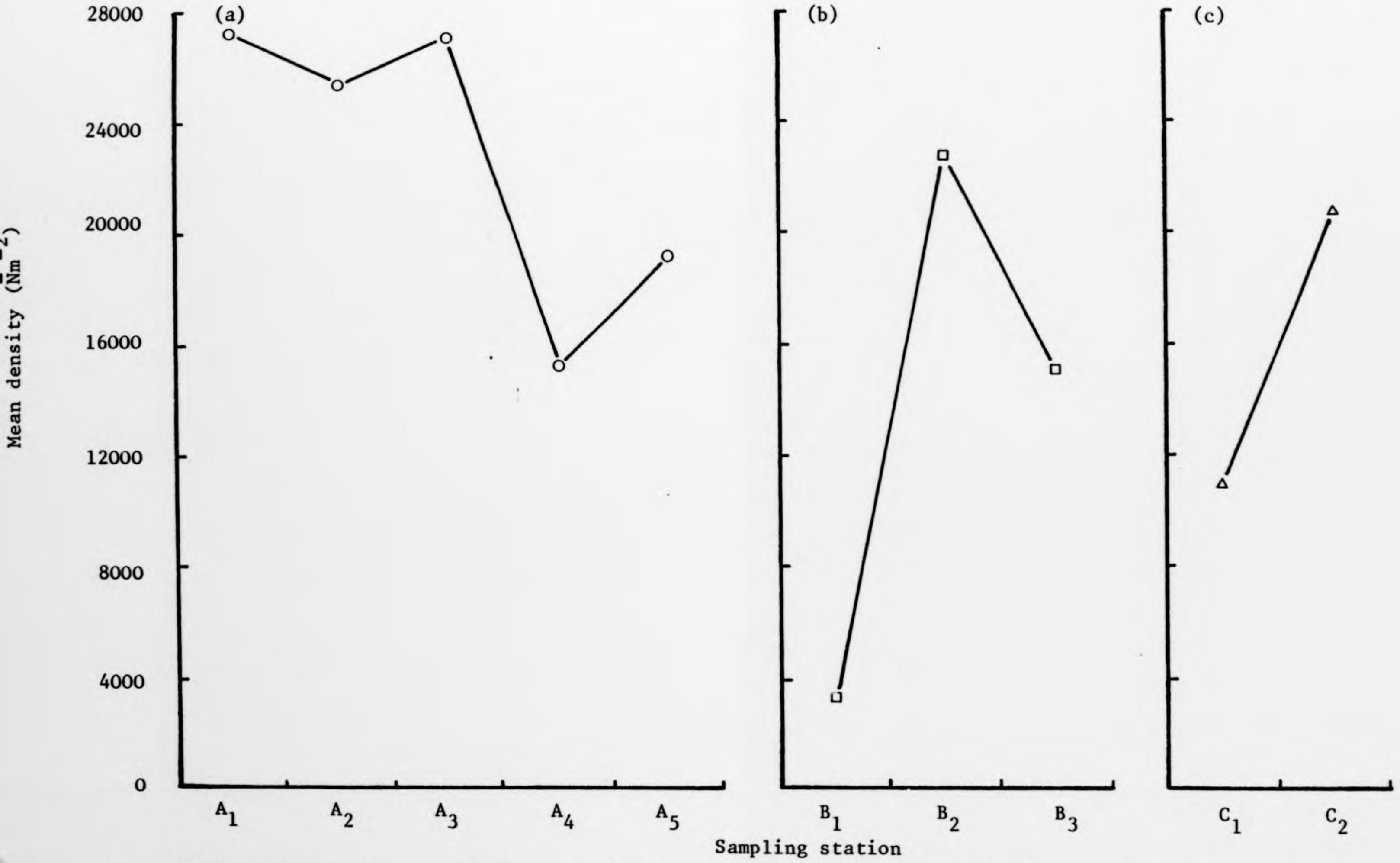

FIGURE 3.4.16: The mean density of oligochaete spp at each sampling station during the study period

TABLE 3.4.11: Computation of the biomass (mgm^{-2}) of Tubificoides benedeni

	Density $\bar{n}\ m^{-2}$	Biomass $\bar{B}$ (mgm^{-2})
July 1976	22200 ± 13718	4417.8
August	19400 ± 9530	3860.6
September	25000 ± 13000	4975.0
October	17960 ± 9070	3547.0
November	21160 ± 11567	4210.8
December	23800 ± 13447	4736.2
January'77	24440 ± 11236	4863.3
February	19280 ± 14105	3836.7
March	20240 ± 12206	4027.8
April	10440 ± 5783	2077.6
May	20880 ± 15790	4155.1
June	19920 ± 9662	3964.1

Tubificoides benedeni (= Peloscolex benedeni). It had a mean individual weight there of 199 µg (Teare 1979). Assuming a P:B ratio of 3:1 after Haka et al (1974) (in Warwick et al 1978), then 12.2 g dry weight m^{-2} was produced from a mean annual biomass of 4.06 g dry weight m^{-2} during the period July 1976 - June 1977 (Table 3.4.11).

3.4.8 Corophium volutator

3.4.8 (i) Distribution and density

The distribution and occurrence of Corophium during the study period was patchy. The mean density per month showed a summer peak in both study years with the peak in July 1977 of 2480 ± 4211 m^{-2} lower than that in 1977 (5800 ± 5344 m^{-2} September 1976) (Fig 3.4.17). The subsequent decrease in density from these peaks was dramatic. The minimum density was found in May 1977 with a mean of only 320 ± 620 m^{-2} being present.

Density at each station varied considerably owing to the sporadic occurrence of Corophium. The mean density was highest at A_3 ($\bar{x}$ = 2591 ± 2678) and B_3 ($\bar{x}$ = 4435 ± 4438) where it was recorded most frequently (Fig 3.4.18). The abundance at A_5, B_1 and C_1 was particularly low with corresponding low frequency of occurrence.

(ii) Population structure and growth

In December 1975 91% of the Corophium population consisted of individuals less than 6 mm long and by February 1976 all individuals measured less than 5 mm (Fig 3.4.19). There was little or no growth during this winter period as shown by the size-frequency histogram. By April growth was resumed and this continued through June when the mean individual/

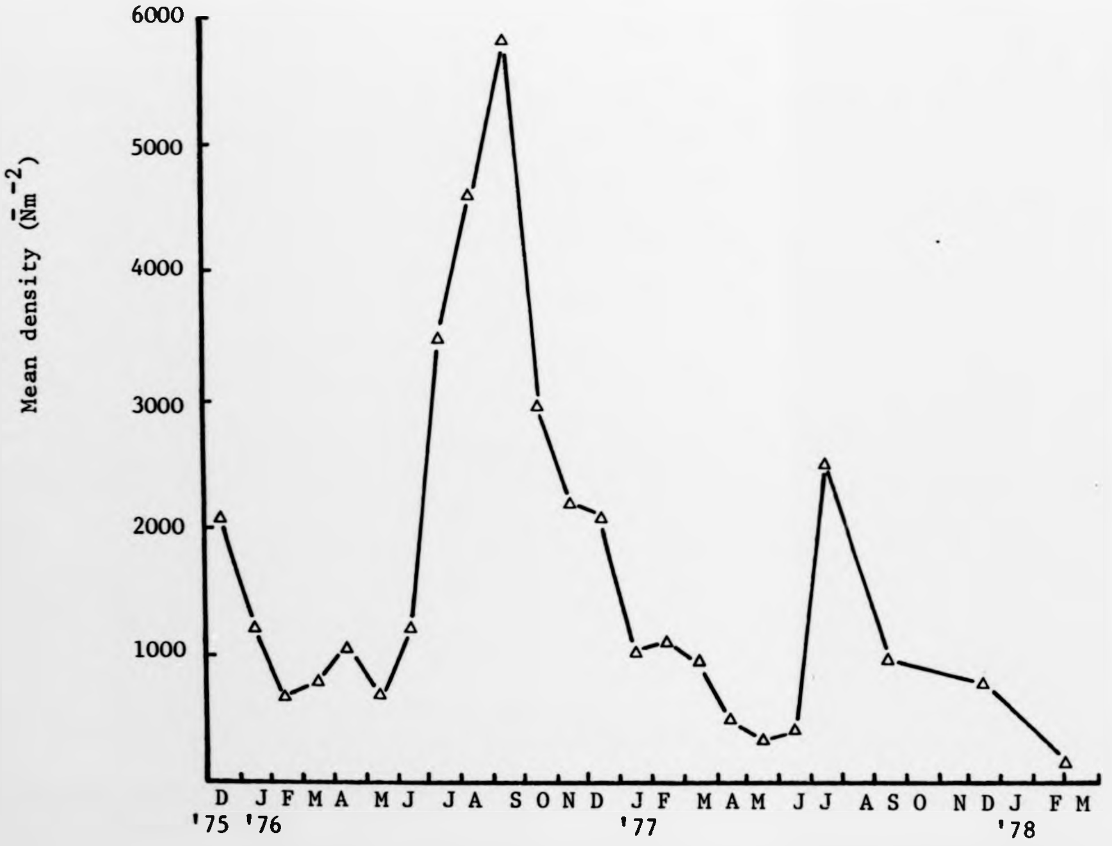

FIGURE 3.4.17 : The mean density of <u>Corophium</u> at Skinflats during the sampling period

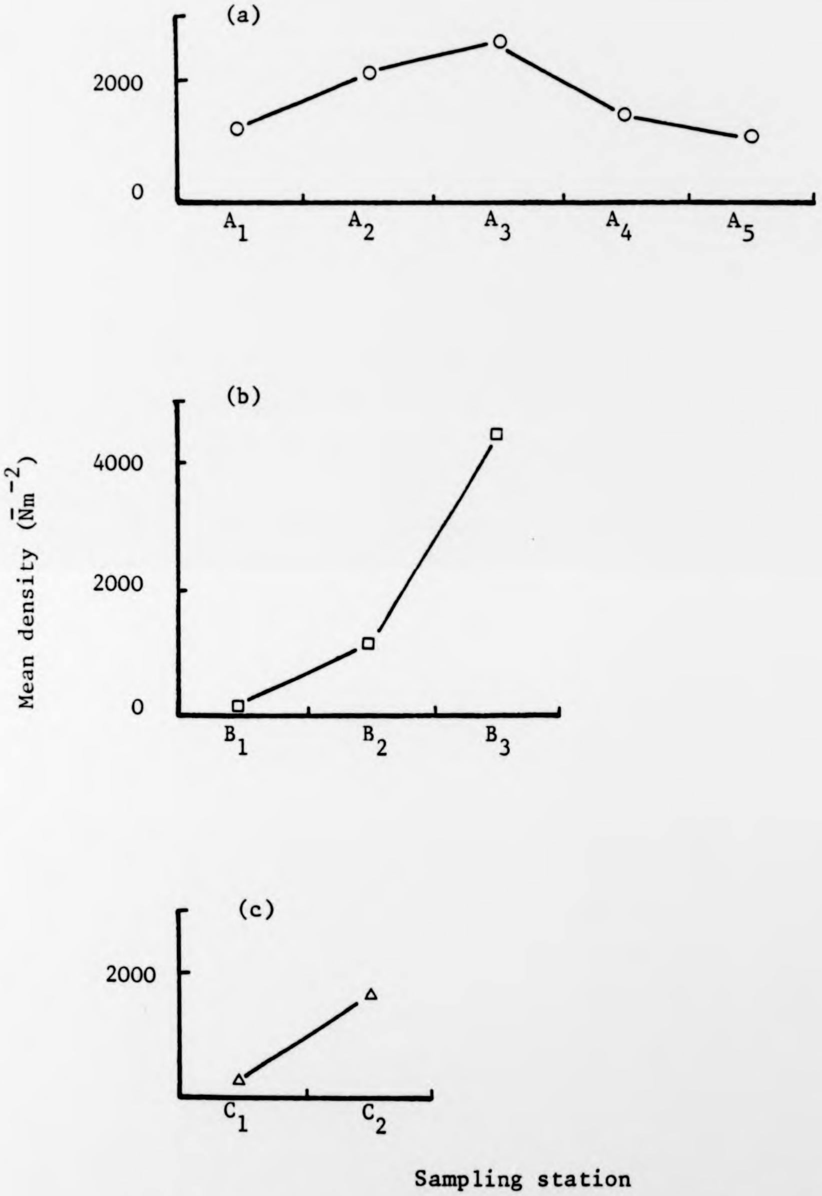

FIGURE 3.4.18: The mean density of *Corophium* at each sampling station during the study period. (a) Transect A (b) Transect B and (c) Transect C

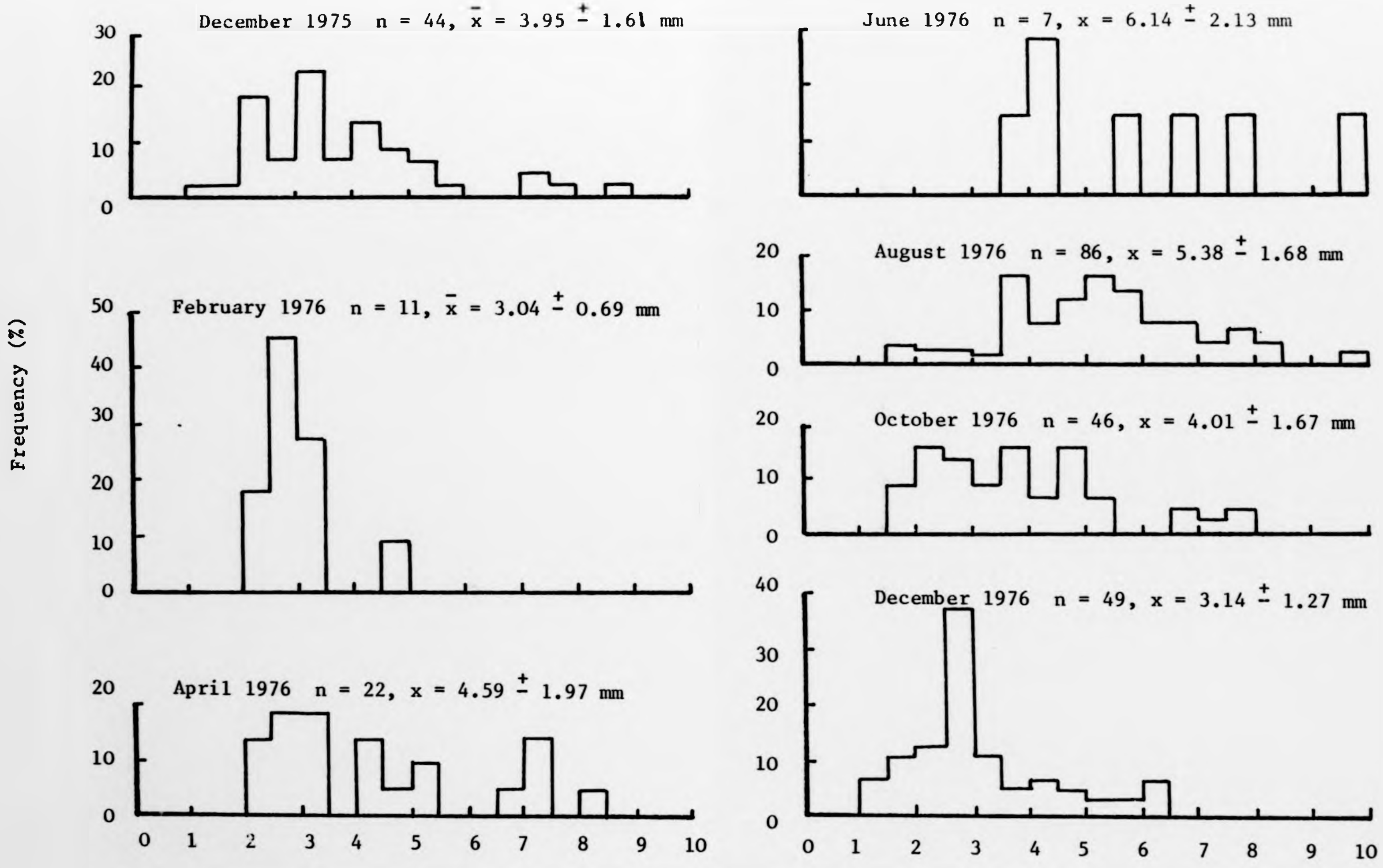

FIGURE 3.4.19: Size-frequency histograms of *Corophium* at Skinflats during the study period December 1975 - December 1976

TABLE 3.4.12: Computation of the biomass (mgm^{-2}) of <u>Corophium</u>

	Density $\bar{n}\ m^{-2}$	Biomass $\bar{B}\ mgm^{-2}$
July '76	3440 ± 3725	1857.6
August	4660 ± 4786	2521.1
September	5800 ± 5344	3132.0
October	2960 ± 2076	1598.4
November	2160 ± 1979	1166.4
December	2080 ± 1807	1123.2
January '77	1000 ± 660	540.0
February	1080 ± 707	583.2
March	920 ± 823	496.8
April	480 ± 880	259.2
May	320 ± 620	172.8
June	400 ± 706	216.0

$\bar{B} = 1139 \pm 965$

$P = 8769.5$ mg dry wt $m^{-2}\ yr^{-1}$

individual length was 6.14 ± 2.13 mm. In August, the first spat were taken to the sieves, reducing the mean body length of the population to 5.38 ± 1.68 mm but increasing the population density to 4600 ± 4780 m^{-2}. The density increased until October thereafter remaining fairly constant until December when mean density was similar to that in December 1975. The decrease in mean body length during this period following spatfall (August x = 5.38 ± 1.68 mm, December x = 3.14 ± 1.27) reflects the post-reproductive mortality of the larger adults and the recruitment of small individuals into the population.

(iii) Biomass and production

Dry weight determinations were made on 60 animals taken at random from the samples. A mean of these gave an individual weight of 0.541 ± 0.409 mg. This estimate was used in all biomass calculations. Since the $P:\bar{B}$ ratio of 7.7:1 found by Mossman (1977) refers to a population having more than two broods per year, a $P:\bar{B}$ ratio of 4.57:1 determined from Robertson (1979) was used in a production estimate of Corophium. The latter gave an annual production of 5.21 g dry wt flesh from a mean annual biomass (Table 3.4.12) of 1.14 g dry wt m^{-2} during the period July 1976 - June 1977. A production of 8.77 g m^{-2} yr^{-2} was achieved if Mossman's $P:\bar{B}$ ratio of 7.7 was utilised.

3.4.8 (iv) Depth distribution

In both November 1977 and January 1978 all Corophium occurred in the top 4 cm.

3.4.9 Discussions

The distribution, density, size-distribution and production of Macoma, Cardium, Nereis, Manayunkia, Pygospio, T benedeni and Corophium, together with the study of the depth distribution of several of these species, gave the basis for assessment of

the/

the distribution and availability of food available to wading birds and Shelduck at Skinflats. The sampling programme was less intense than for Hydrobia, the principal invertebrate studied.

3.4.9 (a) Distribution and density

The mean density range for Macoma of 240 - 480 individuals m^{-2} at Skinflats was in the middle range of densities recorded in other estuaries (Clay 1967b) and was similar to the densities at many stations at Torry Bay (Elliott 1979). It was, however, lower than the mean density in the preferred Macoma areas at Torry Bay, where up to 2000 small animals $<$ 2.5 mm occurred, but higher than the densities recorded nearby at Kinneil between 1976 and 1979 (McLusky 1979b).

The distribution of Macoma at Skinflats during this study was wider than had previously been recorded in autumn 1974 (Moffat 1975). At that time, the species was restricted to the area south of transect A but a high density at upshore stations in the vicinity of that transect was also recorded, the abundance decreasing with decreasing tidal height as in the present study. This is an atypical distribution since most Macoma populations have their peak densities around mid-tide regions (Elliott 1979, Spooner and Moore 1940). The cause of the northerly extension of the range is unknown.

In contrast to the wide distribution and elevated densities of Macoma upshore, C. edule had a very limited distribution together with a sporadic occurrence. The highest densities were recorded at the outer stations of transect A where the clay sediment was hard-packed beneath a shallow fluid-mud layer/

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In contrast to the wide distribution and elevated densities of Macoma upshore, C. edule had a very limited distribution together with a sporadic occurrence. The highest densities were recorded at the outer stations of transect A where the clay sediment was hard-packed beneath a shallow fluid-mud layer/

layer of 1-2 cm depth and so contrasting with other sediment textures at Skinflats. The occurrence of small *C.edule* individuals at B_3 and C_2 in August 1976 and their subsequent elimination indicates that conditions were suitable for settlement but not for long-term survival. Even at A_4 the 1976 population, consisting almost entirely of individuals $<$ 6 mm, was unable to sustain itself throughout the following year and the 1977 spatfall was eliminated, or was so small that it was not recorded in the samples, by March 1978. In general, the distribution of *C.edule* is known to be limited by low salinity (Muus 1967) and in winter at Skinflats, the salinity may fall below the level of tolerance. Spatfall was also erratic at Kinneil (McLusky and Bryant 1975 - 80) and similar decreases were found in winter on the Wash (Goss-Custard *et al* 1977) and the Ythan (Joffe 1978). This was possibly due to predation by overwintering birds which may also have partly accounted for the dramatic decline in numbers at Skinflats (see section 3.6.2). One causal factor in limiting the distribution of *C.edule* to the low tidal levels may have been immersion period. Only in these outer areas would immersion be greater than the four hours required to provide an adequate feeding period (Kristensen 1957). It thus seems likely that the combined influences of immersion period, lowered winter salinity and predation prevent *C.edule* from extending its distribution and increasing its population size at Skinflats.

Nereis, like *Macoma*, was widely distributed at Skinflats and its mean density in the top 10 cm (maximum 381.5 ± 364 m^{-2}) was similar to those densities found on the polluted Tees estuary (Gray 1976) but far lower than those recorded in a brackish/

brackish water pool in Belgium (Heip and Herman 1979) or in the intertidal areas of estuaries such as the Severn (Boyden and Little 1973) and the Medway (Wharfe 1977). The levels of abundance were similar, however, to those recorded at Kinneil during the same period (McLusky 1979) and had not changed significantly since the sampling at Skinflats in the autumn 1974 (Moffat 1975). Thus despite a decrease in mean density throughout the present study, the population of <u>Nereis</u> appears to be stable.

The dramatic increase in the density of <u>Manayunkia</u> at Skinflats during the study period was concurrent with increases at Kinneil. At the latter site, the population was still rising in January 1980 (McLusky 1980) when over 10^6 m^{-2} were recorded at one station. The influence of high densities of these tube-dwelling polychaetes on the infaunal community is unknown but it has been suggested by Woodin (1974) that suspension and infaunal deposit feeders will be excluded when they dominate the population. There is no evidence to support this suggestion from data collected at Skinflats. At Kinneil it colonised areas adjacent to industrial effluents which were avoided by the species more sensitive to pollution prior to the establishment of <u>Manayunkia</u> populations (McLusky 1979 a and b, 1980a). Thus there is no evidence of <u>Manayunkia</u> excluding other benthic infauna.

Concurrent with the increase in <u>Manayunkia</u> density at Skinflats was an increase in the abundance of spionid worms. However, the sudden increase was rapidly succeeded by a decline which continued until the end of the sampling period. Again, the/

the reasons for the increase are unknown but the high levels recorded in 1976 at Kinneil were not maintained subsequently (McLusky 1979b) suggesting that similar causal factors were operating at both sites.

In contrast to the large fluctuations in density of small polychaetes the abundance of oligochaetes during the study was remarkably constant, with mean numbers principally ranging from 15000 - 25000 m^{-2}. As with Manayunkia, densities were highest upshore on transect A and also on B_2. The mean densities were similar to those recorded in other British estuaries (eg Gray 1976, Warwick et al 1978) and to those found at Kinneil 1976-79 where the population density was also fairly constant (McLusky 1979b).

The patchiness and the marked variations in density of Corophium between months and sampling stations at Skinflats is characteristic of the species (Muus 1967) as is a summer peak in density (McLusky 1969, Mossman 1977). The lower population levels in 1977 compared to 1976 parallels the differences in density seen in Hydrobia and Nereis suggesting that similar factors may be influencing the reproduction of all three species. Only Macoma spatfall was higher in 1977 than 1976 but the causal factors in these are unknown.

The overall density of Corophium at Skinflats was low compared to that at Benfleet Creek, Essex (Mossman 1977) but higher than that recorded at Kinneil during the same period of study (McLusky 1979b). The possible adverse effects of pollution cannot be ruled out at Kinneil (McLusky 1968). A preference for muddy-sand (Meadows 1964) indicates that the fine-mud/

fine-mud sediment at Skinflats is not a favoured habitat for *Corophium*, although the salinity is within the range of tolerance of the species (McLusky 1968).

In general, the distribution and density of the common benthic invertebrates at Skinflats are similar to those reported in other estuaries with the exception of *Corophium*. Its density is generally low on the Forth estuary as a whole (McLusky *et al* 1976). The factors controlling dramatic increases in *Manayunkia* and spionids are unknown and further work into interspecific interactions within a single mudflat system are required. Character displacement between different species of co-existing mudsnails (eg Fenchel 1975a) and resource partitioning in deposit-feeding *Hydrobia* and *Corophium* (fenchel *et al* 1975) indicate ways in which community structure and coexistence between members of a community may be achieved but research in this field is still in its infancy particularly where small polychaetes and oligochaetes are concerned (Gray 1976).

(b) Population structure and growth

The population structure and growth of *Macoma*, *Nereis*, *Corophium*, and to a lesser extent, *C. edule* at Skinflats were described in this study. In the *Macoma* population at least five year classes were present in both years studies. A reduced spatfall in 1976 resulted in a small contribution of this cohort to the total population density and biomass. The recruitment at Torry Bay was also low in 1976 compared to the previous year (Elliott 1979) suggesting that factors controlling spatfall levels were similar on the estuary as a whole and not restricted/

restricted to one area. This is to be expected for a species relying on planktonic larval dispersion. Similar differences in annual recruitment were noted by Hughes (1970) for a population of Scrobicularia plana and he stated that this is a common phenomenon amongst tellinds. Although he also suggests that recruitment success is probably caused by local conditions he offered no explanation. The 'local' conditions influencing Macoma recruitment may also have influenced Hydrobia recruitment since the patterns of spatfall density were also similar between the two Forth estuary sites. Since growth of first year Hydrobia influences reproduction, environmental constraints on Macoma growth may also be responsible for variations in its spatfall although the data presented here are not sufficient to support this idea.

Growth of all age-classes was maximal between June and December 1977, followed by a winter period of minimal growth. This growth pattern was similar to that at Torry Bay(Elliott 1979) and in the Ythan estuary, Aberdeenshire, (Chambers and Milne 1975). All exhibit long growing seasons compared with the Macoma populations at lower latitudes (see Elliott 1979 for review). Even with this long growing season annual growth increments at both Torry Bay and Skinflats are smaller than at lower latitude localities and are only higher than arctic populations. Growth ceases at 15°C with an optimum temperature of 10°C (de Wilde 1975) suggesting that winter growth cessation is due not to temperature, but to other limiting factors such as food availability and internal rhythms.

The small individual size of C. edule at Skinflats with

a/

a maximum shell length of 18 mm (16.7 mm height) reveals that animals more than 3 yrs old were not found, since at Torry Bay the maximum height attained by 3 yr old animals was 18 mm (Elliott 1979). This is consistent with the finding of McLusky et al (1976) for the Forth as a whole.

Small Nereis (jaw size 0.2 mm) were recorded on all sampling occasions but the peak abundance was in August 1976 and September 1977 indicating a late summer settlement. The majority of these worms probably spawn in the following summer but some may live for about two years before spawning and dying. It is impossible to confirm the second spawning suggested in March 1978 without information on the occurrence of eggs in the coelom of individual worms but a similar peak was found to be present in the Nereis population in the Ythan estuary (Chambers and Milne 1975b). The life-cycle of Nereis shows marked differences with locality. In the Thames and at St Andrews (Dales 1950 and McIntosh 1907), the populations showed one spawning, in Spring, but in a brackish pool in Belgium spawning continued from spring to autumn (Heip and Herman 1979) and in Cherbourg it was found in every month (Herpin 1925). Since the data presented here were largely exploratory, an intensive study of Nereis is required to confirm the proposed life cycle.

Growth of Corophium began in April, probably in response to the increase in temperature (Segerstrale 1940) and followed a period of little growth from December. The occurrence of spat in August and subsequent decline in density is indicative of a single brood per year, similar to that found on the Ythan estuary/

estuary (McLusky 1968). This contrasts with the two or more broods suggested by Mossman (1977) and Watkin (1941) in Southern Britain and the four broods proposed by Muus (1967) in Denmark. The overwintering mean size was small compared to that in the Baltic (Segerstråle 1940) and may reflect adverse conditions in the Forth and the diversion of energy into growth rather than producing more than one brood per year. Once again, a detailed study of Corophium on the Forth is required to examine the growth and reproduction specifically.

(c) Biomass and production

A summary of mean biomass production and P:B ratios of all invertebrate species studied at Skinflats is shown on Table 3.4.13. Accurate estimates of secondary production are time-consuming and, although the use of a $P:\bar{B}$ ratio in determining production does not offer the same degree of precision, it has the advantage of being rapid. $P:\bar{B}$ ratios have been found to vary little in groups of similar organisms provided the same methods are employed (Waters 1977) but there are inevitable sources of innaccuracy. The determination of a $P:\bar{B}$ ratio in one locality and applied to another to estimate production are subject to innaccuracies arising from varying environmental conditions, which can influence growth rates (Elliott 1979), differences in the number of generations produced per unit time, and changes in predation regimes between localities (Robertson 1979).

When computed on an annual basis, the $P:\bar{B}$ ratio varies according to the life-span of the animal in question (Robertson 1979, Sanders 1956, Waters 1977), those with short life-spans having/

TABLE 3.4.3: Summary of biomass, production and $P:\bar{B}$ ratio of a number of invertebrates at Skinflats

	1 HYDROBIA	2 MACOMA	3 CARDIUM	4 NEREIS	5 MANAYUNKIA	6 PYGOSPIO	7 TUBIFICOIDES	8 COROPHIUM
Mean biomass gm^{-2}	3.320 Jul '76 - Jun '77	1.290 Aug '76 - Sep '77	0.072 Aug '76 - Sep '77	0.355 Aug '76 - Sep '77	0.115 Jul '76 - Jun '77	0.133 Jul '76 - Jun '77	4.06 Jul '76 - Jun '77	1.14 Jul '76 - Jun '77
Production gm^{-2}	3.900	0.748	0.073	1.07	0.63	0.734	12.2	5.21
$P:\bar{B}$ ratio	1.17:1	0.59:1	1.011:1	3:1	5.46:1	5.46:1	3:1	4.57:1

1 Original data

2 Original data

3 $P:\bar{B}$ (Elliott 1979)

4 $P:\bar{B}$ (Chambers and Milne 1975b)

5 $P:\bar{B}$ (Warwick _et al_ 1978)

6 $P:\bar{B}$ (Warwick _et al_ 1978)

7 P:B (Haka _et al_ 1974)

8 $P:\bar{B}$ (determined from Robertson (1979))

having a higher $P:\bar{B}$ ratio than long-lived species. Additionally, older cohorts contribute substantially to the total biomass but little to the annual production as a result of slower growth rates. Younger, but rapidly growing, animals will conversely produce large quantities of flesh relative to their small biomass (eg Chambers and Milne 1975, Elliott 1979, Hibbert 1976, Nichols 1975).

In the present study, with the exeption of Hydrobia and Macoma, it has been necessary to compute production either from $P:\bar{B}$ estimates of the same species but at a different locality, or from the $P:\bar{B}$ ratio of a similar species exhibiting a similar life-history. Production for all species except Macoma, Cerastoderma and Nereis was estimated for the annual cycle beginning in July 1976. Annual production for the latter began in June 1977 and the populations were sampled four times during the year. More frequent sampling was practically not possible and the limitations were inevitable. The exact timing of spatfall was impossible to judge as was the prediction of maximum and minimum levels of biomass.

In view of the limitations the annual production estimates were considered to be reasonably accurate (Fig 3.4.20 summarises the contribution of each species to the total production). The most productive animals were the oligochaetes. From a mean biomass of 4.056 g dry weight m^{-2} yr^{-1}, they produced 12.168 g dry weight m^{-2} yr^{-1}. Small specimens were undoubtedly lost through the 300 μm sieve but the production value is close to the 11.59 gm^{-2} estimated for the Firth of Forth in general (Teare 1979). Since 95% of oligochaetes are located in the top/

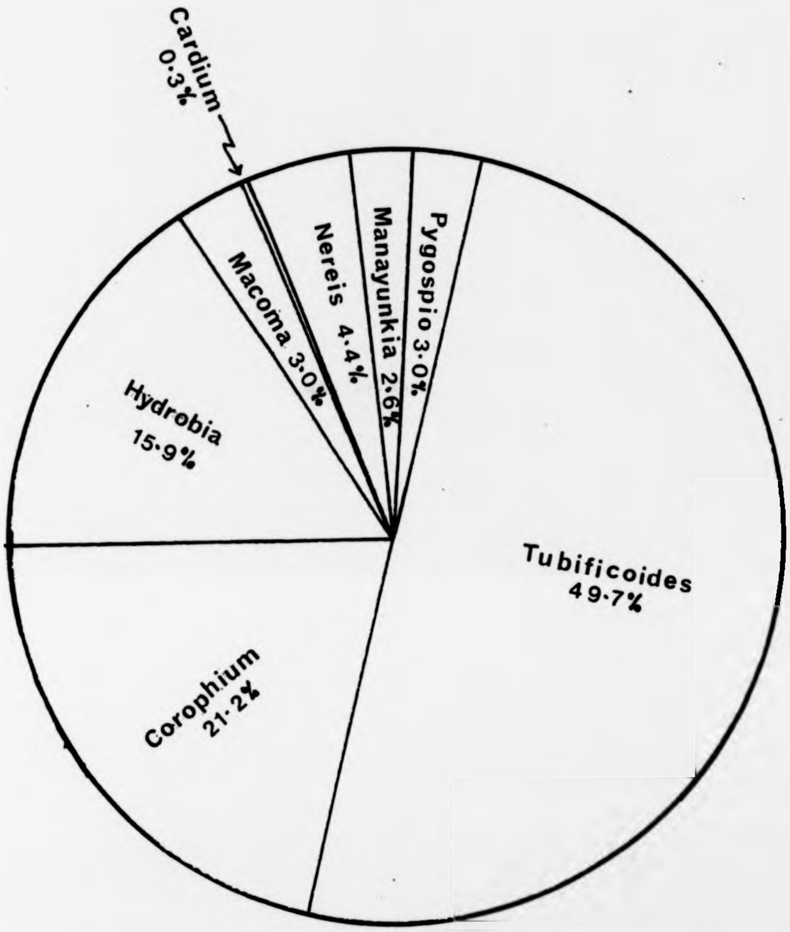

FIGURE 3.4.20: The contribution of each invertebrate species to the total production at Skinflats

top 5 cm (Ann Bagheri pers. comm.) the samples were representative of the population as a whole. The production was higher than that on the Lyhner (Warwick et al 1978) where 0.783 gm^{-2} dry wt were produced from a mean annual biomass of 0.261 gm^{-2}, most probably attributable to organic enrichment on the more industrialised Forth estuary.

By comparison to the oligochaetes, the population of Manayunkia and spionids had a low productivity of 0.63 gm^{-2} dry wt yr^{-1} and 0.73 g m^{-2} dry wt yr^{-1} respectively. The estimates were made over a period when the populations were expanding and the $P:\bar{B}$ ratios may thus have been higher than those published elsewhere since growth rates relative to mortality would be high. Nevertheless, the production from small polychaetes and oligochaetes was estimated at 13.528 g dry wt m^{-2} yr^{-1} which was higher than the total macrofaunal production (see below).

Of the macrofaunal species, Corophium contributed the largest proportion of the total production, despite its small and patchy population. However, the production estimates are likely to be unreliable for several reasons and should be treated with caution. Firstly, the mean individual weight will have varied throughout the year and the dry weight determinations did not take this into account. Secondly, the longevity of the species and the number of broods per year were not determined, so the application of $P:\bar{B}$ ratios calculated by Mossman (1979) and Robertson (1979) may not be appropriate to the Skinflats population. At Benfleet Creek, Essex, 95.6 gm^{-2} dry wt yr^{-1} were produced (Mossman 1971), emphasising/

emphasising the small size of the population at Skinflats.

With the exception of *Hydrobia*, which produced 3.9 g AFDW m^{-2} yr^{-1} (section 3.3.5) the remaining macrofaunal species contributed little to the total production of the species considered. *Nereis* produced a total of 1.01 g dry wt m^{-2} yr^{-1} from a mean biomass during the study period of 0.355 gm^{-2} in the top 10 cm. The mean annual biomass was low compared to the 4.2 gm^{-2} on the Ythan (Chambers and Milne 1975) but similar to that on the polluted Tees estuary (0.025 - 0.509 g dry wt m^{-2}, Gray 1976) although sampling in the former extended to 20 cm and this may have accounted for some of the difference. Other annual biomass estimates of 15.7 g dry wt m^{-2} on Zwin Saltmatsh in Belgium (Govaere 1969) and 24.3 g dry wt m^{-2} in a shallow brackish pond (Heip and Herman 1979) are significantly higher.

The low mean biomass of *Nereis* was accompanied by low production compared with that produced on the Ythan (12.783 g dry wt m^{-2} yr^{-1}) (Chambers and Milne 1975b) where the $P:\bar{B}$ ratio was 3:1. The value was also well below the 61.3 g dry wt m^{-2} yr^{-1} produced in a shallow brackish pool where the $P:\bar{B}$ ratio was 2.5:1. (Heip and Herman 1979). Owing to the lack of tidal conditions and probably differences in predation pressure, it is difficult to equate populations in a pool and on an intertidal mudflat.

The production of 0.748 g AFDW m^{-2} from a mean biomass during the study period of 1.29 g gave a $P:\bar{B}$ ratio for the *Macoma* population of 0.59:1. This is in the range expected for a long-lived benthic bivalve and was similar to that found at/

at Torry Bay by Elliott (1979). There, production ranged from 0.055 to 2.5 gm^{-2} AFDW which, from a biomass of -0.48 to 6 g m^{-2} AFDW, gave a $P:\bar{B}$ ratio of 0.116 - 1.108. Area differences there were a result of differential settlement and the influence of environmental factors. The uniformity of the sediment at Skinflats precluded exploration of these factors.

The $P:\bar{B}$ ratio of Macoma at Skinflats (0.59) was slightly higher than the average values from Torry Bay (0.354, 0.489) (Elliott 1979) but below the values for other intertidal populations (Beukema 1971, Burke and Mann 1974, Chambers and Milne 1975a, Warwick and Price 1975, Wolff and de Wolf 1977). The value was only slightly higher than $P:\bar{B}$ ratios found in sublittoral populations (Ankar and Elmgren 1976, Cederwall 1977, Segestråle 1960 by Bergh 1974) and it has been suggested by Elliott (1979) that high levels of heavy metals and other pollutants may be responsible for this.

The production of C.edule was, not surprisingly, low, 72.74 mg AFDW m^{-2} yr^{-1} being produced from a mean biomass during the study period of 71.95 mg m^{-2}. This was a direct result of the limited distribution and extinction by March 1978. On the Lyhner 0.205 gm^{-2} was produced (Warwick and Price 1975) and in Southampton Water, where cockles dominated the community, 20 - 71 gm^{-2} flesh dry wt were produced (Hibbert 1976). A still higher value of 119.82 g dry wt m^{-2} was produced on the Grevelingen estuary (Wolff and de Wolf 1977) further illustrating the instability of the Skinflats population. The $P:\bar{B}$ value of 1.011:1 estimated at Torry Bay (Elliott 1979) was also low compared to 0.69 - 8.92:1 on the Grevelingen and 1.1 - 2.61:1/

2.61;1 in Southampton Water (Wolff and de Wolf 1977, Hibbert 1976), further illustrating the poor condition of cockle populations on the inner Forth estuary.

(d) Depth distribution

The depth distribution of invertebrates is important for assessment of the availability of prey species to wading birds and Shelduck. The depth distribution of Macoma, Nereis and Corophium was investigated and the results demonstrated that Macoma size increased with sediment depth. This was consistent with the hypothesis that burying depth is restricted by siphon length since siphons have to be extended onto the mud surface for feeding (Reading and McGrorty 1978, Vassallo 1971). The consistently high percentage of Macoma occurring in the top 4 cm in both November and January 1978 (81% and 88% respectively) does not indicate an increase in burying depth as environmental conditions became more severe, although this was recorded on the Wash (Reading and McGrorty 1978). Some support for this idea comes from the increased burying depth of the < 3 mm and +8 mm size classes in January but the higher proportion of 3 - 8 mm animals dwelling in the surface 1 cm zone in January confounds this.

Reading and McGrorty (1978) demonstrated a seasonal vertical movement with only 59% Macoma occurring in the top 3 cm in December compared with 98% in June, although small 0 - 2 mm size class animals always remained in the surface 1 cm. The cause of the migration was attributed to a day-length response but on the Ythan estuary (Chambers and Milne 1975), Macoma gave a reversed response by burying deeper in the/

the summer. A long term experiment on the Forth is required if consistent patterns in the seasonal burying depth and availability of Macoma to wading birds are to be shown.

There was an increase in the size of Nereis with increase in sediment depth but animals with burrows extending deeper than 10 cm were not sampled. However, although Vader (1964) found burrows extending to 25 cm, Muus (1967) recorded 50 - 70% of the population in the top 5 cm, despite a maximum burrowing depth of 35 cm, suggesting that a high proportion of Nereis present at Skinflats were sampled. Nereis with a jaw length of up to 0.7 mm were recorded at Skinflats in the top 10 cm but the occurrence of larger sized jaws in the pellets of Redshank (Section 3.5.2) indicates that larger deeper dwelling worms are available to Redshank at certain times.

All Corophium were located in the top 4 cm as found by both McLusky (1969) and Mossman (1977) at other sites.

3.5 The Diets and Feeding Habits of Several Shorebird Species

3.5.1 Introduction

Shorebirds feeding on large intertidal areas are difficult to observe at close range. Often the food items taken are too small or are ingested at such high rates that accurate descriptions of their diets are not possible. Alternative, indirect methods of quantifying the diets of shorebirds have consequently been developed and include gut, pellet and faecal examination. These methods are biased against soft-bodied animals which are rapidly digested leaving no identifiable remains and can only be used in conjunction with observation to give a quantifiable analysis.

The problems inherent in gut, pellet and faecal examination have been discussed by Hartley (1948) and for wading birds by Goss-Custard (1973). In a more recent study, Goss-Custard and Jones (1976) have shown that, for Redshank at least, an analysis of pellets egested on roosting and feeding grounds can give a rapid, qualitative estimate of the diet, and one which is adequate for general surveys of shorebird diets. Coupled with direct observation of feeding birds, it is often satisfactory for more detailed studies.

In the present study, pellet and gut examination coupled with direct observation were used where possible. The most numerous shorebird species at Skinflats were Redshank, Knot, Dunlin and Shelduck. At this site, pellets of Redshank, Knot and Dunlin were collected and in addition eleven Dunlin were shot under licence from the N.C.C. The Redshank was studied in most detail and, in addition, to the four common species, the diets of Oystercatcher, Curlew and Turnstone were investigated. Since these three species were more common elsewhere on the Forth estuary, it was found necessary to qualify/

qualify the diets in other intertidal areas. Oystercatcher and Turnstone are more numerous on the north shore of the Forth, although Curlew occurred at all the major intertidal sites (Bryant - unpublished counts). Shelduck diets were studied at Kinneil since shooting birds on the RSPB Reserve at Skinflats was not possible.

The diets of Redshank, Dunlin and Knot at various localities are discussed together with the results from the study at Skinflats (Section 3.5.2, 3.5.3 and 3.5.4). The following account of the diets of Curlew, Oystercatcher, Turnstone and Shelduck summarises the results for these species from other locations.

The Curlew feeds mainly by day (Burton 1974) in both intertidal and inland habitats. The diet on intertidal feeding grounds has been described for estuaries in Essex (Burton 1974), the Tees (Evans *et al* 1979), the Wash (Goss-Custard, Jones and Newberry 1977) and Morecambe Bay (Prater 1970). At these locations large, polychaete worms and bivalve molluscs were the main prey species. *Lanice*, *Arenicola*, *Macoma*, *Scrobicularia* and *Cardium* were important on the Wash whilst *Nereis* was the principal prey item at other sites. *Carcinus* was also taken commonly on the Wash in autumn and on mussel beds and stony areas of Morecambe Bay.

Other, less important prey items include *Littorina* (Fenton 1958), *Talitrus*, *Thais*, *Pilumnus* (Madon 1935), *Balanus* sp. (Prater 1970), *Crangon*, flounders and blennies (Witherby *et al* 1943).

Few studies on the diet of Shelduck can be found in the literature. Olney (1965) found a variety of food items in the guts of Shelduck from the Medway estuary and Bridgewater Bay, including *Macoma*, *Corophium*, *Nereis* and plant material but the principal prey was *Hydrobia*. On the Ythan estuary in summer Buxton (1975) and Young (1964) also found

Hydrobia/

Hydrobia to be the most important prey with Macoma, Nereis, Littorina sp, Mytilus, Cardium, Corophium, insects and seeds comprising the rest of the diet. Earlier studies have also shown the importance of Hydrobia (Campbell 1947, Goethe 1961), together with Littorina rudis (Campbell 1947) and both juvenile Mya sp and Macoma (Goethe 1961).

The importance of Hydrobia in the diet of Shelduck at Skinflats on the Forth estuary was inferred from the relationship between feeding intensity and Hydrobia density (Bryant and Leng 1975). On the Tees estuary, however, oligochaete worms are thought to be of greater significance in the diet, as Shelduck do not concentrate their feeding only in areas of high Hydrobia density (Evans et al 1979).

The principal foods of the Oystercatcher are the cockle, Cardium, the mussel, Mytilus, and Macoma, (Dare 1966, Hulscher 1964). The predation pressure exerted by Oystercatchers on the edible cockle and mussel populations has been the subject of several fisheries investigations (Davidson 1967, Drinnan 1958, Horwood and Goss-Custard 1977). On the mussel beds in Morecambe Bay, the Wash, the Conway Estuary and Teesmouth, they feed almost exclusively on mussels (Dare and Mercer 1973, Drinnan 1958, Goss-Custard, Jones and Newberry 1977, Pienkowski 1973). Whilst on sandflats cockles are the most important prey, Macoma were only taken at high beach levels on the Wash, contributing little to the overall diet (Goss-Custard, Jones and Newbery 1977).

Other prey recorded include Nereis on the Tees and in the Bury Inlet (Davidson 1957, Pienkowski 1973) and Littorina, small crustaceans Tellina tenuis, shore-crabs and brown shrimps on Morecambe Bay (Dare and Mercer 1973). The latter two items were especially important in the autumn.

Inland feeding in winter appears to be a recently acquired habit, the diet consisting mainly of earthworms (Dare and Mercer 1973, Heppleston 1971 (a) and (b)). Heppleston (1971b) showed that Oystercatchers tended to feed in fields with the highest density of earthworms. In general, these were fields that had been under pasture for at least six years. Leatherjackets (Tipulidae larvae), together with other insects and their larvae made up the rest of the diets (Dare and Mercer 1973, Heppleston 1971a).

Studies of the winter diets of the Turnstone in Britain have been made on the Wash (Jones 1975), Morecambe Bay (Davidson 1971, Prater 1970) and Beaumaris, Anglesey (Harris 1979). On the Wash, the main feeding grounds are the mussel beds, where *Carcinus* is the most frequently taken prey. *Mytilus* spat, *Littorina sp*, *Nereis*, *Macoma*, *Cardium*, *Hydrobia*, *Calliostoma zizyphinum*, *Lepidochitone cinereus*, *Euphagurus sp*, Cirripedia and insects are also eaten (Jones 1975). The stony scars, mussel beds and rocky beaches support most of the feeding Turnstones in Morecambe Bay (Prater 1970) and there, also, *Carcinus* is the most important prey. A wide variety of prey were found there as well including: *Macoma*, *Hydrobia*, Cirripedia, *Littorina*, *Gammarus*, *Nereis* and *Mytilus*. The diet at Beaumaris (Harris 1979) depended on the tidal cycle. At high tide, dipteran larvae, amphipods and dead *Mytilus* were important items and on the ebb tide, a good correlation between Turnstone and amphipod distribution was shown. Barnacles, as well as amphipods, were taken at low tide and, on the flow, a correlation between the distribution of feeding birds and *Littorina* was found.

There are several reports of Turnstones feeding on carrion (MacDonald and Parmalee 1962, Mercer 1966, Selway and Kendall 1965) and after/

after a storm they will scavenge along the high tide line in search of dead or moribund cockles and mussels (Jones 1975).

MacDonald and Parmalee (1962) also recorded the taking of household scraps.

The Forth estuary holds a wintering population of up to 200 birds. These are mainly found on the north shore of the estuary between Torry Bay and Charlestown.

3.5.2 The Redshank (Tringa totanus)

3.5.2 (i) Feeding methods

Two feeding strategies were employed by Redshank at Skinflats: methods involving sight detection and those involving the location of prey by touch. Sight-feeding birds occurred either as individuals or in loose flocks and were distinguished by a slow, steady pacing over the mud interrupted only occasionally by short runs. They fed by making distinct probes interspersed with pecks; some deeper probes often extended to the base of the bill. Nereis and Macoma were the only prey taken by probing whilst many small items, presumed to be mainly Hydrobia, were obtained through pecking at and just below the surface. The poor spatfall of Macoma in 1976 (Section 3.4.2) indicated that few would be available in the surface 1 cm and that most prey items taken from the surface would indeed be Hydrobia. Nereis and Macoma could be distinguished within 300 m through a 25-40x telescope and often worms were shaken and dropped before being eaten. Occasionally, a prey item was rejected. During the field observations only one Carcinus was seen to be eaten by a Redshank. All prey recorded were swallowed whole.

When/

When foraging in dense flocks, Redshank used touch-feeding methods which often involved continuous pecking at or just below the surface. An alternative method, sweeping the bill from side to side through the fluid upper layer of the sediment whilst vibrating the lower jaw, was occasionally seen.

Successful captures arising from the touch-feeding methods were identified by a backwards jerk of the head accompanied by the swallowing of small, but often unidentifiable, prey items.

During mild winter conditions when the air temperature was at least 4°C, the proportion of the total number of feeding birds engaged in either sight or touch feeding methods was largely tide related. As birds dispersed from the roosts on the ebbing tide, Redshank were the first species to begin to feed: the first birds to arrive fed belly-deep at the waters edge. As soon as a small area of mud was exposed the majority of Redshank began feeding in dense flocks along the tideline. They mainly pecked in the newly exposed mud but a few remained wading and probing.

The area of exposed mud rapidly increased and about 1.5 hrs after high water approximately one third of the total area was exposed, the exact area depending on the height of high water. Redshank flocks then began to disperse widely into a regular pattern of sight feeding birds although a diminishing number continued to follow the tide edge. All birds fed by sight once the tide had receded from the area.

During spells of severe weather the mudflat at Skinflats became/

became frozen and, since the surrounding fields were also frozen and not available for feeding, Redshank were forced to roost until rising temperatures and/or flooding tide melted the ice. They then fed at the tide edge or exposed mud in dense touch-feeding flocks and many swept their bills through the sediment rather than surface pecked. Some birds fed as individuals or in loose groups but all used the touch-feeding strategy.

Swishing was also predominantly utilised by Redshank when the air temperature was below 4°C but not severe enough for the mudflat to freeze.

3.5.2 (ii) Feeding rates

The feeding rate and the proportional contribution of each prey species to the diet above 4°C (air temperature) varied with respect to the tidal cycle and feeding site (Table 3.5.1). During the low tide period, all Redshank were widely dispersed using sight-detection to locate their prey. Small prey were assumed to be *Hydrobia* and were the most frequently taken prey at both Carron and Powfoulis feeding sites (7.13 min^{-1} and 5.33 min^{-1} respectively). The site varied considerably. At Powfoulis, the ratio of *Nereis*: *Macoma* taken was 12.52 whereas at the Carron site it was only 0.82.

When feeding 0.75 - 1.5 h either side of high water, Redshank formed dense flocks and fed almost exclusively on *Hydrobia* by touch. The only exception was the taking of a *Macoma* by one individual.

On the flow tide (27.2.78) at the Carron site, feeding rate/

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On the flow tide (27.2.78) at the Carron site, feeding rate/

TABLE 3.5.1: The diet of Redshank at Skinflats determined by observations at air temperature $\geqslant 4^{o}C$

tidal state	feeding method	area	no days total no. observations	total no. minutes observation	total number of items taken			no items taken hr^{-1} no.items taken min^{-1}		
					Small (Hydrobia)	Nereis	Macoma	Small (Hydrobia)	Nereis	Macoma
L.T.	Sight	Carron	4 61	40.56	289	83	102	427.5 7.13	122.8 2.05	150.0 2.51
L.T.	Sight	Powfoulis	2 45	21.87	121	74	6	332.0 5.53	203.0 3.38	16.5 0.27
H.T.	Touch	Carron	2 37	12.89	356	0	1	1657 27.62	0	4.65 0.08
H.T.	Touch	Powfoulis	2 12	3.03	120	0	0	2376 39.6	0	0
Flow	Touch/ Sight	Carron	1 11	8.86	83	28	5	562 9.37	189 3.16	33.9 0.56
Ebb	Touch/ Sight	Powfoulis	1 12	4.97	82	9	0	990.0 16.50	108.7 1.81	0

rate increased substantially between tidal position 2 and 3 above 4°C (Table 3.5.2, Fig 3.5.1). This increase resulted from a larger number of small items ingested. The proportion of Nereis taken fluctuated between 10 and 37.5% only falling to zero with the formation of dense feeding flocks at position 5. The percentage of Macoma ingested was low.

On the ebb tide at Powfoulis (5.3.78) all birds fed by touch detection methods at a high rate on small items until the tide reached position C (Fig 3.5.1). At this stage, Redshank were dispersing and a higher percentage of worms were taken by those feeding by sight.

3.5.2 (iii) The effect of severe weather on feeding rates

During a period of severe weather (Feb 1978), when ice and snow covered the mudflats above the strand line, Redshank made extensive use of tactile feeding methods at all stages in the tidal cycle. They either pecked at the surface or swept their bills through the surface layers. Small items were taken, almost to the exclusion of Nereis and Macoma (Table 3.5.3). Feeding rates were similar to those around H.W. on milder days.

3.5.2 (iv) Pellet analysis

Samples of pellets were collected from Redshank roost sites (sites 1 and 3: Fig 3.6.1) at Skinflats on three occasions (Table 3.5.4). The number of prey fragments representing individuals of each species varied considerably within samples (Appendix 11). Hydrobia, Nereis and Macoma occurred most frequently, the percentage occurrence differing between sites and with ambient temperature. Nereis and Macoma were present in/

TABLE 3.5.2: Feeding rates of Redshank in relation to ebb and flow tides at Skinflats $> 4^{o}$C

	position of the tidal edge	total observation period (min)	total number of observations	total number of items taken	total number of each prey taken			percentage of items taken			total number of prey items taken min^{-1}
					Hydrobia	Nereis	Macoma	Hydrobia	Nereis	Macoma	
flow-tide observations Carron site (27.2.78)	1	5.9	5	50	32	17	1	64	34	2.0	8.47
	2	1.0	1	8	4	3	1	50	37.5	12.5	8.0
	3	1.16	3	30	27	3	0	90	10	0	25.8
	4	0.95	2	20	13	5	2	65	25	0	21.1
	5	2.70	8	70	69	0	1	98.6	0	1.4	25.9
high-tide observations Carron site	5	1.59	5	50	50	0	0	100	0	0	31.4
ebb-tide observations Powfoulis (5.3.78)	a	2.61	10	100	100	0	0	100	0	0	38.3
	b	1.45	6	60	60	0	0	100	0	0	41.4
	c	3.52	6	30	21	9	0	70	30	0	8.5

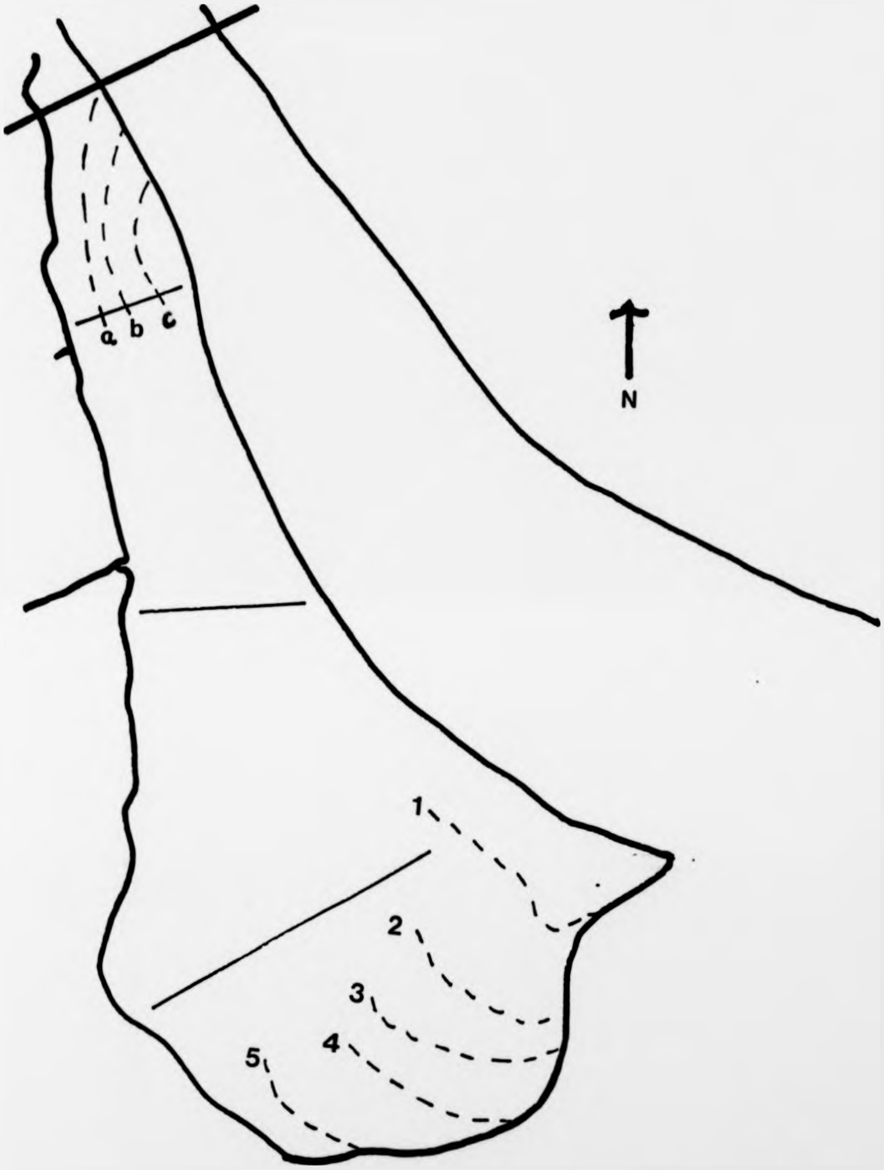


FIGURE 3.5.1: Observation sites for Redshank feeding rates. 1 - 5 are positions for observations taken on a flow, spring tide and a - c on ebb, neap tides

TABLE 3.5.3: The diet of Redshank at Skinflats determined by observations at air temperature < 4^oC

tidal state	feeding method	area	no days total no. observations	total no. minutes observation	total number of items taken			no items taken hr^{-1} no. items taken min^{-1}		
					Small (<u>Hydrobia</u>)	<u>Nereis</u>	<u>Macoma</u>	Small (<u>Hydrobia</u>)	<u>Nereis</u>	<u>Macoma</u>
L.T.	Touch/ Sight	Carron	1 13	5.38	128	1	1	1428 23.79	11.15 0.19	11.5 0.19
H.T.	Touch	Carron	1 6	2.27	60	0	0	1586 26.43	0	0
H.T.	Touch	Powfoulis	1 17	7.45	165	0	0	1328.9 22.15	0	0
Flow	Touch/ Sight	Carron	1 19	11.74	131	1	5	669.5 11.16	5.11 0.09	25.55 0.43
Flow	Touch	Powfoulis	1 24	7.97	227	0	0	1709 28.48	0	0
Ebb	Touch	Carron	3 50	17.78	494	0	0 (+ 1 crab)	1667 27.78	0	0 (crab 0.06)
Ebb	Touch	Powfoulis	1 35	12.60	348	0	0	1657 27.62	0	0

TABLE 3.5.4: The analysis of Redshank pellets collected at Skinflats

sample no.	sample description	air temp ^{o}C	no. of pellets	*Hydrobia*	*Nereis*	*Macoma*	*Carcinus*	mysids	*Cardium*	oligochaetes	spionid tubes	seeds/veg matter	nematodes	unidentified gelatinous objects
1	18.11.77 Carron Mouth roost site	7	11	73.0	100.0	100.0	73.0	9.0	9.0	18.0	63.3	18.0	9.0	18.0
2	11.2.79 Carron Mouth Orchardhead roost site	2	6	100.0	16.7	50.0	-	-	-	-	-	-	-	-
3	13.11.79 Kincardine Bridge roost site	4	6	100.0	83.3	33.3	-	-	-	-	-	16.7	16.7	-

in all pellets collected from the site 1 at 7°C but only in a smaller percentage, (16% and 50% respectively) of those collected at 2°C. Nereis, in particular, was poorly represented in the pellets collected at low temperatures but the percentage containing Hydrobia increased to 100%. At site 3 few pellets contained Macoma, (33%), indicating that Redshank roosting here had been feeding on the adjacent mudflat (since few Macoma were seen taken by feeding Redshank in this area).

Carcinus were present in a large proportion of pellets from site 1 (sample 1) but were absent from the other samples. The importance of oligochaetes and spionids cannot be assessed since they are easily digested. Additionally, those present in the pellets may have been collected accidentally from the sediment surface with the pellets, as some pellets were collected from roost sites on the mud, above the neap high-tide line. They are unlikely to be important during surface pecking but may well be ingested during sweeping. Since their biomass is very small over the whole tidal cycle, they are unlikely to be an important food item.

3.5.3 (v) Gut analysis

The gizzards of four Redshank collected from the Kinneil Open Pan in December 1975 contained only fragments of Hydrobia shells (Appendix 12).

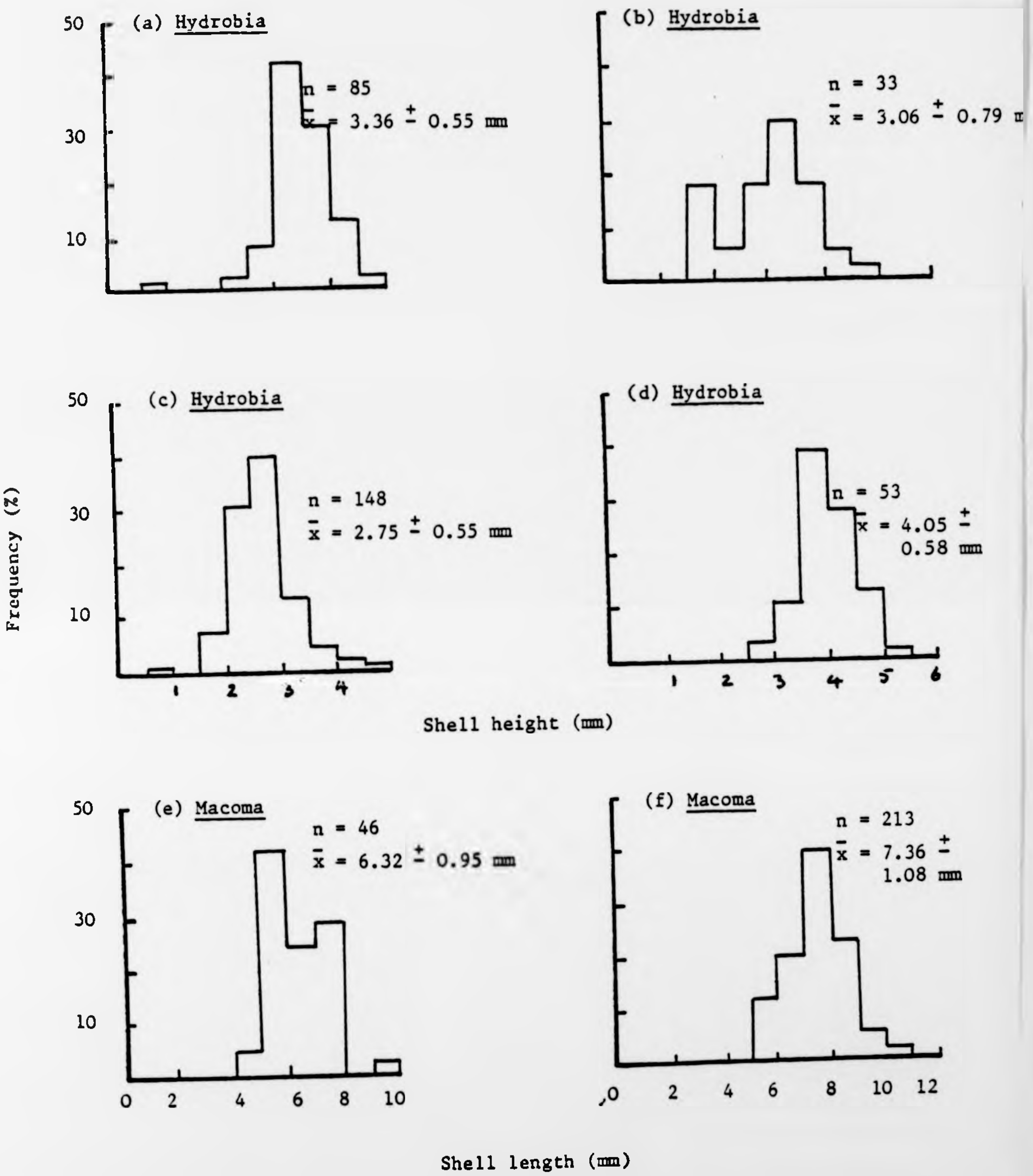
3.5.3 (vi) The size of items in the diet

Hydrobia

The size of Hydrobia from pellets ranged from 0.9 - 4.8 mm (Figs 3.5.2 a-c) and the mean size of those from site 1 and site 3 samples were similar at temperatures above 4°C ($p > 0.05$). However/

FIGURE 3.5.2: Size-frequency histograms of _Hydrobia_ (a-d) and _Macoma_ (e-f) taken from Redshank pellets and guts.

(a) Pellets; Site 3; 15.12.79; 4°C
(b) Pellets; Site 1; 18.11.77; 7°C
(c) Pellets; Site 1; 11.2.79; 2°C
(d) Guts; Kinneil;
(e) Pellets; Site 1; 13.11.79
(f) Pellets; Site 1; 18.11.77.


(a) Hydrobia
n = 85
x̄ = 3.36 ± 0.55 mm
(b) Hydrobia
n = 33
x̄ = 3.06 ± 0.79
(c) Hydrobia
n = 148
x̄ = 2.75 ± 0.55 mm
(d) Hydrobia
n = 53
x̄ = 4.05 ± 0.58 mm
(e) Macoma
n = 46
x̄ = 6.32 ± 0.95 mm
(f) Macoma
n = 213
x̄ = 7.36 ± 1.08 mm
Frequency (%)
50
30
10
1 2 3 4
1 2 3 4 5 6
Shell height (mm)
0 2 4 6 8 10
0 2 4 6 8 10 12
Shell length (mm)

However, the mean size of Hydrobia from pellets collected at site 1 at 2^oC (Fig 3.5.2c) was smaller than that collected at 7^oC ($x = 3.06 \pm 0.79$ mm 7^oC, $x = 2.75 \pm 0.55$ mm 2^oC $p < 0.05$).

The size of Hydrobia from the gizzards of Redshank from Kinneil included larger individuals than were found at Skinflats (range 3.0 - 5.4 mm); the mean size (4.045 ± 0.58 mm) was significantly larger ($p < 0.001$) than those collected from the Carron mouth pellets at 7^oC.

A Forage Ratio (FR) was calculated to indicate any selectivity of prey sizes (after Buxton 1975). It was obtained by dividing the percentage frequency of each size class of Hydrobia in the pellets by the corresponding size-class frequency in the sediment. A $FR > 1$ for any given size class suggested that this was being selected; a $FR < 1$, that the size class was taken in smaller proportions than it occurs in the sediment; a FR of 1, that no selection occurred. The results (Fig 3.5.4a) indicated a preference by Redshank for snails > 2.5 mm shell height, representing 1+ year class Hydrobia. The smaller 1+ and all 0+ year class snails were not selected.

Macoma

The mean shell lengths of Macoma in pellets from site 1 on two sampling occasions (Fig 3.5.2 e-f) were similar ($x = 6.32 \pm 0.95$ mm Nov 79; $x = 7.36 \pm 1.08$ mm Nov 77, $p > 0.05$). Animals in the range 4.8 - 10.8 mm were taken by Redshank.

A Forage Ratio (Fig 3.5.4b) showed selection for Macoma of/

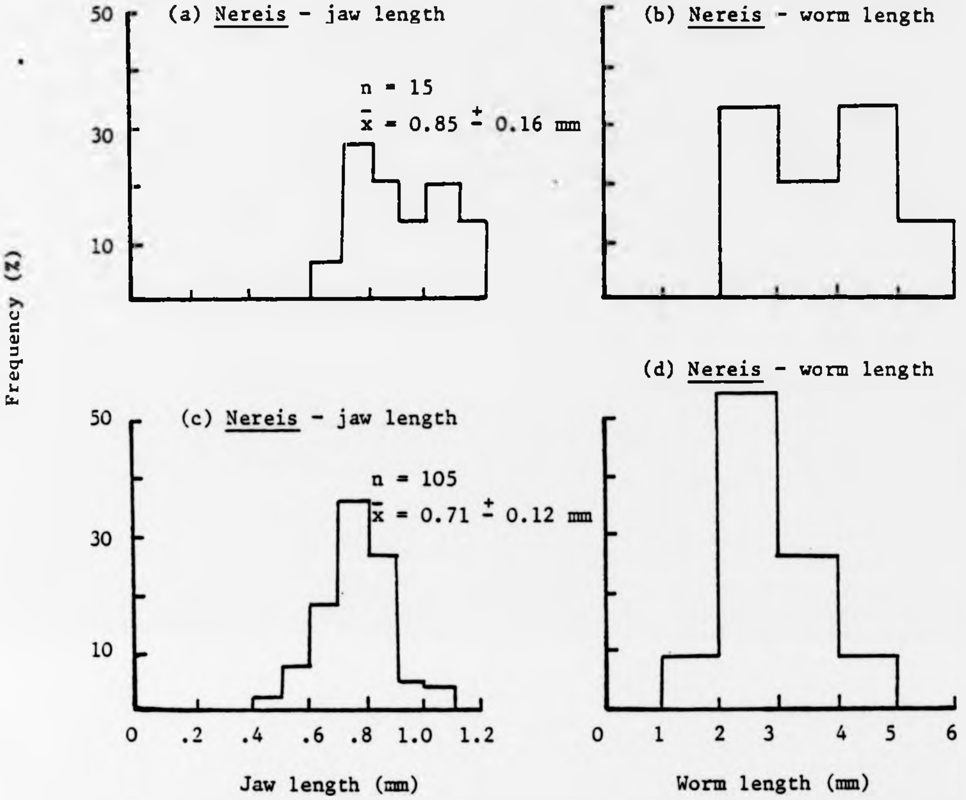


FIGURE 3.5.3: Size-frequency histograms of jaw-length of *Nereis* from pellets collected from (a) Kincardine Bridge and (c) Carron mouth roost sites. (b) and (d) depict equivalent worm lengths.

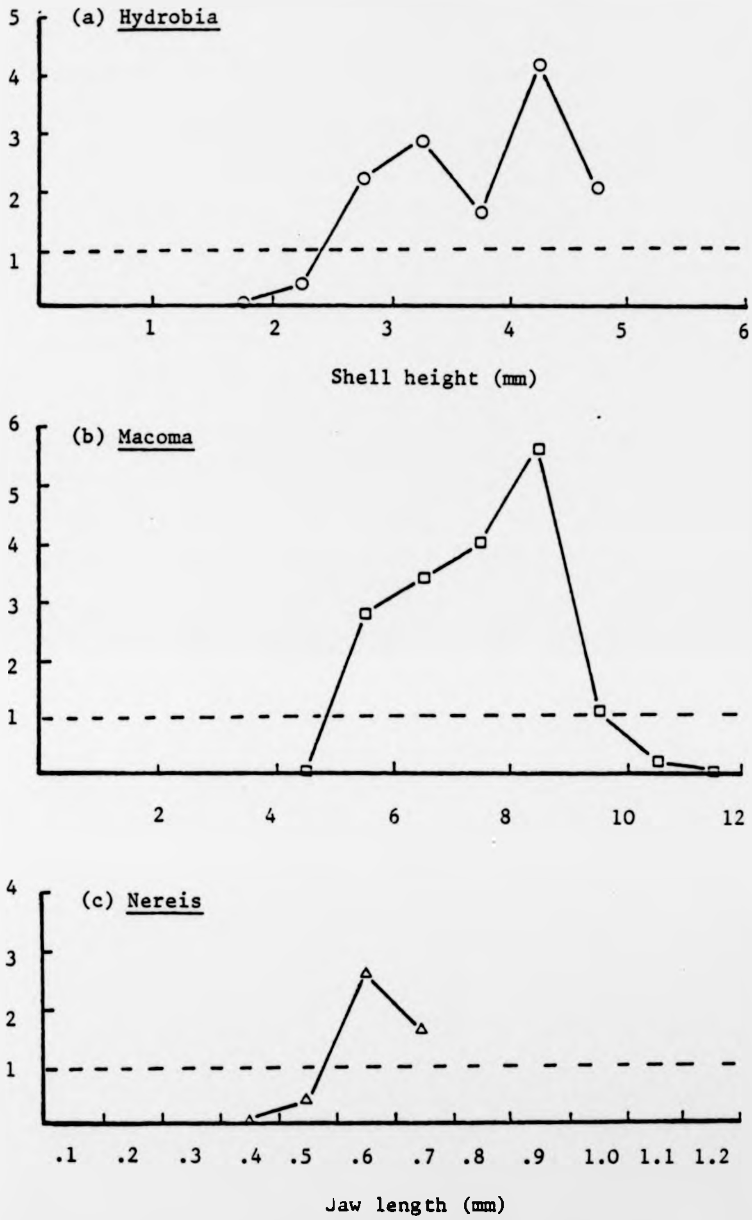


FIGURE 3.5.4: Forage ratios for Redshank feeding on (a) *Hydrobia*, (b) *Macoma* and (c) *Nereis* at Skinflats

of 5 - 9 mm shell length. Above 9 mm shell length, Macoma were taken in smaller proportions than they occurred in the sediment. The small Macoma (< 5 mm) were available in the top 4 cm but selected against whilst the poor availability of animals larger than 9 mm accounted for their being poorly represented in the diet. Only 44% of Macoma 10 mm and larger were found in the top 4 cm in November ($n = 9$) (Section 3.4.2 and Appendix 13).

Nereis

The mean size of Nereis jaws from pellets collected at sites 1 and 3 (Fig 3.5.3 a,c) were similar ($p > 0.05$), the range including 0.4 - 1.2 mm jaws (1.15 - 6.44 cm worms Fig 3.5.3 b,d).

The availability of Nereis to Redshank could not be assessed by taking sediment samples since the worms withdrew into their burrows. Thus the depth distribution samples (Section 3.4.4) showed that the burrows of the majority of worms selected by Redshank extended beyond the reach of a probing Redshank bill, 7 - 10 cm below the surface. They must therefore have been taken when feeding or irrigating their burrows, activities which would bring them within reach of Redshank. Smaller worms, available in the top 4 cm, were not taken.

3.5.2 (vii) Discussion

The catholic diet of Redshank overwintering in Britain includes not only intertidal organisms but also invertebrates from adjacent saltmarshes and agricultural land (Table 3.5.5). Of the intertidal organisms, Hydrobia, Nereis and Macoma occur universally/

TABLE 3.5.5: Summary of the diets of Redshank from different localities in winter

AUTHORITY	LOCALITY	SOURCE	MOLLUSCA Gastropods	 Bivalves	ANNELIDA	CRUSTACEA	INSECTA	OTHER
BURTON (1974)	Essex	gizzards n = 22	L. rudis H. ulvae	M. edulis M. balthica C. edule	Nereidae Lumbricus*	Isopoda Corophium Caridea Carcinus	Coleoptera* Diptera*	Gobius Grass*
CABOT (1968)	Galway Bay	gizzards n = 37	H. ulvae	Nereis sp	Crangon	Coleoptera "small crabs"		
CAMPBELL (1935)	West Mersey Essex	gizzards n = 2	H. ulvae L. saxatilis					
DAVIDSON (1971)	Morecambe Bay	gizzards n = 5	H. ulvae	M. balthica C. edule	Polychaetes			
EVANS et al (1979)	Teesmouth	gizzards n = 25	H. ulvae Littorina sp	M. balthica M. edulis Modiolus sp	N. diversicolor small polychaetes small oligochaetes	Corophium sp. C. maenas	Insecta	Invertebrate eggs Plant material
GREENHALGH (1975)	Ribble	gizzards n = 95	H. ulvae Littorina sp Gastropoda*	M. edulis	Nereis sp Lumbricids[1]*	Sphaeroma Gammarus Corophium sp.	Insect larvae[1]	Araneida[1]* Enteromorpha Chaetomorpha Myriapoda[1]* Barley-oat seeds*
		pellets n = 731	H. ulvae	Mytilus spat Macoma	Nereis Pygospio Oligochaeta[1]	Carcinus Sphaeroma[1] Gammarus[1] Corophium sp.	Insect larvae[1]	Nematoda seeds[1] Other vegetable matter
GOSS-CUSTARD (1969)	Ythan Estuary Aberdeen	observ-ation + gizzards	H. ulvae	M. balthica	N. diversicolor	C. volutator		

(cont'd over)

TABLE 3.5.5 (cont'd)

AUTHORITY	LOCALITY	SOURCE	MOLLUSCA Gastropods	MOLLUSCA Bivalves	ANNELIDA	CRUSTACEA	INSECTA	OTHER
Goss-Custard (1976) + Goss-Custard Jones and Newbery (1977)	The Wash	pellets n = 1151	H. ulvae	M. balthica C. edule	N. diversicolor	Corophium sp Orchestia sp Crangon sp C. maenas		Small fish
Goss-Custard (1979)	Taw estuary Devon	pellets n = 10	H. ulvae		N. diversicolor	C. volutator C. maenas		
	Tavy estuary Devon	pellets n = 8	H. ulvae	M. balthica S. plana	N. diversicolor N. hombergii	C. maenas Cyathura		
	Millbrook Creek Devon	pellets n = 9	H. ulvae		N. diversicolor N. hombergii	C. volutator C. maenas		
Joffe (1978)	Ythan Estuary Aberdeen	gizzards	H. ulvae Littorina sp	Macoma Mytilus	Nereis Lumbricus sp	C. volutator C. maenas Gammarus Crangon Ostracods	Coleoptera Diptera - adults and larvae	Plant remains
Prater (1970)	Morecambe Bay	gizzards n = 51	H. ulvae Littorina sp	M. balthica T. tenuis C. edule M. edulis	N. diversicolor	C. volutator C. maenas Gammarus sp Crangon sp Mysidae Balanus sp	Coleoptera Dolichopodidae larvae	Coelenterata Aranae Fish
Present Study	Forth Estuary	pellets n = 11 gizzards n = 4	H. ulvae	M. balthica C. edule	N. diversicolor Pygospio tubes? oligochaetes	C. maenas Mysidae		Vegetable matter Seeds

NB * from fields

1 from saltmarsh

universally and their overiding importance as food for Redshank at Skinflats, indicated by field observations and pellet analysis, is in accordance with findings elsewhere (eg Burton 1974, Evans et al 1979, Goss-Custard 1967, Prater 1970). At some localities, Corophium is an important prey item and is probably preferred to Nereis where it occurs in greater abundance (Goss-Custard 1977(b)). However, the small size of the Corophium population and small individual size at Skinflats (Section 3.4.8) together with a patchy distribution on the Forth as a whole (McLusky et al 1976) accounts for its absence from the diet in the present study. It may, nevertheless, be of local importance elsewhere on the estuary as positive associations with feeding distributions of Redshank have indicated (Bryant 1979).

In addition to the main prey species, Redshank exploit seasonally abundant prey such as small Carcinus which are often available in late autumn (Evans et al 1977, Goss-Custard, Jones and Newbery 1979). As Carcinus occurred in a high proportion of pellets collected in late autumn at Skinflats but were rarely seen to be eaten by Redshank during subsequent observations in mid-winter, it seems likely that seasonal exploitation of crabs also occurs on the Forth.

The extent to which smaller polychaetes and oligochaetes are exploited is difficult to assess because of their digestibility but they were presumed to be taken during sweeping on the Tees (Evans et al) and at other sites on the Forth estuary (Speakman pers. comm. Warnes et al 1980). It is likely that they were similarly taken by Redshank when sweeping at Skinflats.

The/

The ability of Redshank to exploit readily available food resources is further illustrated by examples on the Forth estuary (Warnes et al 1980). Cardium are usually swallowed whole (eg Goss-Custard, Jones and Newbery) but Redshank were regularly observed removing fragments of flesh from cockles opened by Oystercatchers at Kinneil and Bo'ness. Only one bird associated with a particular Oystercatcher as it fed on cockles and approaching Redshank were aggressively attacked by the bird already in attendance. Also, throughout the winter, a Redshank fed on the Stirling D. C. Refuse Tip (A Turner pers. obs.) further illustrating the flexibility of Redshank feeding behaviour.

It appears that Redshank are opportunistic foragers. The main prey species taken in estuaries are those which are also widely distributed and relatively abundant, but seasonally and temporarily abundant prey are also exploited.

On the feeding grounds within an estuary, this study and those elsewhere (eg Goss-Custard 1969, 1970b, 1976) have shown that the feeding strategy of Redshank varies with feeding dispersion, tidal state and environmental conditions. These factors also influence the behaviour of the more mobile prey (Goss-Custard 1970b, Vader 1964) which largely accounts for the predator's change in feeding strategy.

Sight detection is incompatible with dense feeding flocks since the surface activity of prey such as Nereis or Corophium is reduced by disturbance (personal observation, Goss-Custard 1970, 1976). Thus around high water, the switch from sight to touch feeding at Skinflats indicated a response to the increased bird density/

bird density reducing the availability of Nereis. Macoma would still be available in the top 4 cm at this time but visual clues revealing their presence may have been reduced by the dense flocking.

On the ebb and flow tides, Nereis feed at the surface (Evans 1979, Vader 1964) and if flocking is not limiting, will be available to feeding Redshank. This is supported by the results from Skinflats, since the percentage of Nereis taken remained high on the flow tide prior to the formation of dense flocks. Similarly, on the ebb, Nereis were taken as dispersion began.

On the basis of this study and others elsewhere, it appears that low temperatures, heavy rain and high wind speeds reduce the feeding efficiency of birds (Evans 1979, Goss-Custard 1969, 1976, Pienkowski 1973, Warnes et al 1980). Redshank commonly adopted a method of sweeping the bill through the surface layers at Skinflats under such conditions. In these layers only prey such as Hydrobia, small worms and bivalves would be available and of these, Hydrobia were most important.

In the fluid muds of both the Tees estuary (Evans et al 1979) and the Forth (J. Speakman per. comm.) however, sweeping is adopted under all environmental conditions. As these muds are associated with high oligochaete and small polychaete abundance, sieving mud may be more efficient than searching by sight in the soft mud since the biomass is high (see also: Shelduck Section 3.5.9). The method is also adopted by Redshank feeding at night (Goss-Custard 1970b, Greenhalgh 1975) in a variety of substrates.

Availability of prey in different substrates may also account for the high proportion of Nereis taken by Redshank at Powfoulis compared with the Carron Mouth site, where almost equal numbers of Macoma and Nereis were taken when the mudflat was exposed. The mechanism of prey selection is unknown but a preference for Corophium over Nereis at other sites, despite a potentially higher energy intake from Nereis (Goss-Custard 1969, 1977(a)) suggests that factors other than simply maximising energy intake are involved. In general, Corophium are taken in sandy areas (eg Greenhalgh 1975, Prater 1970) and Nereis where muddy conditions prevail.

The size distribution of Hydrobia, Macoma and Nereis taken from pellets and gizzards of Redshank are in general similar to those recorded elsewhere (eg Burton 1974, Goss-Custard, Jones and Newbery 1977, Prater 1970) although methods of measuring Nereis jaw fragments differed, making comparison with some studies difficult.

Feeding rates on Nereis were similar to those found elsewhere (Goss-Custard 1977b) but comparison of feeding rates over a range of densities could not be made. No data was available for comparison of feeding rates on Macoma and Nereis together since feeding rates were not related to invertebrate density changes over small areas.

3.5.3 The Knot (calidris canutus)

3.5.3 (i) Field observations

At Skinflats, Knot usually fed in large dense flocks over 1 km from the nearest observation point. Thus feeding methods were assumed similar to those used elsewhere on the Forth where substrate/

substrate type was similar but observation distances less. Shallow and deep probing were the most commonly used methods in muddy substrates and surface pecking occurred frequently on sandy-mud (Warnes et al 1980). On one occasion at Torry Bay, feeding by Knot over the high tide period as the mudflats thawed, mainly consisted of pecking amongst stones and rocks with the tip of the bill slightly open. Other birds either probed or pushed their bills forward through soft mud, rapidly running between each series of probes. All these methods of feeding were used by a flock of 50 Knot foraging for 15 minutes near Powfoulis, when there were also several aggressive encounters. Bivalves presumed to be Macoma were also seen taken.

No feeding rate determinations were made.

3.5.3 (ii) Pellet analysis

Macoma and Hydrobia were the only species to be represented in Knot pellets (n = 10) collected from the ICI pipeline roost at Skinflats (site 2 Fig 3.6.1). Of these pellets, 70% contained Hydrobia and 80% Macoma (Appendix 14). The number of Hydrobia per pellet was highly variable, ranging from 1 - 136 ($\bar{x} = 38.25 \pm 49$, n = 8).

3.5.3 (iii) Gut analysis

No Knot were collected from Skinflats but five birds were shot whilst feeding at Crombie Point, in muddy-sand, over H.W. period. Hydrobia, Littorina rudis and Macoma were present in all their guts (Table 3.5.6). The alga was thought to have originated from the guts of Hydrobia and Littorina.

The/

TABLE 3.5.6: Analysis of gut contents of 5 Knot collected at Torry Bay (p = present in sample)

KNOT	HYDROBIA	LITTORINA		MACOMA		OTHER
		whole/terminal whorls	operculae	hinges	fragments	
1	7	22	3	8	p	Algae
2	32	21	1	-	p	"
3	35	7	-	-	p	"
4	4	35	1	-	p	"
5	17	22	-	-	p	"

The mean number of Hydrobia per gizzard was 19.0 ± 14.1 and of Littorina, 21.4 ± 9.9. The Littorina operculae were from smaller individuals. The Macoma shells were fragmented, preventing an estimate of the number present to be made. However, eight hinge fragments were found in one gizzard.

3.5.3 (iv) The size of items in the diet

Hydrobia:

The mean size of Hydrobia taken from pellets (3.95 ± 0.7 mm n = 26) was larger than that of those from gizzards (2.35 ± 0.55 mm n = 19). As shown in Fig 3.5.6 a and b, there was little overlap in the size classes taken. The size range of Hydrobia from the pellets was used in subsequent analysis since birds that ejected these at Skinflats had almost certainly fed at Skinflats and probably Kinneil.

Assuming that the Hydrobia in the Knot pellets originated from Skinflats, the forage ratio (Fig 3.5.8) shows a preference by Knot for Hydrobia above 4 mm, although the sample (n = 26) was small.

Macoma:

The mean length of Macoma from Knot pellets collected at Skinflats (5.48 ± 0.78 mm, n = 8) was smaller than that from the gizzards of birds collected at Crombie Point (8.45 ± 1.42 mm n = 8) (Fig 3.5.5 a and b). Since the sample size was small the results were combined and indicated that the size range taken by Knot on the Forth was 4.2 - 9.8 mm. Although not sufficient to calculate a Forage Ratio at Skinflats, it is clear that Knot will take the middle size range of the Macoma population (Fig 3.5.9). Macoma in their first winter were absent from/

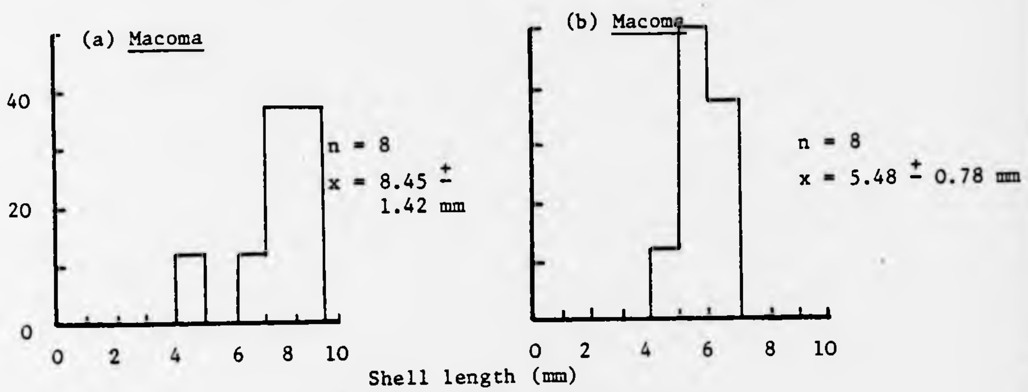


FIGURE 3.5.5: Size-frequency distribution of Macoma from (a) guts and (b) pellets of Knot

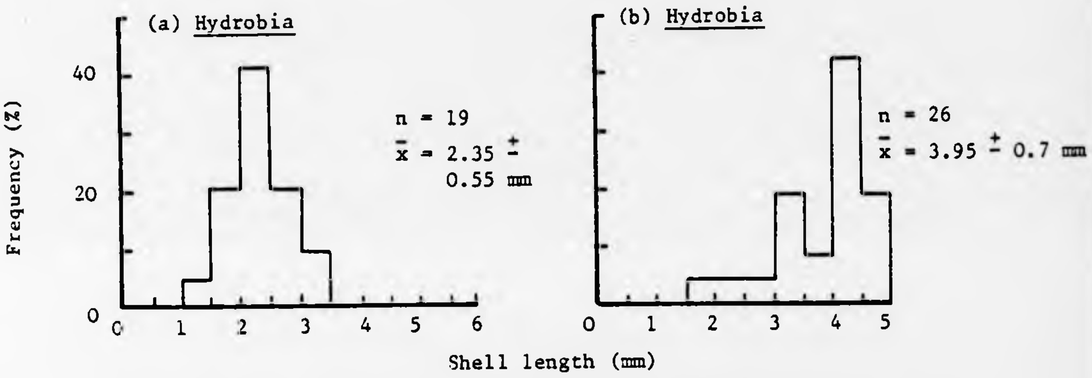


FIGURE 3.5.6: Size-frequency distribution of Hydrobia from (a) guts and (b) pellets of Knot

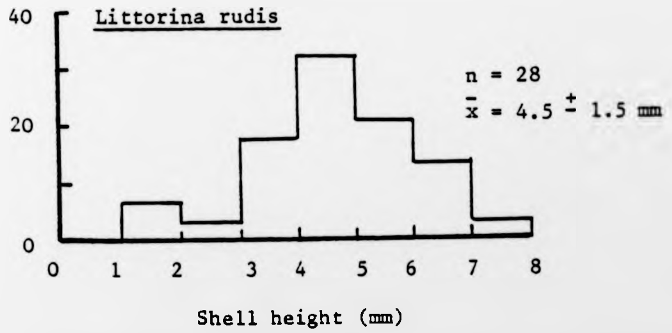


FIGURE 3.5.7: Size-frequency distribution of Littorina from Knot guts

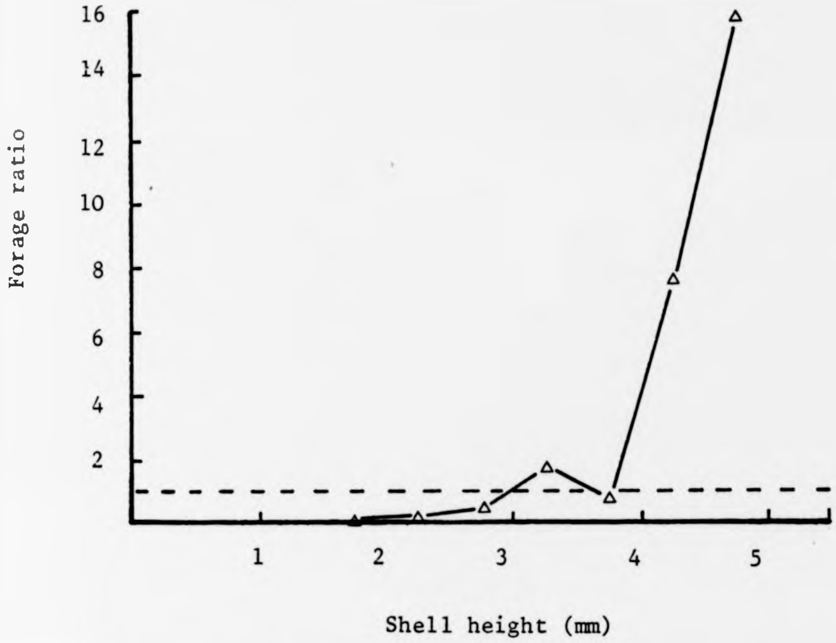


FIGURE 3.5.8: Forage ratio for Knot feeding on Hydrobia

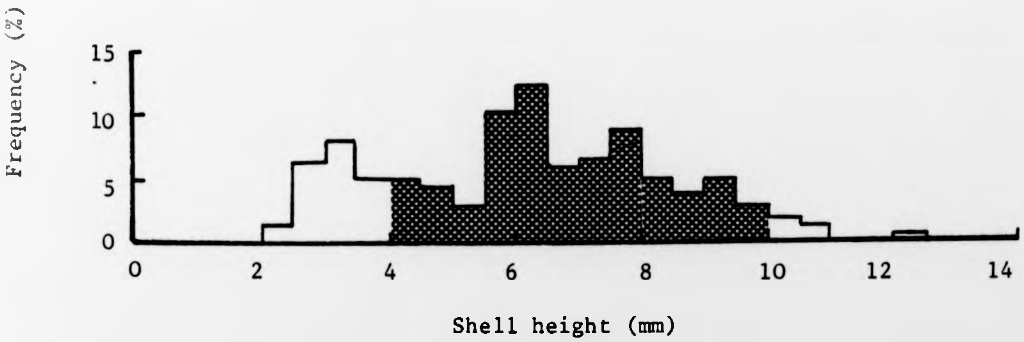


FIGURE 3.5.9: Size-frequency distribution of Macoma at Skinflats (November 1976). Shaded area = size-range included in Knot diets on the Forth estuary.

from the diet but the 1+ to 5+ year classes were exploited (Section 3.4.2).

The mean length of the bills of 15 Knot caught on the Forth in December 1976 was 32.37 ± 2.48 mm (Davies unpubl.). Thus the majority of animals dwelling in the top 4 cm of sediment would be available to foraging Knot. At Skinflats 76% of the Macoma population were 4 - 10 mm long and 88% of these were available in the top 4 cm of sediment (Section 3.4.2).

Only 44% of Macoma larger than 10 mm were available in this zone the density of which was small (19.8 m^2) compared to that of other size classes. Thus, if only 44% of these were available to Knot, only 8.7 m^2 would be within reach compared with 284.6 m^{-2} 4 - 10 mm animals.

The most frequent size-class of Macoma in the population in November 1976 were those between 5.5 and 6.5 mm (23%) since the mean size found in pellets was 5.48 ± 0.78 mm. This indicates that Knot were taking the most abundant size classes within the range available.

Littorina:

The mean size of Littorina from the gizzards of Knot collected at Crombie Point (Fig 3.5.7) was 4.5 ± 1.5 mm, representative of the smaller individuals of the population (B.Ross pers. comm.).

3.5.3 (v) Discussion

The results of this study suggest that Macoma and Hydrobia are the most important foods of the Knot on the estuarine Forth. The importance of Littorina is probably limited to areas of the upper/

TABLE 3.5.7: Summary of the diets of Knot from different localities in winter

AUTHORITY	LOCALITY	SOURCE	MOLLUSCA		ANNELIDA	CRUSTACEA	INSECTA	OTHER
			Gastropods	Bivalves				
CAMPBELL (1935)	N. Uist	gizzards n = 1	L. saxatilis H. ulvae	C. exiguum				
DAVIDSON (1971)	Morecambe Bay	gizzards n = 23	H. ulvae	M. balthica C. edulis		C. maenas		
EHLERT (1964)	German Waddensea	gizzards n = 151	L. littorea H. ulvae	M. balthica		Decapoda	larvae and pupae	Vegetable matter
EVANS et al (1979)	Teesmouth	gizzards n = 33	Littorina sp H. ulvae	M. balthica M. edulis Modiolus sp	N. diversicolor Oligochaetes Small polychaetes	C. volutator		Vegetable matter Invertebrate eggs
FEILDEN (1897)	N Norfolk Coast	gizzard	L. rudis H. ulvae A. myostis					
GOSS-CUSTARD (1970)	Ythan Aberdeen	gizzards n = 4 observ-ation	H. ulvae	bivalves				
GOSS-CUSTARD JONES AND NEWBERY (1977)	Wash	pellets droppings gizzards	H. ulvae	M. balthica C. edule	N. diversicolor	C. maenas Crangon sp		
GREENHALGH (1975)	Ribble	pellets n = 266	Littorina sp H. ulvae.	Tellina sp M. balthica	N. diversicolor	C. maenas Corophium sp		
		guts n = 43	H. ulvae	M. balthica C. edule Tellina sp	N. diversicolor	C. maenas Corophium sp		

(cont'd over)

TABLE 3.5.7 (cont'd)

AUTHORITY	LOCALITY	SOURCE	MOLLUSCA		ANNELIDA	CRUSTACEA	INSECTA	OTHER
			Gastropods	Bivalves				
PRATER (1972)	Morecambe Bay	gizzards n = 90	L.saxatilis H.ulvae	M.balthica T.tenuis C.edule M.edulis	N.diversicolor	C.maenas Crangon sp		
ROOTH (1967)	Dutch Waddensea	?	H.ulvae	C.edulis				
SPERRY (1940) (C.canutus rufus)	N.America	gizzards	Littorina sp Nassariidae Melampus sp	M.edulis Donax sp G.gemma			Unident	
WARNES et al (1980)	Firth of Forth	gizzards n = 5	L.rudis H.ulvae	M.balthica				
THIS STUDY	Firth of Forth	pellets n = 10	H.ulvae	M.balthica				

upper shore where these small snails are abundant.

The similarity in the composition of the diets of Knot from the Forth and elsewhere (Table 3.5.7) is striking. Molluscs are taken most extensively. In North America Nassarids occupy a similar niche to Hydrobia in N.W.Europe and are an important food for Knot (Sperry 1940), together with other gastropods and bivalves. Polychaetes and oligochaetes have not been extensively recorded from any study.

The size distribution and mean sizes of Hydrobia in the diet of Knot from the Forth estuary are similar to those from the Wash, Ribble and Morecambe Bay (Goss-Custard, Jones and Newbery 1977, Greenhalgh 1975, Prater 1972b)with Knot taking all sizes of Hydrobia over 1.8 mm. The preference for the larger sizes of Hydrobia at Skinflats indicates that only Hydrobia in their second year are exploited.

The size range of Macoma taken by Knot on the Forth is small compared to that comprising the diet of Knot on the Wash. There, 80% of Macoma were in the range 9 - 13 mm (Goss-Custard, Jones and Newbery 1977). It is similar, however, to the range of sizes taken on Morecambe Bay where 91.2% were less than 12 mm, 78.5% less than 9 mm (Prater 1972b). Macoma on the Wash are probably larger with many dwelling in the top 4 cm.

3.5.4 Dunlin (Calidris alpina)

3.5.4 (i) Field observations

It was not possible to determine the diet of Dunlin by direct observation. They fed very actively, turning frequently, rapidly probing and pecking. This method was particularly common on the ebb and flow tides where most Dunlin fed in dense flocks/

flocks at the tide-edge, both in shallow water and on moist mud. A slower pecking rate was noted for individuals and small groups on the Carron shore. Here, single or series of deep probes, often to the base of the bill, sometimes resulted in a worm being taken. Small items were swallowed too rapidly to be identified. Occasionally birds fed by making a rapid series of pecks interspersed by a burst of running.

3.5.4 (ii) Pellet analysis

Although Nereis and Hydrobia occurred most frequently (90.9%) in the eleven pellets collected from the ICI pipeline roost (Roost 2) at Skinflats, Macoma, oligochaetes and Manayunkia also featured (Table 3.5.8 Appendix 15). Dipteran larvae and vegetable matter occurred occasionally (9.1% of pellets).

3.5.4 (iii) Gut analysis

The importance of Nereis and Hydrobia in the diet of Dunlin is further illustrated by the gut analysis (Table 3.5.8 Appendix 16). Four birds were collected in November 1975 at Kinneil 'Open Pan' and eleven from Skinflats in February 1976. Two corpses, raptor casualties, were also examined: one from Kinneil and a second from West of Kincardine Bridge (Table 3.5.8). Oligochaetes ~~alone~~ were present in the gizzards from Kinneil, although both oligochaetes and Manayunkia were found in pellets from Skinflats. These may have been collected from the sediment surface with the pellets. The occurrence of Corophium in the birds from W. Kincardine Bridge was the only record of this prey in any wader diet in the present study. The bird may have been feeding at Kennet Pans where Corophium are abundant (Bryant and McLusky/

TABLE 3.5.8: Pellet and gut analysis of Dunlin

	% occurrence							
	NEREIS	MACOMA	HYDROBIA	OLIGOCHAETES	MANAYUNKIA	DIPTERAN LARVAE	VEG. MATTER	COROPHIUM
Pellets n = 11 (Skinflats) 4.12.77	90.9	18.2	90.9	18.2	27.3	9.1	9.1	-
Gizzards n = 4 (Kinneil) 21.11.78	75	25	100	25	-	-	-	-
Gizzards n = 11 (Skinflats) 13.2.76	90.9	27.3	90.9	-	-	9.1	18.2	-
Gizzard raptor casualty Kinneil	p	p	-	-	-	-	-	-
Gizzard raptor casualty W. of Kincardine Br.	p	p	p	-	-	-	-	p

McLusky 1976).

3.5.4 (iv) Size of items in the diet

Hydrobia:

The mean size of Hydrobia from pellets ($\bar{x}$ = 2.2 ± 0.77 mm) and gizzards ($\bar{x}$ = 2.4 ± 0.77 mm) was similar, ($p > 0.05$), the range of 0.6 - 3.5 mm shell heights (Fig 3.5.11 a and b) being equivalent to 0+ and 1+ yr classes of Hydrobia (Section 3.3.4). A Forage Ratio greater than 1.0 indicated that 2 - 3 mm Hydrobia were selected by Dunlin (Fig 3.5.12a). Other size classes between 0.5 and 3.5 mm were taken non-selectively, with the exception of the 1 - 1. 5 mm class.

Nereis:

The size-frequency distribution of Nereis jaws is shown in Fig 3.5.10 a and c, and the equivalent body lengths derived from the jaw measurements in Figs 3.5.10 b and d. The mean size of the Nereis jaws from pellets ($\bar{x}$ = 0.56 ± 0.11 mm) and from the gizzards ($\bar{x}$ = 0.55 ± 0.25 mm) were similar ($p > 0.05$) and the majority of worms these represented (> 80%) were less than 3 cm long.

A Forage Ratio greater than 1 for Nereis with jaws 0.5 - 0.6 mm long indicates selection by Dunlin for these size classes (Fig 3.5.12b). Worms smaller than 0.5 would largely be available in the top 4 cm (Section 3.4.4) but were selected against.

The selection for larger worms whose burrows extend into the 4 - 7 cm zone indicates that they were taken by Dunlin when extended into the shallower zones.

3.5.4 (v) Discussion/

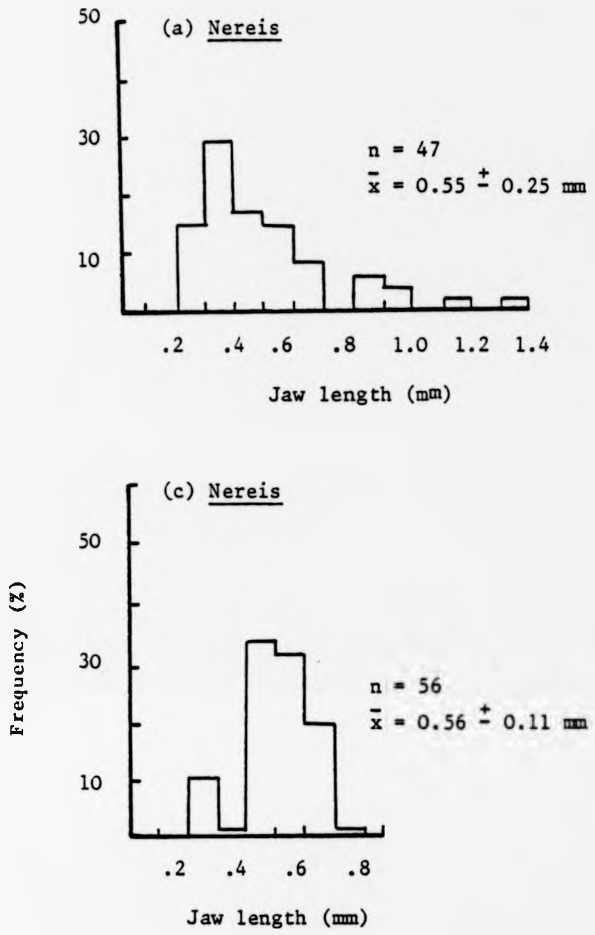


FIGURE 3.5.10: Size-frequency distribution of Nereis jaws from (a) guts and (c) pellets of Dunlin and the equivalent worm lengths (b and d)

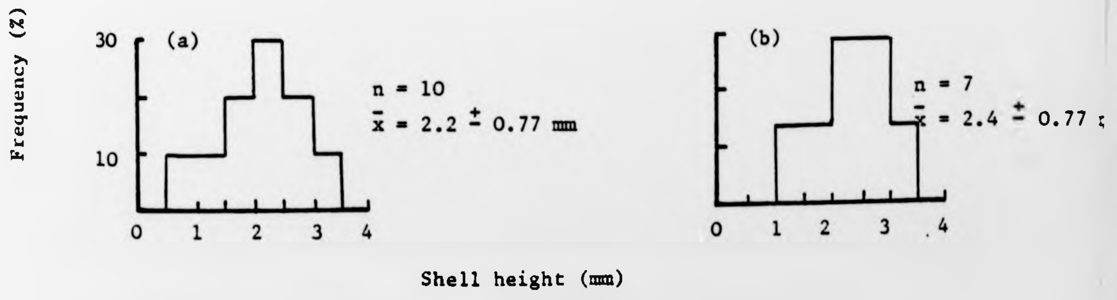


FIGURE 3.5.11: Size-frequency distribution of Hydrobia from (a) pellets and (b) guts of Dunlin

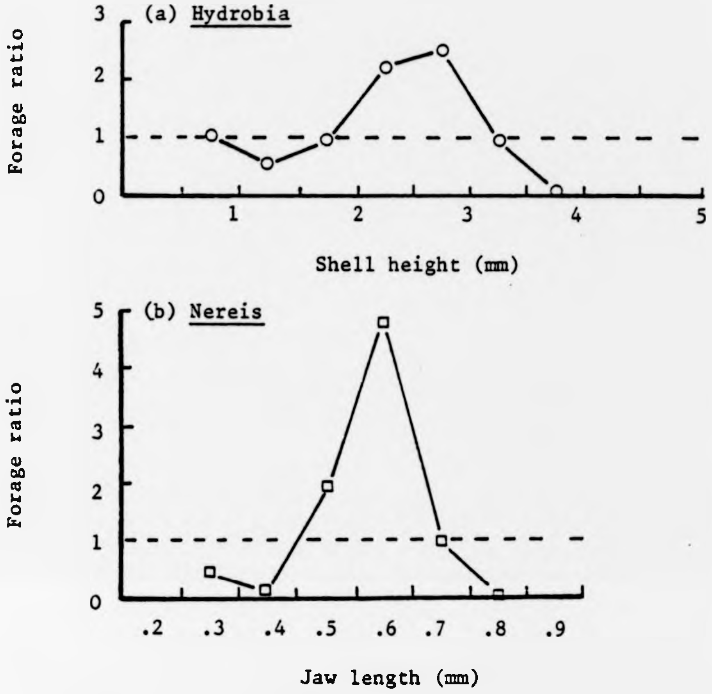


FIGURE 3.5.12: Forage ratios for Dunlin feeding on (a) Hydrobia and (b) Nereis

3.5.4 (v) Discussion

The ability of Dunlin to exploit a wide range of prey has been demonstrated in this study and in those elsewhere (Table 3.5.10). On one of the breeding grounds, in northern Alaska, insects and their larvae are the major food items (Holmes 1970, Holmes and Pitelka 1968) and they continue to feature, to a lesser degree, in the diets of overwintering Dunlin in N W Europe. There is close agreement between locations concerning the prey species. *Nereis* appears to be the major prey (eg Bengston and Svensson 1968, Ehlert 1964, Goss-Custard 1970b) with *Hydrobia* also of importance.

The contribution of oligochaetes and small polychaetes cannot be assessed, for reasons outlined for Redshank, but their preference in the guts of birds from Kinneil indicates a potential importance at this site at least. The fluid, oligochaete-rich muds (McLusky 1976-80) in the vicinity of the BP effluent outfall are similar to those on the Tees where small worms are considered important in Dunlin diets (Evans *et al* 1979).

Since Dunlin prefer the size classes of *Nereis* whose burrows extend beyond the reach of the birds' bills, disturbance of worms by dense flocking must be important and, as for Redshank, most likely explains their feeding dispersion at low tide. Although not so widely spaced as Redshank, they do not forage in large dense flocks like Knot (pers. obs., Goss-Custard 1970b). At high beach levels Moffat (1975) noted a high incidence of pecking and shallow probing at Skinflats compared to the high incidence of deep probing at low levels. Also, on Morecambe/

TABLE 3.5.9: Comparison of the size of Nereis and Hydrobia in the diets of Dunlin from different localities

AUTHORITY	LOCATION		HYDROBIA	NEREIS
Burton 1974	Essex	Gizzard	mean size 2.08 ± 0.03 n = 288	mean size jaw length 0.9 n = 64
Evans et al 1979	Teesmouth	Gizzard	0 - 1 yr class	0 - 1 yr class
Goss-Custard Jones and Newbery 1977	Wash	Gizzard	2 - 3 mm age class most frequent n = 71	mainly 3 cm although 8 cm worm recorded
Greenhalgh 1975	Ribble	Gizzard	mean size 2.04 ± 0.11 n = 615	mean jaw length 0.27 ± 0.018 mm n = 37
Present Study	Forth	Pellets	mean size 2.2 ± 0.77	jaw length 0.56 ± 0.11 mm worm length 1.95 ± 0.63 cm n = 56
		Gizzard	mean size 2.4 ± 0.77 n = 7	jaw length 0.55 ± 0.25 mm worm length 2.07 ± 1.56 cm n = 47

TABLE 3.5.10: Summary of the diets of Dunlin from different localities in winter

AUTHORITY	LOCALITY	SOURCE	MOLLUSCA Gastropods	 Bivalves	ANNELIDA	CRUSTACEA	INSECTA	OTHER
BENGTSTON & SVENSSON (1968)	Saltviken S. Sweden	gizzards n = 23	*H. ulvae*		*N. diversicolor*	*Gammarus sp*	Coleoptera Heteroptera Hymenoptera Diptera	Seeds Vegetable matter
BURTON (1974)	Essex estuaries	gizzards n = 26	*L. neritoides* *Crepidula* *H. ulvae*	*M. balthica* *C. edule*	*N. diversicolor*	*T. saltator* *C. volutator* Decapoda	Unidentified insect	Vegetable matter Fish
CABOT (1968)	Galway Bay	gizzards n = 28	*H. ulvae*		*N. diversicolor*			
DAVIDSON (1971)	Morecambe Bay	gizzards n = 24	*H. ulvae*	*M. balthica*	Polychaetes	*Bathyporeia* sp *C. volutator*		
DEWAR (1909)	Forth?	observation	univalves from rocks and sand		"Worms"	"mud crustacea"	Insects	Spiders
EHLERT (1964)	German Waddensea	gizzards n = 151	*L. littorea* *H. ulvae* *R. truncululata*		*N. diversicolor* *S. armiger* *P. elegans*	Amphipoda	Coleoptera Diptera and their larvae	Seeds Vegetable matter
EVANS *et al* (1979)	Teesmouth	gizzards n = 48	*H. ulvae*	*M. balthica* *Mytilus* sp. *Modiolus* sp.	*N. diversicolor* Oligochaetes Small Polychaetes	*C. volutator* *C. maenas*	Insects	Vegetable matter Invertebrate eggs
FUCHS (1975)	Camargue	gizzards n = 9	*H. ulvae*		Polychaetes	*Artemia*	Insects inc. Diptera and Coleoptera Larvae	
GOSS-CUSTARD	Ythan	gizzards n = 13				*Corophium* most important		

TABLE 3.5.10 (cont'd)

AUTHORITY	LOCALITY	SOURCE	MOLLUSCA		ANNELIDA	CRUSTACEA	INSECTA	OTHER
			Gastropods	Bivalves				
GOSS-CUSTARD JONES AND NEWBERY (1979)	Wash	observ-ation + gizzards n = 59	*H. ulvae*	*M. balthica* *C. edule* *M. edulis*	*N. diversicolor* *Nephthys* sp	*C. volutator* 'Crabs'		
GREENHALGH (1975)	Ribble	gizzards n = 45	*H. ulvae*	*M. balthica*	*N. diversicolor*	*C. volutator*		
MADON (1935)	'France'	gizzards n = ?	Small Molluscs		*N. diversicolor*	Crabs Small crustacea	Dipteran larvae	Vegetable matter
PRATER (1970)	Morecambe Bay	gizzards n = 56	*H. ulvae*	*M. balthica* *C. edulis* *Tellina* sp.	*N. diversicolor*	*Corophium* sp *Carcinus* *Bathyporeia* unid Crustacea	Dolichopodidae larvae Hymenoptera	Vegetable matter
THIS STUDY	Forth	pellets n = 11 gizzards n = 15	*H. ulvae*	*M. balthica*	*N. diversicolor* *Manayunkia* Oligochaetes		Dipteran larvae	Vegetable matter

Morecambe Bay, 91% of Dunlin pecked from the surface close to HW when flocks were densely packed, (Prater 1970). This strongly suggests that Hydrobia and probably small Macoma are taken when the birds feed in large dense flocks and that the majority of the preferred sizes of worms are unavailable at such times.

A comparison between the size classes of prey taken by Dunlin at various locations (Table 3.5.9) shows similarity between areas. Nereis body lengths differ little where the same methods of measurement have been employed (Evans et al 1979, Goss-Custard, Jones and Newbery 1977, this study) but differences in the methods of measuring jaws may account for discrepancies at other sites.

No Macoma hinges were available for measurement but on Morecambe Bay (Prater 1970) the mean shell size was 4.77 ± 0.06 mm in February, corresponding to small 0+ and 1+ year classes, occurring in the surface layers.

3.5.5 The Curlew (Numenius arquata)

The number of Curlew feeding at Skinflats was small and, since pellet and gut analysis from this site was not possible, the species was studied at several sites on the Forth.

3.5.5 (i) Field observations

The results of observations to determine the food type taken at five sites around the estuary are shown in Table 3.5.11. Those at Longannet were made by J. Speakman (Speakman 1980) while those made during this study at Torry Bay and Newmills Bay were at upshore sites only.

TABLE 3.5.11: The prey items and feeding rates of Curlew at five sites on the Forth estuary

Site	total no. items taken	total no. mins observation	items taken min^{-1}	% of each species taken				
				Arenicola	Bivalves	*Nereis*/ *Nepthys*	Crabs	Unidentified
Longannet ♂	85	23.82	3.57	-	35.3	63.5	1.2	-
♀	254	84.83	2.99	-	61.8	36.6	1.6	-
Newmills Bay	15	5.83	2.57	-	-	100	-	-
Torry Bay	9	-	-	88.9	-	11.1	-	-
Skinflats	130	50.08	2.6	-	0.8	80.8	-	18.5
Kinneil	80	35.45	2.26	-	7.5	58.8	-	20.7

Nereis/Nepthys were taken by Curlew at all study sites and exclusively at Newmills Bay, although the sample size at the latter was small. Bivalves were taken at all other sites except at Torry Bay where Arenicola was favoured. Only at Longannet was Carcinus observed being eaten.

A high percentage of the prey taken at Longannet was Macoma, in contrast to the proportion taken elsewhere, while at Skinflats, Nereis was taken almost exclusively.

The feeding rates (Table 3.5.11) were highest at Longannet foreshore where the diet consisted of bivalves, Nereis and a few crabs. Male Curlew fed at a higher rate than females at this site. When feeding mainly on worms, the feeding rates were lower.

3.5.5 (ii) Pellet Analysis

The results from the pellet analysis are summarised in Table 3.5.12. The appearance of the pellets varied greatly. Some consisted only of stones, occasionally bound by vegetable matter. Others formed distinct, oval pellets 2.2 - 3 cm long containing bivalve and Carcinus fragments together with vegetable matter. Occasionally the whole gizzard lining was ejected. One pellet, from Newmills Rock, contained only crab remains.

Nereis was the only prey species to be found in pellets from all sites. Cerastoderma occurred in 58.3% of those from the Newmills roost but, in general, the pellets at any site were diverse in their species composition but with few prey occurring frequently in any sample.

Three/

TABLE 3.5.12: % frequency of each prey species in Curlew pellets

	LITTORINA	CERASTODERMA	NEREIS	CARCINUS	MACOMA	MYTILUS	STONES ETC VEGETABLE MATTER
n = 12 Newmills	25%	58.3	33.3	41.7	16.7	16.7	66.7
n = 4 Kinneil	0	25	25	25	25	0	insects 25
n = 18 Charlestown	0.5	-	16.6	16.6	gizzard linings 16.6	barley grains 16.6 plastic pellets 16.6	insects 11.1 stones 33.3 veg 77.7
n = 5 Torry	-	40	20	-	40	20	veg 80.0 stones 100.0 3 unidentified 'worms' semi-digested

TABLE 3.5.13: gizzard contents of Curlew from Kinneil (✓ = present)

	Macoma	Cerastoderma	Nereis	Unidentified	Stones
Gizzard Contents	fragments	fragments	512 jaws	semi-digested flesh	✓

Three of the five Torry Bay Curlew pellets contained stones plus terrestrial vegetable matter, whereas all but two from the Newmills roost contained intertidal invertebrates exclusively, these two consisting entirely of stones. Insect remains occurred in one pellet from Kinneil. Plastic pellets, similar to those found in the Shelduck guts were found in 16.6% of pellets from Charlestown.

3.5.5 (iii) Gut analysis

The results of the gizzard analysis for a single Curlew collected at Kinneil are shown in Table 3.5.13. Macoma, Cerastoderma and Nereis were all represented.

3.5.5 (iv) Size of items in the diet

Nereis

The size-frequency distributions of Nereis jaws from Curlew pellets and gizzard are shown in Figs 3.5.13 a-b and 3.5.14 a-b. The equivalent worm lengths of Nereis, estimated from jaws found in the gizzard, is shown in Fig 3.5.13c. The mean jaw lengths from the pellets from the various sites were similar ($p > 0.05$) but the difference in mean jaw length of Nereis obtained from the gizzard and pellets at Kinneil was significant ($p < 0.05$) with those from the gizzard being smaller.

Macoma

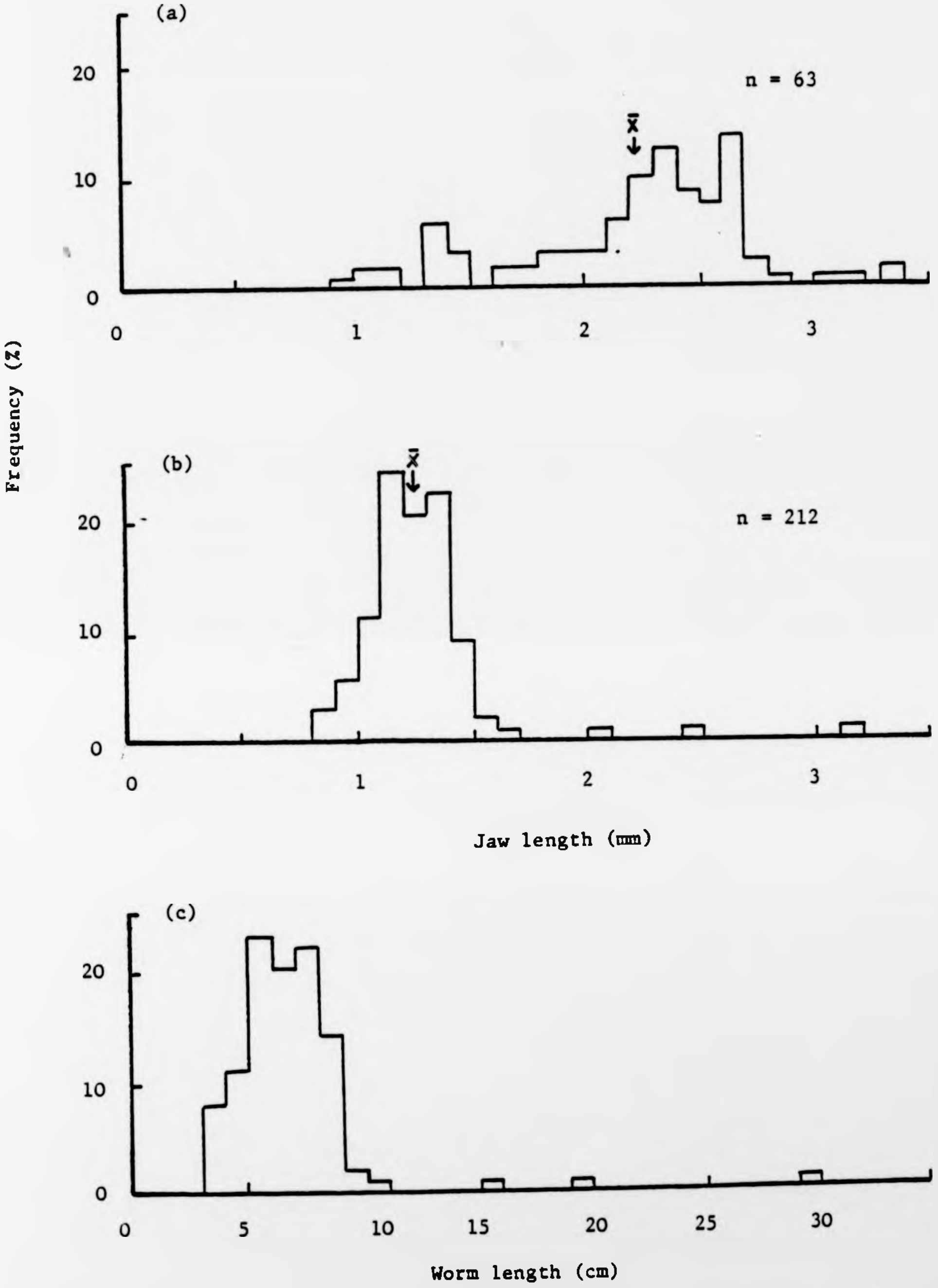
Fig 3.5.15 shows the size range and frequency of Macoma found in pellets from the Newmills Rock roost-site. The mean size is 12.27 ± 3.02 mm, range 8 - 21 mm.

Carcinus

Fig 3.5.16 shows the length frequency distribution of the dactyles/

FIGURE 3.5.13: Size-frequency distributions of Nereis jaws from (a) a pellet and (b) a gut of Curlew from Kinneil.

The equivalent worm lengths of Nereis from the gut are shown in 3.5.13 (c).


(a)
20
10
0
n = 63
x̄
0
1
2
3
Frequency (%)
(b)
20
10
0
n = 212
x̄
0
1
2
3
Jaw length (mm)
(c)
20
10
0
0
5
10
15
20
25
30
Worm length (cm)

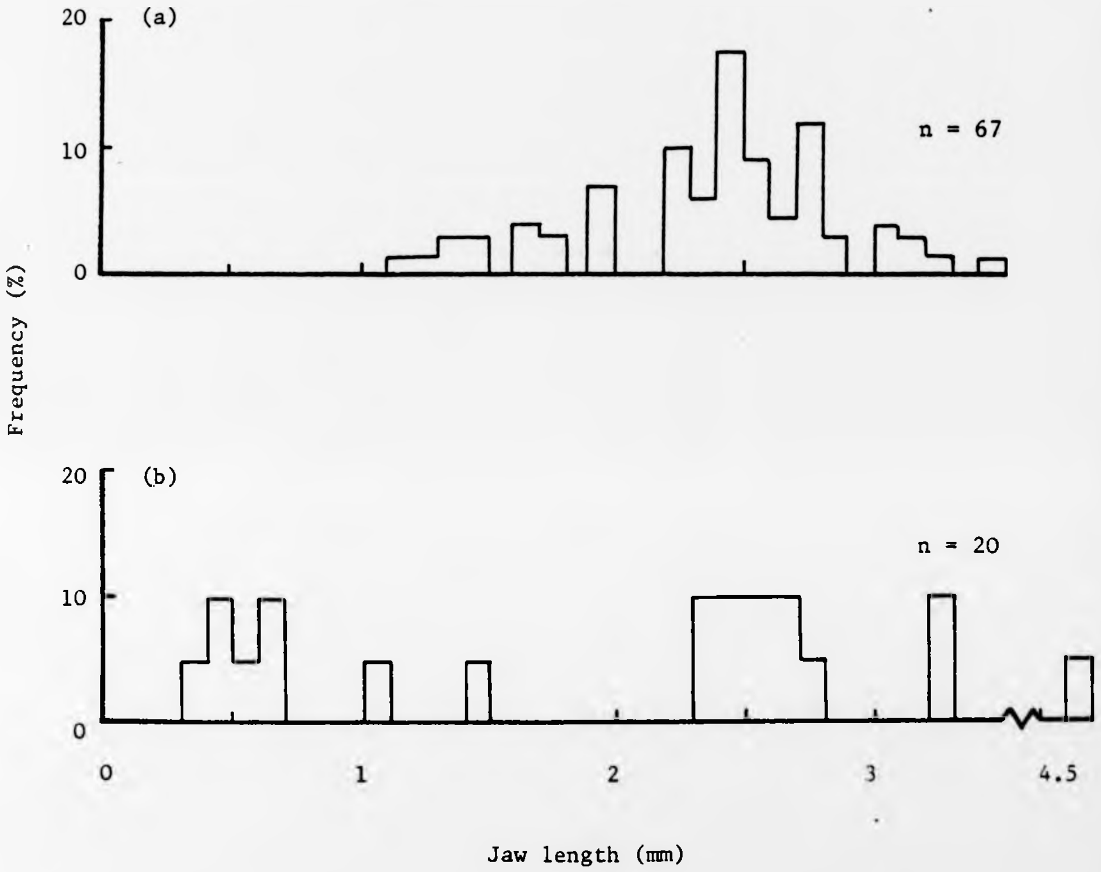


FIGURE 3.5.14: Size-frequency distribution of <u>Nereis</u> jaws in pellets from (a) Newmills Rock roost and (b) Charlestown Harbour roost

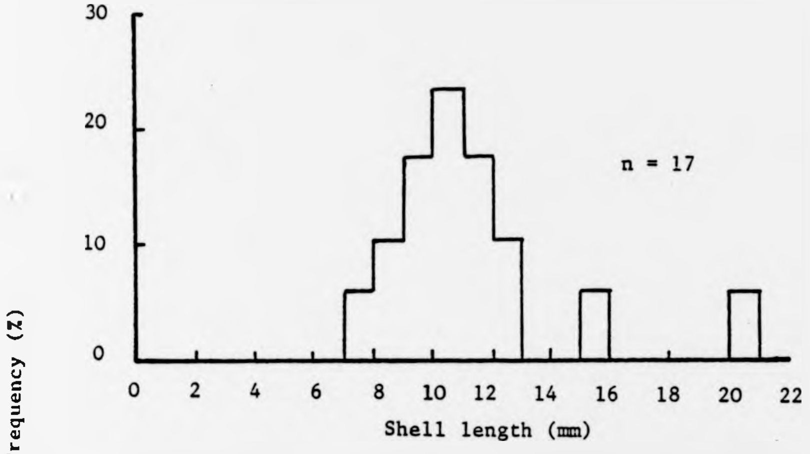


FIGURE 3.5.15: Size-frequency distribution of Macoma, from Curlew pellets, Newmills Rock roost

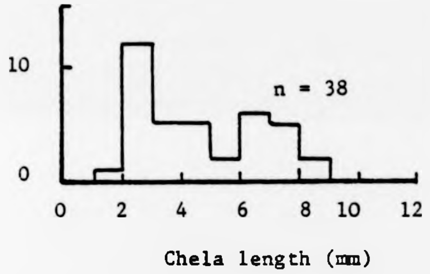


FIGURE 3.5.16: Size-frequency distribution of Carcinus chelae from Curlew pellets, Newmills Rock roost

dactyles of the cheliped of *Carcinus* from pellets. Four *Carcinus* taken by Curlew at Longannet were estimated to be c. 2 cm in carapace width (Speakman 1980).

3.5.5 (v) *Discussion*

The combined results of observations on feeding birds, pellet and gizzard analysis strongly suggest that *Nereis* is the most important prey taken by Curlew on the Forth with bivalves also being important at most sites. This confirms the diet suggested from associations between feeding birds and prey density (Bryant 1979a). *Carcinus* may be an important prey on the North Shore feeding grounds, amongst the mussel beds and in the more marine habitats, as on Morecambe Bay (Prater 1970). They may also be seasonally important as found on the Tees estuary and on the Wash (Evans *et al* 1979, Goss-Custard Jones and Newbery 1977). The wide range of species present in the diet supports the suggestion made by Goss-Custard, Jones and Newbery (1977) that, by following the tide across the mudflats, Curlew will encounter and exploit a wide variety of prey types. *Nepthys* are more common than *Nereis* at Torry Bay and Newmills Bay and may thus be the more important prey items there. Many Curlew feed amongst the mussel beds at Torry Bay (Fig 3.5.17), where *Carcinus* are probably common, and also on the sandy areas beyond, where *Cerastoderma* abound (M. Elliott pers. comm.). Near the top of the shore is an *Arenicola* zone (Elliott 1979) and Curlew feeding there probably concentrate their feeding on this large polychaete. The whole area of Torry Bay is utilised to some extent by Curlew emphasising the variety of prey available.

On the South Shore, the fauna is less diverse and there *Nereis*/

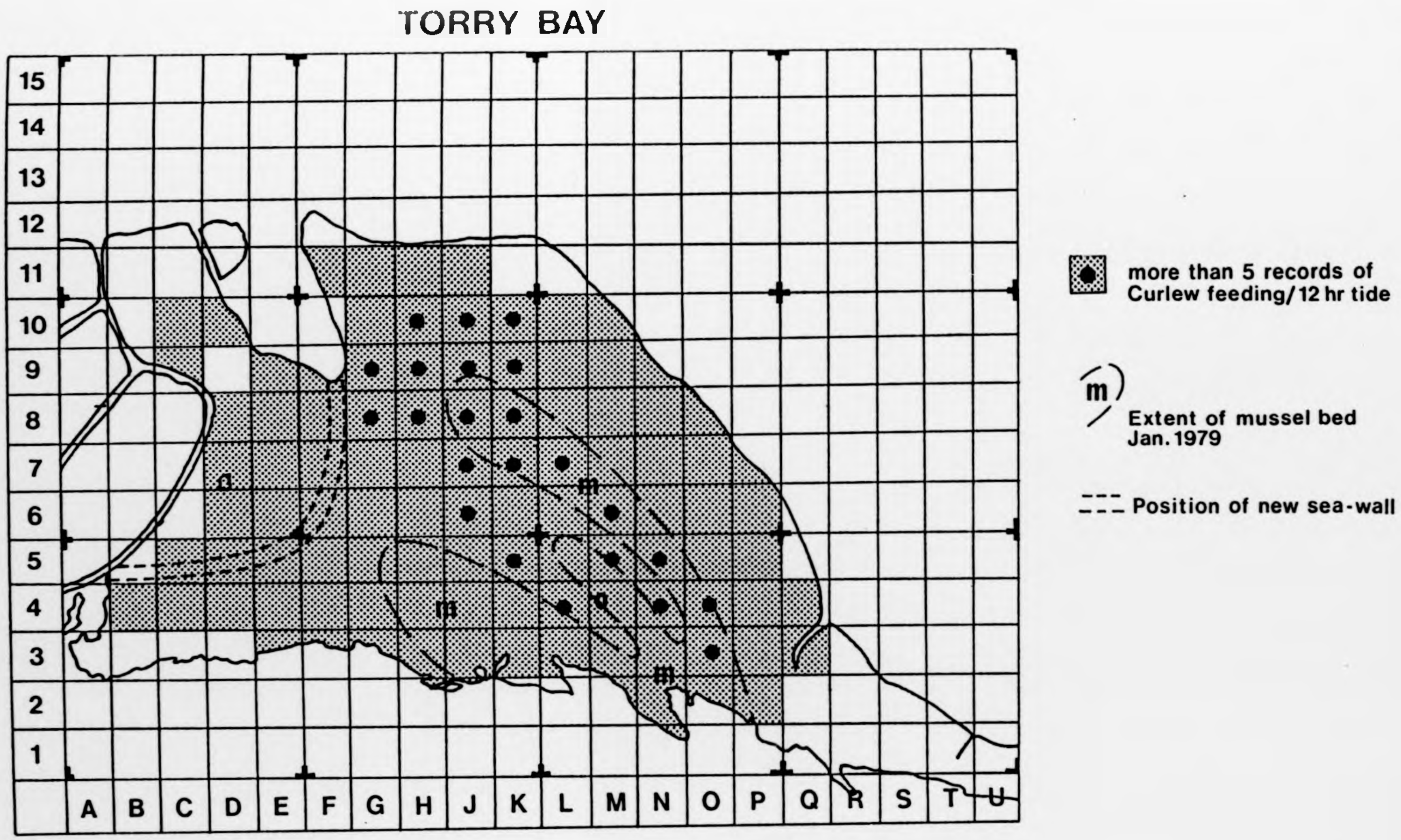


FIGURE 3.5.17: The feeding distribution of Curlew during January 1976 Survey (shaded)

Nereis and bivalves are probably the principal prey items, although Carcinus also features in the diet.

Prater (1970) and Goss-Custard and Jones (1975) noted a contrast between the large number of Nereis and Arenicola seen to be eaten by Curlew and the small number found in guts and pellets. This emphasises the need to combine field observations with gut and pellet analyses to fully describe the diet of the Curlew.

The feeding rates of Curlew on Nereis conform with those on the Tees ($x = 2.1\ \mathrm{min}^{-1}$, Pienkowski 1973) and on Morecambe Bay ($x = 2.23\ \mathrm{min}^{-1}$, Prater 1970). Rates of feeding on a mixed diet cannot be compared with those of a single prey. Feeding on Macoma in Morecambe Bay (Prater 1970) yields a mean rate of $2.8\ \mathrm{min}^{-1}$ which is also similar to the rates of feeding on the Forth estuary.

The differences in mean sizes of Nereis jaws from the pellets and the gizzard from the Kinneil bird suggest that the smaller ones were of Nereis diversicolor, the larger from N. virens. Prater (1970) found a 4 mm jaw in the gut of one Curlew and MacDonald (1971) found a bimodality in the size distribution of jaws which corresponded to the small and large size-classes found in this study. N. virens is found in more marine habitats than that at Kinneil suggesting that the pellets collected there were from birds that had been feeding in part further down the estuary.

The sizes of Macoma in Curlew pellets from the Forth roost-sites are similar to those from the gizzards of Curlew collected on Morecambe Bay (Prater 1970) where 83% measured were/

were between 12 and 16 mm. On the Forth, 88% were between 8 and 14 mm. The mean sizes from the two studies were also similar (13.9 ± 0.15 mm on Morecambe Bay, 12.27 ± 3.02 mm on the Forth).

The largest Carcinus seen to be taken by a Curlew in captivity was 35 mm and 20 - 25 mm Carcinus were taken on Essex estuaries by wild Curlew (Burton 1974). Similar sized Carcinus were taken at Longannet (Speakman 1980)

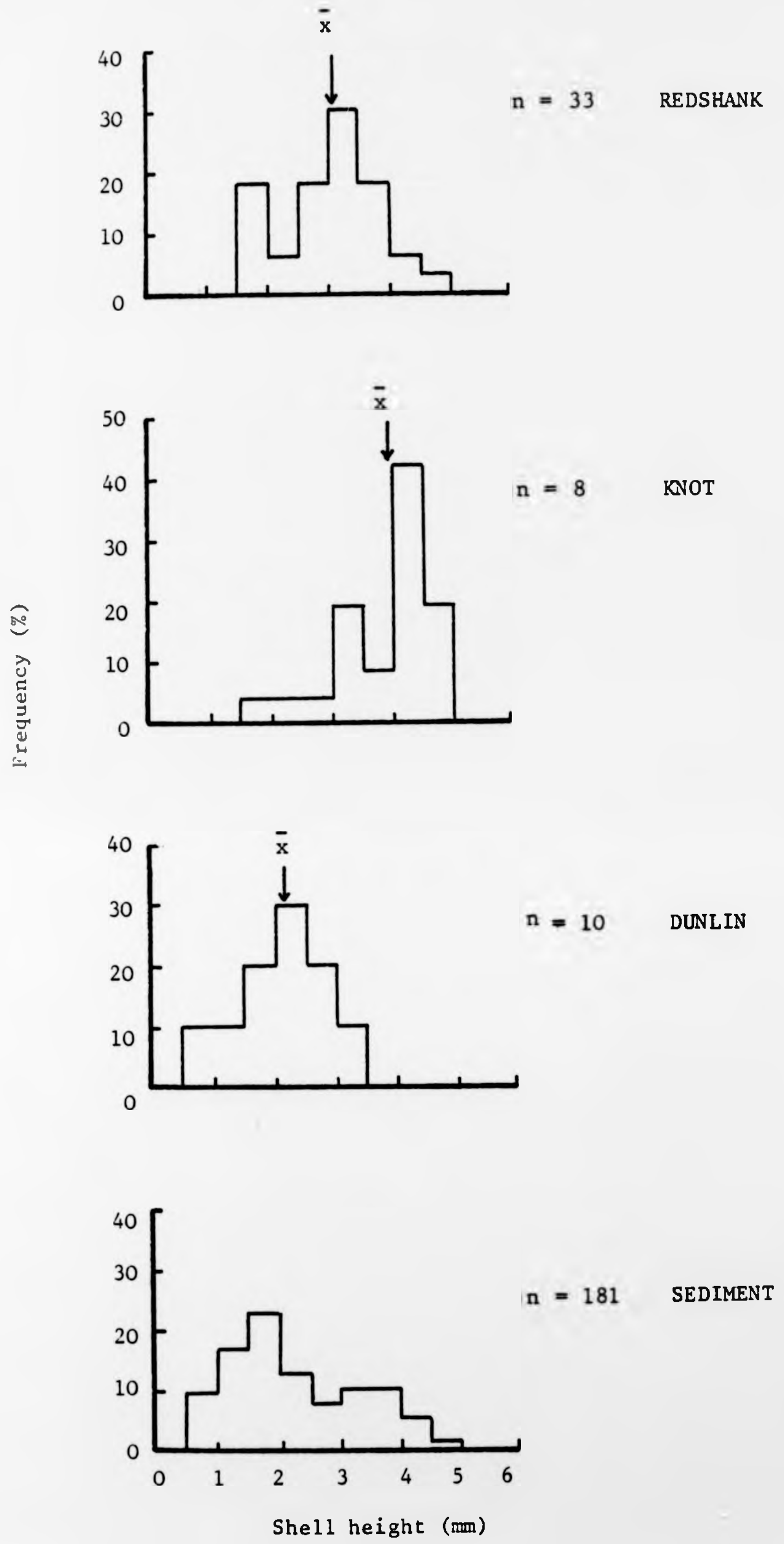
3.5.6 Comparison of the size of prey items in the diets of Redshank, Knot, Dunlin and Curlew

Redshank, Knot, Dunlin and Curlew all feed at Skinflats and thus must differ sufficiently in their ecology to allow co-existence within the area (Lack 1971). Differences in shore level utilisation are discussed in Section 3.6 but differences in diet and in the sizes of the same prey exploited illustrate a degree of resource partitioning.

Figs 3.5.18, 3.5.19 and 3.5.20 illustrate the size distributions of prey taken by the bird predators and the size distributions available in the substrate. Of the three species which include Hydrobia in their diet at Skinflats, Dunlin take the smallest individuals. The degree of overlap is largest between Redshank and Knot but Redshank have a much broader diet than Knot, possibly as the result of competition (see also Section 3.6). All size classes available in the substrate are subject to predation by at least one of the bird predators.

A comparison of the size distributions of Macoma (Fig 3.5.19) also shows considerable overlap between the diets of Redshank and Knot. Macoma is probably the most frequently taken food item of

FIGURE 3.5.18: A comparison of the size-distribution of Hydrobia in the diets of Redshank, Knot and Dunlin and in the sediment at Skinflats.


x̄
n = 33
REDSHANK
n = 8
KNOT
n = 10
DUNLIN
n = 181
SEDIMENT
Frequency (%)
0
10
20
30
40
50
0 1 2 3 4 5 6
Shell height (mm)

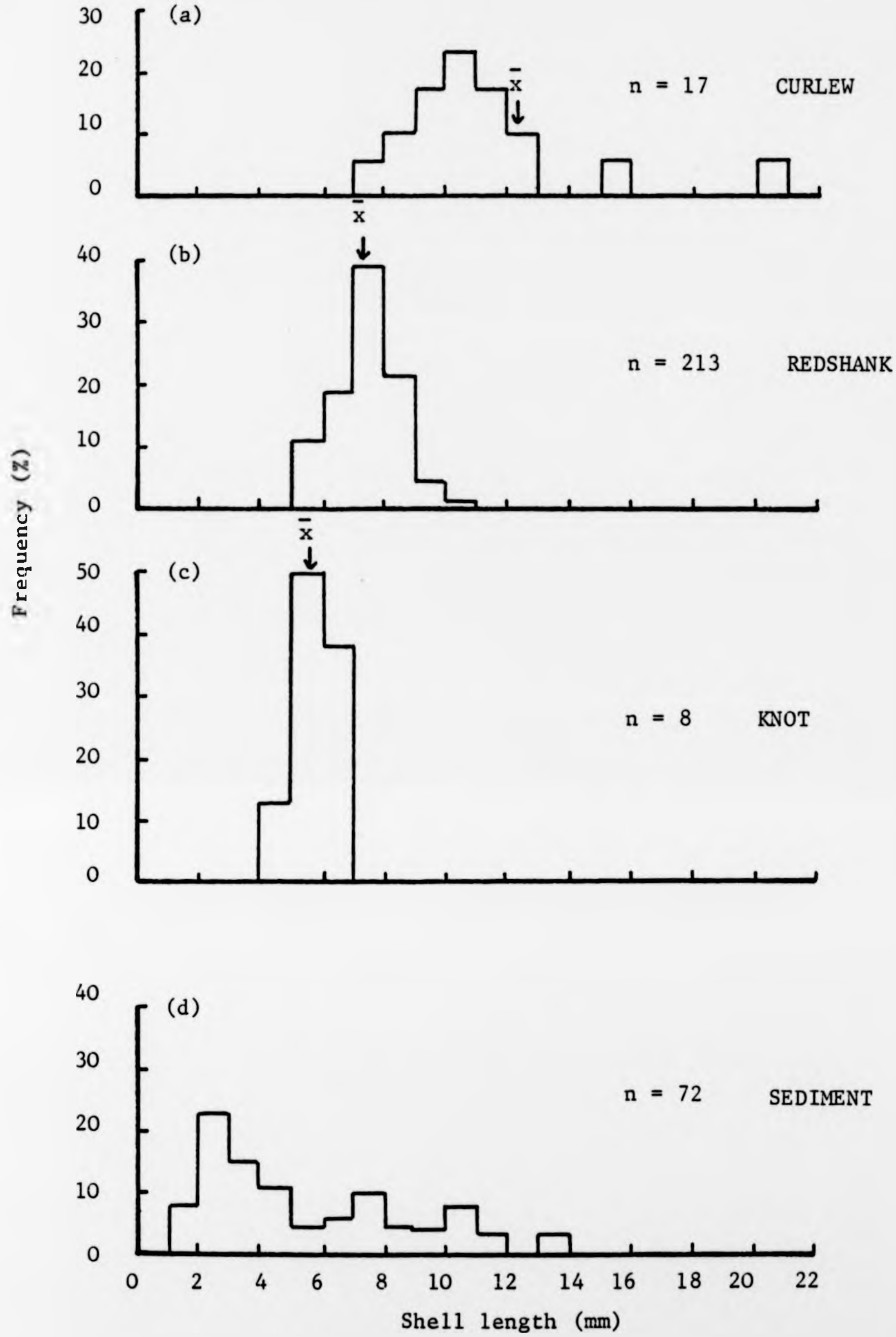


FIGURE 3.5.19: A comparison of the size distribution of Macoma from pellets of (a) Curlew (Newmills Rock roost), (b) Redshank (Skinflats roosts), (c) Knot (Skinflats) and (d) Sediment (Skinflats, December 1977)

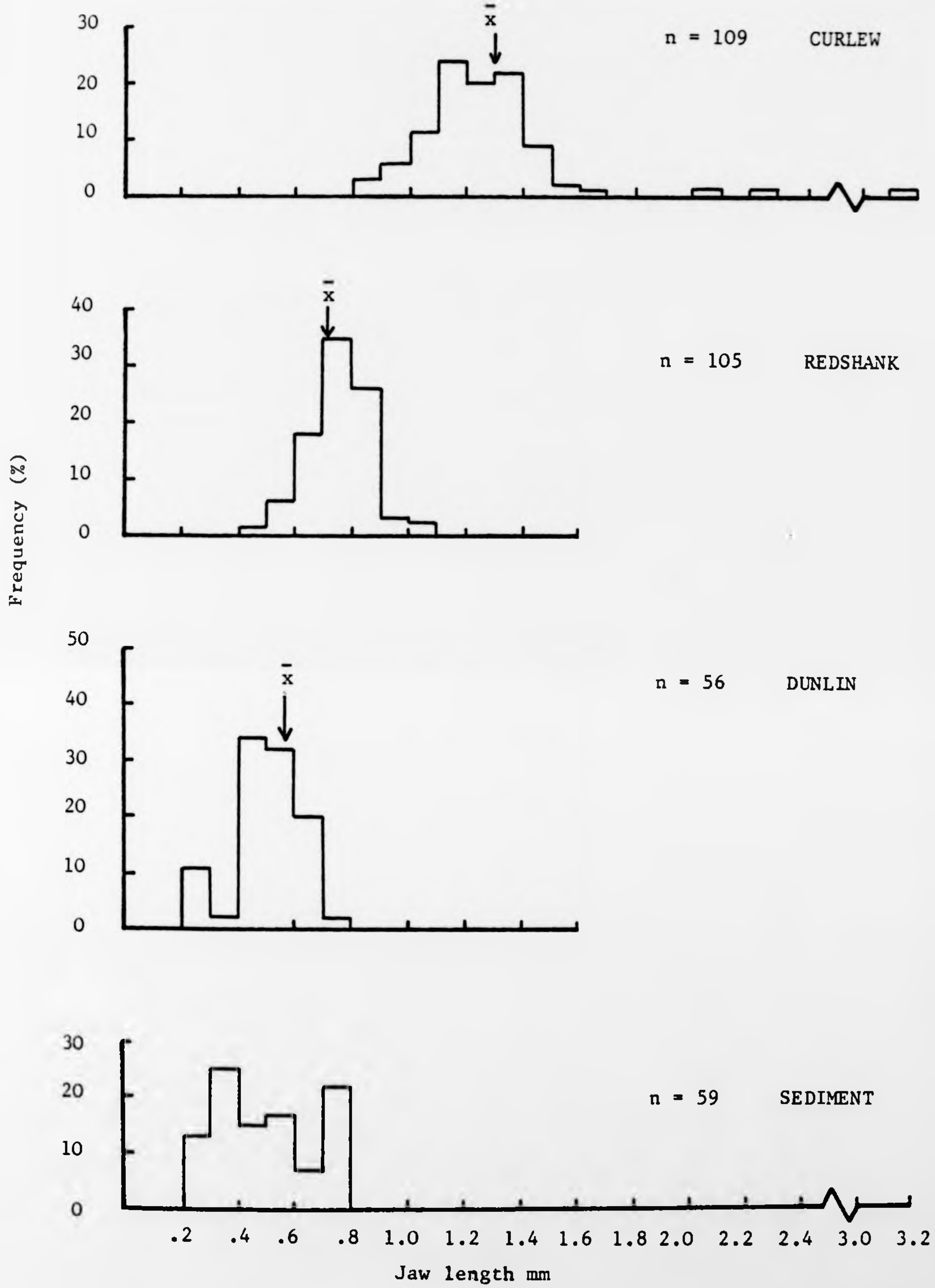


FIGURE 3.5.20: A comparison of the size distribution of Nereis jaws in the diets of Curlew, Redshank and Dunlin and in the sediment (December 1977). (Curlew data from Kinneil, all others from Skinflats)

Knot on the Forth, together with Hydrobia, so that the Redshank's preference for Nereis (Bryant 1979a, Goss-Custard 1969, this study) may prevent any intense competition for these resources. Curlew, with their longer bills can exploit the large, deeper dwelling Macoma and tend to avoid the 0+ and 1+ age classes. Here Macoma may attain a larger size than at Skinflats and so explain the discrepancy between the largest Macoma ingested by Curlew and those sampled in the sediment at Skinflats. Alternately, the sampling technique at Skinflats may have missed the few large Macoma occurring at depths below 10 cm.

Curlew took a wide size-range of Nereis sp. on the Forth but a comparison between the sizes taken at Kinneil (gizzard analysis) and those taken by Redshank and Dunlin (Fig 3.5.20) at Skinflats reveals little overlap with these other species. The sampling technique for the Nereis population was open to improvement since both Redshank and Curlew took larger worms than were sampled from the sediment. A 10 cm depth core appears to be adequate only for worms with less than 0.8 mm jaw length since larger worms will have deeper burrows to withdraw into when disturbed.

3.5.7 The Oystercatcher (Haematopus ostralegus)

3.5.7 (i) Field observations

The results of observations to determine the food items at Culross, Torry Bay and Kinneil are summarised in Table 3.5.14. At Culross feeding was concentrated on the extensive mussel beds and mussels were the only prey seen to be taken. The majority were carried before being opened. Opening consisted of a series of sharp jabs with the bill, followed by a levering action of the head and bill to extract the flesh. The/

TABLE 3.5.14: Prey species and feeding rates of Oystercatcher at three sites on the Forth estuary

	total no mins observation	total no ~~mins~~ observations	total no items seen eaten Mussels	 Cardium/ Macoma	 Unidentified	feeding rate items min^{-1}
CULROSS	34.86	6	40	-	-	1.15
TORRY BAY	18.88	12	-	53	-	2.81
KINNEIL	37.9	11	2	42	10	1.45

TABLE 3.5.15: % Frequency of occurrence of prey species in Oystercatcher pellets at the three sites

	Mytilus byssus threads	Littorina operculae	Macoma shell fragments	Carcinus chelae	Whelk sp operculae	Nereis jaws
Culross Pier n = 23	87	61	4.3	4.3	0	0
MOD Crombie Stub Pier + rocks n = 3	66	100	0	0	67	0
Charlestown harbour walls n = 22	86	59.1	0	0	36.4	4.5

TABLE 3.5.16: Gut contents of three Oystercatchers from Kinneil

	Cardium 'feet'	Mussels (byssus threads)	Coleoptera remains	Macoma	Hydrobia	Veg matter	Stones	Other
Oyster-Catcher 1	-	-	✓	-	-	✓ grass?	-	-
Oyster-Catcher 2	✓ c.100	-	-	✓	✓	-	-	string feathers
Oyster-Catcher 3 Gizzard	48	✓	-	-	-	-	✓	-
Crop	58	-	-	-	-	-	-	-

The extracted flesh was often washed in a pool before being swallowed. On one occasion, as the tide advanced, three Oystercatchers carried mussels several metres from the tide edge before opening them.

At Torry Bay, observations were made on the flow tide, after the mussel beds had been covered. Prey items were mainly opened in situ. The birds rotated 45^{o} - 180^{o} around the bill, presumably to aid shell opening. On one occasion, a cockle was carried before being eaten. Items from probing, opened below the surface, were thought to be Macoma.

At Kinneil, Oystercatchers feeding on a mussel scar fed on cockles which they carried to firmer substrate before opening using 2 - 3 jabs of the bill. Extracted flesh was occasionally washed. Near the Avon channel, Oystercatchers also probed deeply and one Nereis worm was seen taken. Only two incidents of mussels being eaten were recorded and at Bo'ness, bivalves, mainly cockles, were taken.

The feeding rates (Table 3.5.14) were lowest when feeding on mussels and highest at Torry Bay where Macoma was considered to be the main prey item at high beach levels.

3.5.7 (ii) Pellet analysis

The appearance of the pellets from Culross pier, Crombie M.O.D. Stub pier and adjacent rocks and Charlestown harbour walls was similar. They consisted either of mats of Mytilus byssus threads with small stones incorporated or of Littorina operculae held together by mucus.

Mussel pearls were present in 34.8% of the Culross samples and/

and 4.5% of those from Charlestown. Small stones and 'old' shell fragments occurred in the Culross samples (52%), M.O.D. Stub pier samples (33%) and the Charlestown samples (43.5%). They only occurred in pellets containing the byssus threads of mussels. Examination of live mussels showed that they originated from the byssus threads both inside and outside the shells.

The percentage frequency of prey species in the pellet samples (Table 3.5.15), shows that mussels and *Littorina* were found at all sites and whelks from the two more marine sites (M.O.D. Stub pier, Charlestown). *Carcinus* and *Macoma* only occurred in a small proportion of the pellets from Culross and a single *Nereis* jaw was found in a Charlestown Oystercatcher pellet.

3.5.7 (iii) Gut analysis

The results of the gut analysis of three Oystercatchers collected at Kinneil are summarised in Table 3.5.16. Oystercatcher ③ was collected on the feeding grounds in February 1980, the other two during autumn 1979. The bird collected in February contained the flesh of a large number of *Cerastoderma* in both crop and gizzard and a small quantity of byssus threads of *Mytilus* in the gizzard. Oystercatcher ① had probably been feeding inland and ② was in poor condition with a low fat score (Whitmore pers. comm.).

3.5.7 (iv) Discussion

Observation of feeding Oystercatchers on the Upper Forth estuary shows that the diet is similar to that described elsewhere (Dare 1966, Davidson 1967, Drinnan 1958, Goss-Custard Jones and Newbery 1977, Hulscher 1964). Although Dewar (1915) noted/

noted that the majority of mussels were opened in situ by Oystercatchers on the Forth, the habit of carrying mussels and cockles to firm substrates to be opened (eg Drinnan 1958) was noted frequently in this study.

The feeding method to obtain Macoma at high beach levels at Torry Bay was also recorded on the Wash and the pattern of feeding amongst the mussel beds at low tide at this site was also similar. This suggests that Oystercatchers on the Wash and at Torry Bay feed in a similar way. On Morecambe Bay, Macoma was only important as a food source in years when the cockle population was reduced (Dare and Mercer 1973). Nereis appears to be important only on Tees estuary (Pienkowski 1973) and although these worms may be taken frequently by Oystercatchers in the soft mud at Kinneil, they do not contribute significantly to the overall diet of Oystercatchers on the Forth estuary. Only three feeding hours km^{-2} were recorded for Oystercatcher at Kinneil in 1975 and 1977 (Bryant 1979) compared with 198 and 372 at Torry Bay and Culross, emphasising the low usage of this site.

The rate of feeding on mussels at Culross is similar to that found by Drinnan (1958) on the Conway estuary (0.46 - 1.37 min^{-1}). When feeding on Macoma plus a few cockles at Torry, the rate is similar to that on the Wash for Oystercatchers feeding on Macoma (2.84 min^{-1}) (Goss-Custard, Jones and Newbery 1977). The mixed diet at Kinneil cannot be compared with other feeding rate measurements but in general the feeding rates of Oystercatchers on the Forth agrees with those from other studies.

The/

The high incidence of Littorina in the pellets of Oystercatcher was surprising in view of the feeding observations. Their presence was recorded by Adams (1969), in pellets which were similar in appearance to those from Forth roost-sites. They were only found, however, in 10 of the 1229 birds collected on the mussel skears in Morecambe Bay (Dare and Mercer 1973). It is probable that Littorina are only important prey on the Forth when the main feeding areas have been innundated by the tide. As it is only the flesh of most items that is ingested, Littorina ~~operculae~~ will be one of the few species with hard parts to be represented in regurgitated material. Thus, the importance of Littorina, and Buccinum, would be overestimated by pellet analysis alone.

Combining the results obtained from observation and from gut and pellet analysis, it appears that, on the North Shore, Oystercatcher feed mainly on mussels with cockles, Macoma, and possibly Littorina being important when the mussel beds are covered by the tide. On the South Shore, where feeding density and intensity are lower (Bryant 1979) a variety of foods are probably taken with cockles and Macoma predominating. Thus, at Skinflats, where no observations on feeding were possible, it is assumed that the small number of birds present had a similar diet to those at other S. Shore sites.

3.5.8 The Turnstone (Arenaria interpres)

3.5.8 (i) Field observations

It was not possible to identify the prey items taken by Turnstones except at high beach levels. Near the Torry Burn they pecked small items from the surface of mud and stones

and/

and from the undersides of larger stones. These they turned over with their bills. Collection of a random sample of these stones revealed numerous small Littorina rudis. One individual carried a large Littorina to a flat rock before removing the flesh.

Between the Torry Burn and Shoreside house are many flat, weed-covered rocky outcrops within 50 m of the wall. These are surrounded by muddy-sand. There Turnstones searched under seaweed (Fucus spiralis, F. vesiculosis), tossing the weed with head and bill. Examination of the area revealed Gammarus sp and Littorina sp.

At Crombie Point, the Turnstones either pecked small items from the sand surface or fed amongst the strand-line debris.

In Newmills Bay, Turnstones fed on the mud and in a fresh-water run-off channel. They pecked rapidly on one spot and then ran to another area to continue pecking. Only one Littorina was removed from its shell during feeding observations. Examination of the area suggested that Hydrobia and Littorina were the main foods available.

3.5.8 (ii) Pellet analysis

No pellets were available for analysis.

3.5.8 (iii) Gut analysis

The results of analysing three gizzards of Turnstone collected at mid-high tide from Torry Bay are shown in Table 3.5.17. Turnstone ① and ③ were collected near Torry Burn, a fresh-water outflow, and ② from west of Crombie Point. All were collected whilst feeding.

Whole/

TABLE 3.5.17: Prey species and number present from gizzards of three Turnstone collected at Torry Bay

TURNSTONE NO	LITTORINA Whole	Operculae	Terminal Whorls	INSECT REMAINS	GAMMARUS LOCUSTA	NEREIS JAWS
1	13	18	6	Dipteran larvae 1 unidentified larvae 1	0	17
2	0	+500	0	0	0	0
3	1	+500	0	0	6	0

TABLE 3.5.18: Comparison of diets of Turnstone from different locations

			Barnacle	Littorina	Carcinus	Hermit Crab	Amphipoda	Nereis	Insecta	Mytilus	Macoma	Hydrobia	Chiton	Top Shell	Cerastoderma	Veg	Crustacea
JONES 1975	Wash	pellets 37	✓	✓	✓	✓	-	-	✓	✓	✓	✓	✓	✓	✓	✓	-
		guts 1	✓	✓	✓	-	-	✓	-	-	-	-	-	-	-	-	-
PRATER 1972	Morecambe Bay	guts 14	✓	✓	✓	-	G	✓	-	✓	✓	✓	-	-	-	✓	✓
HARRIS 1979	Angelsey	pellets 27	✓	✓	✓	-	✓	✓	C	P	-	-	-	-	-	✓	-
DAVIDSON 1971	Morecambe Bay	guts 14	✓	✓	✓	-	Co G	✓	C	✓	✓	✓	-	-	-	-	-
THIS STUDY	Forth	guts 4	-	✓	-	-	G	✓	L	-	-	-	-	-	-	-	-

KEY:
G - Gammarus
C - Coleoptera
P - Mytillus pearl
Co - Corophium
L - larvae

Whole shells of Littorina rudis and operculae of Littorina sp. were found in all three gizzards. The operculae were from larger snails than the whole individuals present. Insect larvae, Gammarus locusta and Nereis were each found in 37% of the samples.

3.5.8 (iv) Size of items in the diet

Four Littorina rudis taken from the gizzards ranged from 1.9 to 3.2 mm ($\bar{x}$ = 2.63 ± 0.63).

Ten jaws of Nereis from specimen 1 were measured giving a mean worm length of 6.35 ± 1.14 cm. The jaw length ranged from 1 - 1.4 mm ($\bar{x}$ = 1.19 ± 0.14) (Fig 3.5.21 aand b).

Littorina rudis, collected from a random selection of stones from the up-shore feeding grounds at Torry Bay were measured (Fig 3.5.22). The mean size was 4.98 ± 2.79 mm (n = 134) and the size range 2 - 13 mm.

3.5.8 (v) Discussion

A comparison of the diet of the Turnstone from different areas is shown in Table 3.5.18. The range of substrate types and feeding methods (see review: Beven and England 1977) allows a wide range of prey to be taken and this is reflected in the diet analyses. The diet of birds from Torry Bay appears to be more restricted than that from other studies but observations on feeding birds suggest that the prey found in the gizzards is representative of prey taken by Turnstones in up-shore areas. Turnstones are able to adjust their feeding behaviour to take advantage of the available prey (Harris 1979) and to exploit seasonally available prey (Prater 1972a). Littorinids were/

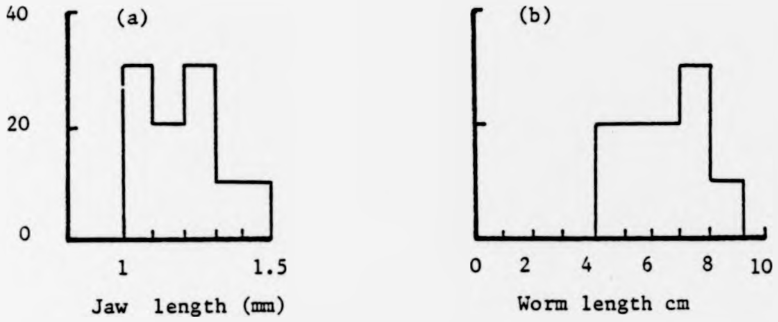


FIGURE 3.5.21: Size-frequency distribution of (a) <u>Nereis</u> jaws and (b) equivalent worm lengths from Turnstone guts

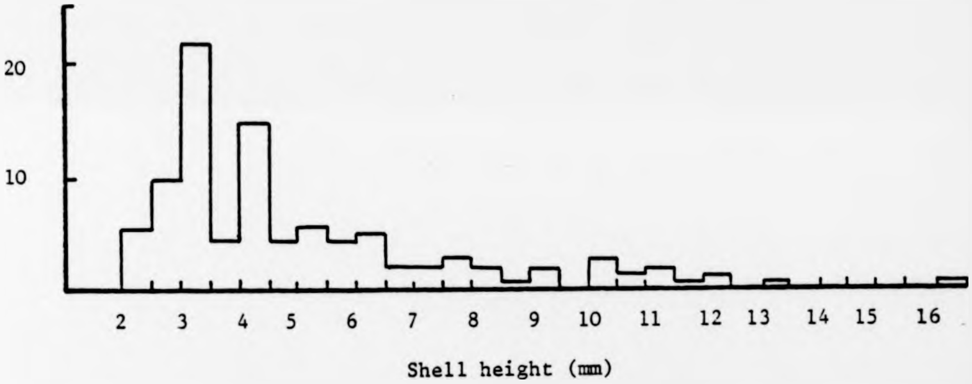


FIGURE 3.5.22: Size-frequency distribution of <u>Littorina rudis</u> from the undersides of stones at Torry Bay

were probably the most abundant and available invertebrates at high tide at Torry Bay during the survey, although Gammarids may have been important in the rocky areas on the ebb tide.

A comparison of the size of Littorinids present under stones and the sample from the gizzards suggests that the smaller individuals are taken whole. The presence of operculae from larger snails in the guts suggests that these are removed from the shells, as verified by observation.

Few Turnstone fed at Skinflats and those observed were restricted mainly to the Carron shore. The diet described for Torry Bay indicated that they would have little impact on the invertebrate populations studied at Skinflats.

3.5.9 The Shelduck (Tadorna tadorna)

3.5.9 (i) Field observations

The diet of Shelduck could not be determined by field observations.

3.5.9 (ii) Pellet analysis

No pellets were available for analysis.

3.5.9 (iii) Gut analysis

The diet of Shelduck was determined by gut analysis: the oesophagus and gizzard contents of four birds were examined. Two birds were collected whilst they were feeding on the mudflats at Kinneil, one whilst flying from its roost-site and a fourth was found recently dead (probably shot).

The prey species and the numbers present in the guts of the/

the four Shelduck are shown in Table 3.5.19. Hydrobia ulvae was the only species to occur in both oesophagi and gizzards of all birds. Oligochaete worms and Manayunkia were found in the two birds collected on the feeding grounds. Macoma was absent from the bird found recently dead. Copepods occurred in one gut as did some plastic pellets which were from a load dumped in Kinneil Open Pan in 1976. Grit and sand completed the list of gut contents.

3.5.9 (iv) Size of items in the diet

The size range of Hydrobia from Shelduck guts and the percentage frequency of each size class is shown in Fig 3.5.23 a-c. The sizes ranged from 0.6 - 4.4 mm with 76.2% between 0.6 and 2 mm. The mean was 1.66 ± 0.8 mm.

Size selection of Hydrobia by Shelduck was estimated by comparing the size-class frequency histogram representing Hydrobia from the two Shelduck shot whilst feeding (Fig 3.5.23 b) with that of Hydrobia occurring in the sediment in the same areas (Fig 3.5.23c). The invertebrate data were from McLusky (1980).

Fig 3.5.23d illustrates the result of the size-selection (FR) analysis. Size-classes of Hydrobia less than 2 mm high representing 0+ year class appear to be selected whilst larger snails are being taken in smaller proportions than they occur in the sediment.

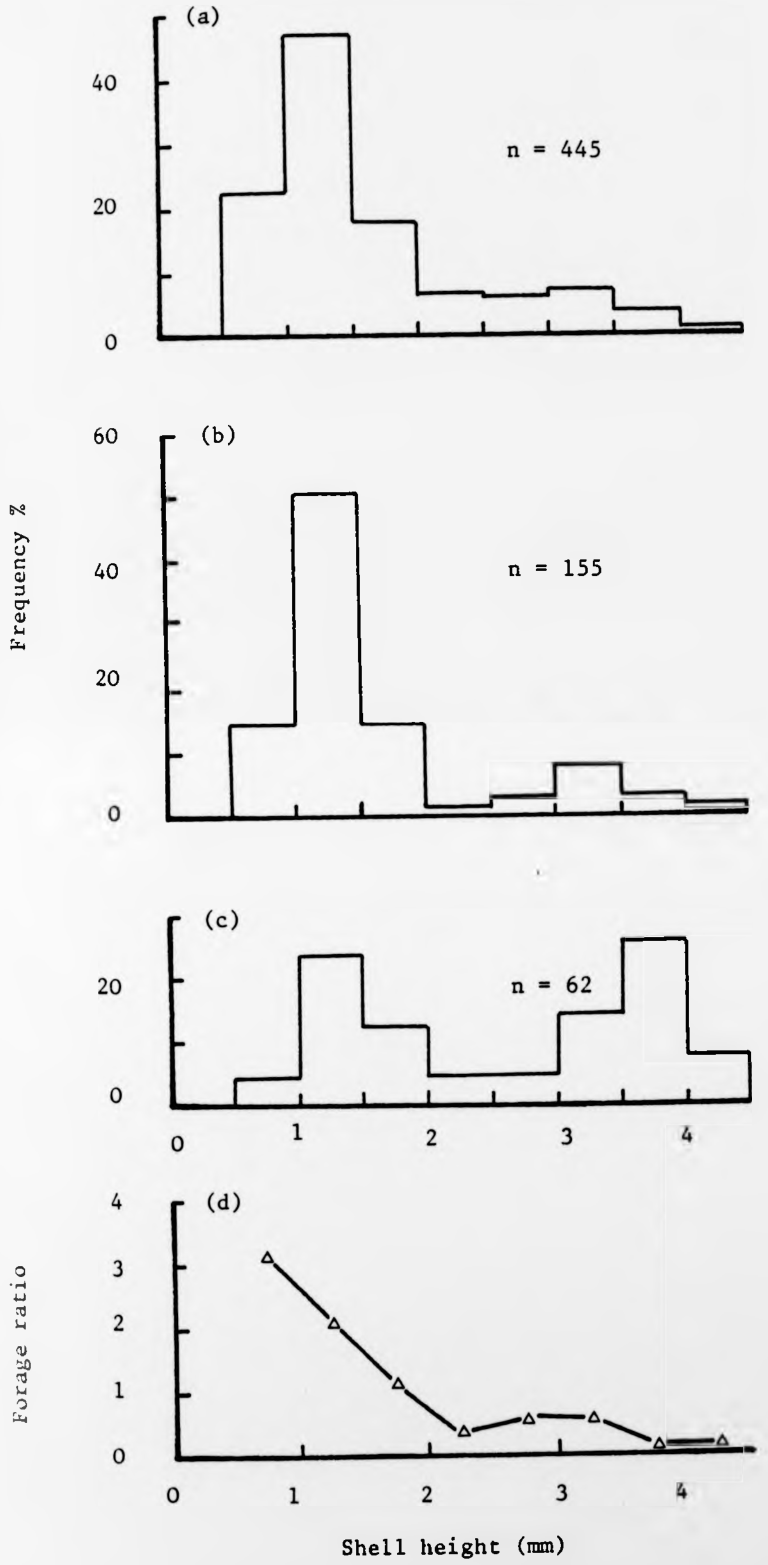
The size range of Macoma from the guts of Shelduck is shown in Fig 3.5.24. Individuals up to 9.5 mm shell length were taken but 80% were below 6 mm. The mean size was 4.8 ± 4.06 SD mm, illustrating the wide variation in sizes taken.

TABLE 3.5.19: Gut contents of 4 Sheldduck from Kinneil ① and ② collected whilst feeding; ③ collected flying from roost and ④ found dead (✓= present)

	Shelduck ①		Shelduck ②		Shelduck ③		Shelduck ④	
	Oesophagus	Gizzard	Oesophagus	Gizzard	Oesophagus	Gizzard	Oesophagus	Gizzard
HYDROBIA	14	158	23	37	150	861	2	3
OLIGOCHAETES:								
T. benedeni	44	8	2	3	-	-	-	-
T. pseudogasta	1	-	-	-	-	-	-	-
Enchytraid sp	-	-	1	-	-	-	-	-
C. capitata	-	-	1	-	-	-	-	-
Manayunkia	52	8	703	80	-	-	-	-
Macoma hinges	2	14	2	2	32	7	-	-
Nereis jaws	-	-	-	-	-	-	-	1
Copepoda	-	-	-	4	-	-	-	-
Plastic pellets	-	-	-	12	-	-	-	-
Grit/Sand	-	✓	-	✓	✓	✓	✓	✓

FIGURE 3.5.23: Size-frequency distribution of Hydrobia from (a) all four Shelduck guts (b) the guts of 2 Shelduck shot on feeding grounds and (c) the sediment where these 2 were feeding.

Figure 3.5.23 (d) depicts the forage ratio for the Shelduck shot on feeding grounds.


(a)
40
20
0
n = 445
(b)
60
40
20
0
n = 155
Frequency %
(c)
20
0
n = 62
0
1
2
3
4
(d)
4
3
2
1
0
Forage ratio
0
1
2
3
4
Shell height (mm)

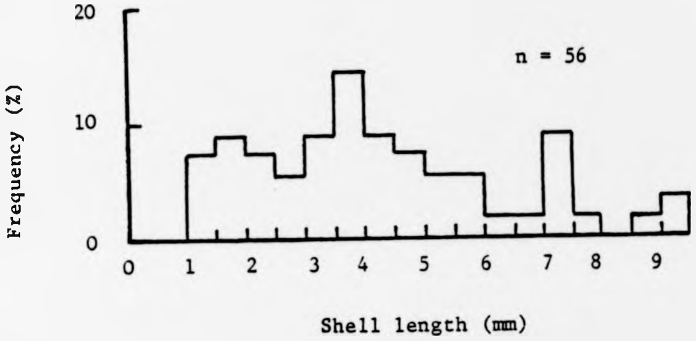


FIGURE 3.5.24: The size-frequency distribution of Macoma taken from four Shelduck guts

3.5.9 (v) Discussion

The occurrence of Hydrobia in all guts is consistent with the findings of previous studies (Buxton 1975, Jenkins et al 1975, Olney 1965, Young 1964). The high numbers of oligochaetes and Manayunkia present in the birds shot whilst feeding lends further support to the idea that these are often important in Shelduck diets but may rapidly become digested and undetectable, (Evans et al 1979, Hall 1971, Murray 1973). The extent to which they contribute to the diet cannot be estimated from the present data but the absence of small worms from the guts of the birds recently roosting and found dead emphasises the importance of fixing the gut contents on collection of the samples. Earlier studies (eg Olney 1965) do not describe any fixing procedure and thus any oligochaetes present may have been digested before the guts were examined.

Evans et al (1979) suggested that, in the liquid mud of the Tees, Shelduck would take any items they could sieve from the mud with their bills. In this study, it appears that, whilst many prey are included in the diet there is a size-selection operating. Feeding involves taking in water and mud at the anterior bill margin and ejecting it near the base. Serrations allow size-selection to operate so that some prey are retained. The different feeding methods enable further selection to take place. Scything the liquid muds of Kinneil would result in all similarly sized prey items in the top 2 cm being taken.

If Hydrobia were the major prey items selected, Shelduck would be expected to take the larger individuals available as on the Ythan (Buxton 1975). The selection for small snails

suggests/

suggests that oligochaetes and Manayunkia are actively selected because selection for large snails would result in many small worms being ejected in the mud/water flow. Thus, as on the Tees (Evans et al 1979), it appears that oligochaetes are an important food item. The possibility that larger Hydrobia were ingested and rapidly crushed was discounted since 78% of snails in the oesophagi of the Shelduck collected from the feeding grounds and 79% of those in the gizzards were less than 2 mm. Also, Hydrobia mainly occur in the top 3 cm of the sediment (pers. obs.) where both large and small snails would be available to the Shelduck.

The wide range of size-classes of Macoma in the diet suggest that they may be taken by a different method, probably by digging or dabbling (Bryant and Leng 1975). Approximately 70% of 3 - 8 mm Macoma and 100% of the 0 - 3 mm sizes occurred in the top 3 cm of the sediment in January, on the Wash (Reading and McGrorty 1978). This represented 64% of the population in the top 7.5 cm but only 17% of the biomass, larger individuals being found deeper. At Skinflats, in January 1978, the mean size of Macoma in the top 1 cm was 2.88 ± 0.98 mm and 61% of those animals $<$ 3 mm long occurred in this zone (75% in November 1977, Section 3.4.2). Also, since 88% of the population occurred in the top 4 cm (81% in November 1977), many of these would be available to feeding Shelduck, a larger percentage than found on the Wash.

Of the oligochaete population, 95% occurs in the top 5 cm (Ann Baghari pers. comm.). The mean $nm^{-2} = 18765 \pm 10832$ at Stations E_2, E_3 and F_2 at Kinneil (McLusky 1980) and Tubificoides benedeni/

Tubificoides benedeni occurred most abundantly, its individual weight being 51 ± 25 μg, (Teare 1979 unpubl.). Thus the biomass available was approximately 2.69 gm^{-2}. Also, at the three sampling stations, the biomass of Manayunkia and Hydrobia was 0.66 gm^{-2} and 1.08 gm^{-2} respectively, emphasising the dominance of small worms at Kinneil and their potential value as a food source.

The contribution of small worms to the diet of Shelduck at Skinflats could not be assessed but the probable importance of Hydrobia is discussed in Section 3.6.

3.5.10 General discussion

The diet of all species studied at Skinflats and elsewhere on the Forth show close agreement with studies on other estuaries in Britain and N.E.Europe. The wide spectrum of prey species taken by most shorebirds indicates their ability to exploit a range of shore habitats and substrate types. Many even feed inland to supplement their diets.

On the shore, bird species occupying the same mudflat areas and feeding on the same species, tend to show a degree of resource partitioning either by feeding on different size classes of prey or, as in the case of Redshank including a wide variety of prey in the diet so that intense competition with Knot appears to be avoided. Similar partitioning of resources occurs in other bird assemblages such as grassland birds (Cody 1974) lending support to the hypothesis of ecological isolation, first proposed by Gause (1934) and subsequently discussed and expanded by ecologists such as Hutchinson (1958), Lack (1971) and McArthur (1968).

3.6 The Factors Influencing the Feeding Distribution and Density of Redshank Knot, Dunlin and Shelduck at Skinflats

Royama (1971) argued that predators would be expected to concentrate their foraging effort in the most profitable parts of a habitat, often assumed to be those areas of highest prey density (Hassell 1966, Holling 1959). Furthermore, shorebirds generally distribute themselves in estuaries in accordance with the distribution of their main prey species (Bryant 1979, Goss-Custard 1977(a), Wolff 1969).

Shorebirds such as Knot, which feed in large compact flocks do not appear to decrease the availability of their prey species. However, the more mobile prey of sight-feeding foragers (eg Corophium and Nereis) generally become less available at high bird densities. Thus it has been suggested that Redshank, and to a lesser extent, Dunlin feed in more widely scattered flocks (Goss-Custard 1970) to maintain a high feeding efficiency. The findings by Bryant (1979a) were also compatible with this.

Other factors which may influence the dispersion and density of shorebirds are physical characteristics such as the size of an area, tidal cover sequence (Bryant 1979a) and substrate type (Evans et al 1979). The aim of this part of the present study was to investigate further the extent to which prey densities and environmental factors influence the feeding distribution and density of shorebirds at Skinflats.

One ultimate aim in studying the densities of shorebirds in relation to food supply and other factors is to predict the densities of birds at sites within any given estuarine environment. Thus the impact of proposed industrial and reclamation developments can be objectively assessed. The feasibility of this is suggested from work on the Forth estuary/

estuary and estuaries in South-East England (Bryant 1979a) Goss-Custard et al 1977) since results from these studies have proved comparable.

3.6.1 Redshank

(i) Tide-related distribution and density patterns

High Tide:

The major Redshank roosts were located on the training wall of the River Carron (Roost 1), the adjacent saltings and the saltings near Kincardine Bridge (Roost 3). The latter was used more extensively on spring tides when sites further east were inundated by the tide. Minor roosts occurred all along the saltmarsh, particularly near Orchardhead and Pocknave Farms (Fig 3.6.1). Redshank occupying these roosts were mainly birds having fed at Skinflats over low tide but some had joined them from sites elsewhere on the estuary, eg Kinneil, which flood sooner than Skinflats (pers. obs., M Davies pers. comm.). The ponds and field behind Skinflats also provided minor roosts.

During two neap-tide observation periods in November, a few birds began to feed belly-deep at the tide edge 0.5 to 1 hour after H.T. Occasionally, these paused to roost but were joined by others as the tide ebbed until a maximum number of feeding birds reached 1.5 - 2 hrs after H.T. (Fig 3.6.2a). On both occasions, the air temperature exceeded 4°C but during a third neap-tide observation period, in mid-winter, the majority of Redshank were feeding 0.5 h earlier than in these mild conditions (Fig 3.6.2a), some less than 0.5 h after H.T. This cold period was part of a prolonged spell of cold weather (max 3.4°C, min-5.4°C) and the flats were frozen and snow-covered above the tidal line (Fig 3.6.3).

The timing of roosting on flow spring-tides was governed by/

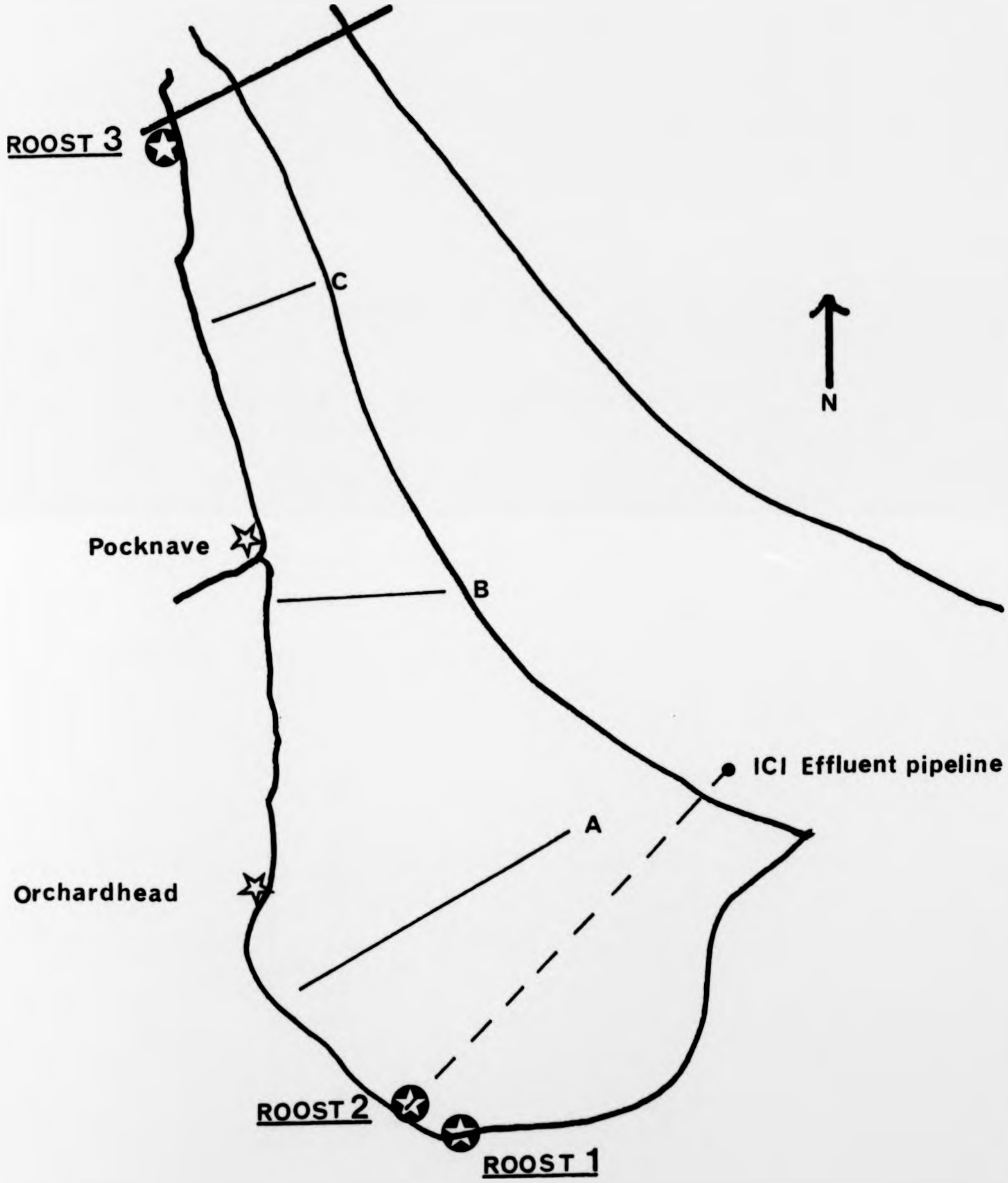


FIGURE 3.6.1: Main roost sites of wading birds at Skinflats

FIGURE 3.6.2: Fluctuations in the density of feeding Redshank on (a) ebb neap tides and (b) & (c) on flow spring tides during the winter

(a) ● 1 - 3.11.76,
■ 27.11 - 1.12.76,
▲ 28.1 - 1.2.77
(b) ○ 7 - 9.11.76,
□ 23 - 26.11.76,
△ 7 - 10.12.76
(c) ● 20 - 22.1.77,
■ 8 - 11.3.77

the density
hank on
des and
ow spring tides
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1.76,
1.12.76,
1.2.77
1.76,
.11.76,
12.76
.1.77,
3.77

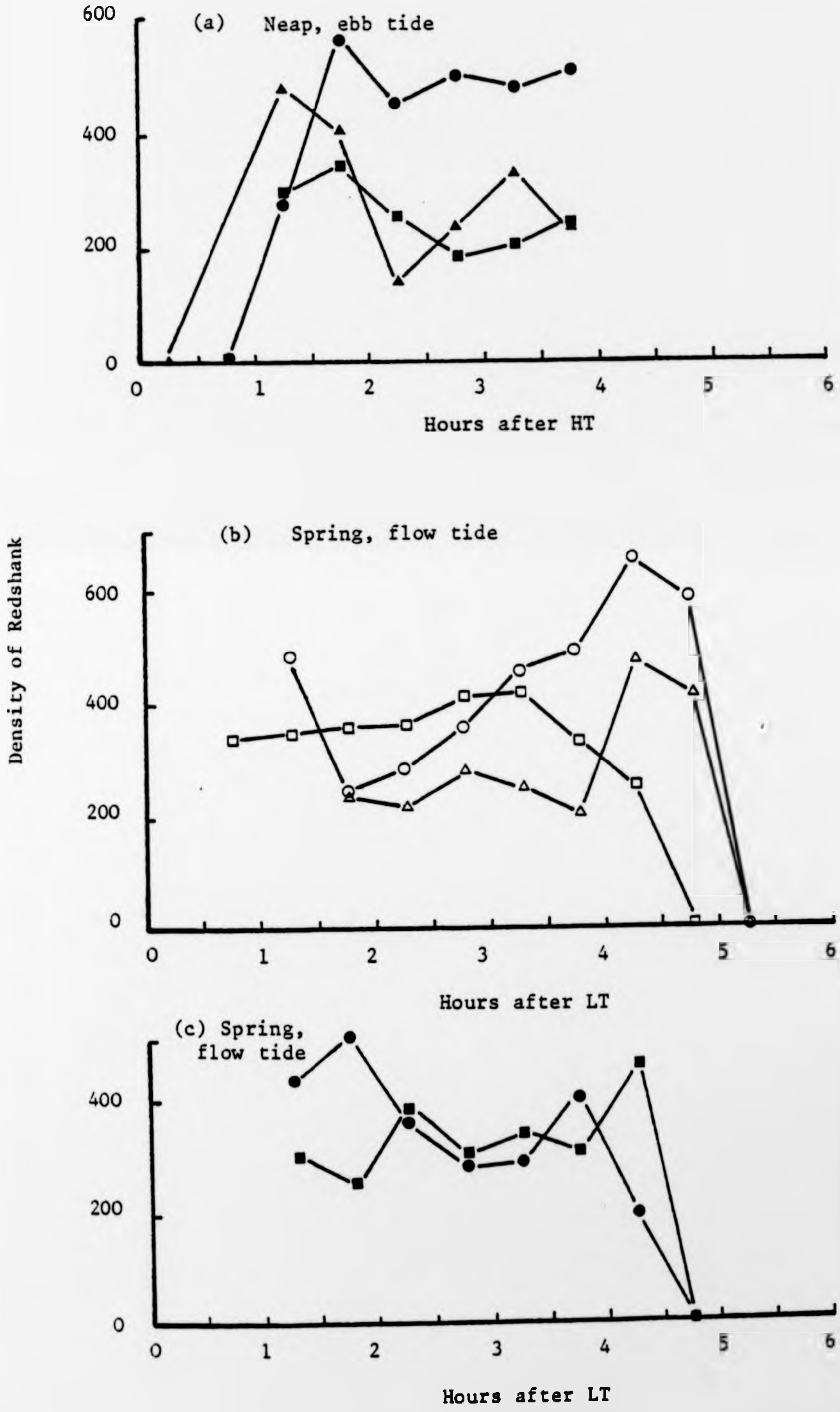


FIGURE 3.6.3: Ice-covered mudflats at Skinflats December 1976

FIGURE 3.6.3: Ice-covered mudflats at Skinflats
December 1976

by the time at which the mudflat became covered (Fig 3.6.2 b and c).

Ebb Tide:

As the tide ebbed the distribution and dispersion patterns of feeding Redshank altered. Initially, high-density Redshank flocks fed at the tide-edge, some belly-deep in water. As the area of exposed mud increased, they dispersed more widely, some continuing to follow the tide, although many remained at high beach levels near the major roost sites (Fig 3.6.4a).

Low Tide:

On neap-tides, the area was completely exposed 3 to 3.5 h after high tide and after a small exodus to Kinneil, the pattern of dispersion remained fairly stable over the low-tide period (Fig 3.6.4a) with the highest feeding intensity adjacent to Roosts 1 and 3 and on the areas of newly exposed mud along the outer edge of the flats. The dispersion of all Redshank at this stage was in loose flocks.

On spring tides 2½ - 3½ h after low tide, the mudflat was still fully exposed and the highest feeding density was again centred around the two major roost-site areas (Fig 3.6.4b)

On neap tides, the area of mud above the M.H.W.N. tide line was not exploited but on spring tides after the whole area had been inundated, feeding occurred at the up-shore levels (Fig 3.6.4). In such areas, on neap tides, the invertebrates were likely to be inactive when not covered at high water and thus not be readily located by predators such as Redshank. The higher concentration of Redshank in the vicinity of Roost 3 on/

FIGURE 3.6.4: Mean LT Redshank feeding densities on (a) neap tides (3 - 3.5 h after HT) and (b) spring tides (2.5 - 3 h after LT) during the winter

<u>Key</u>:-

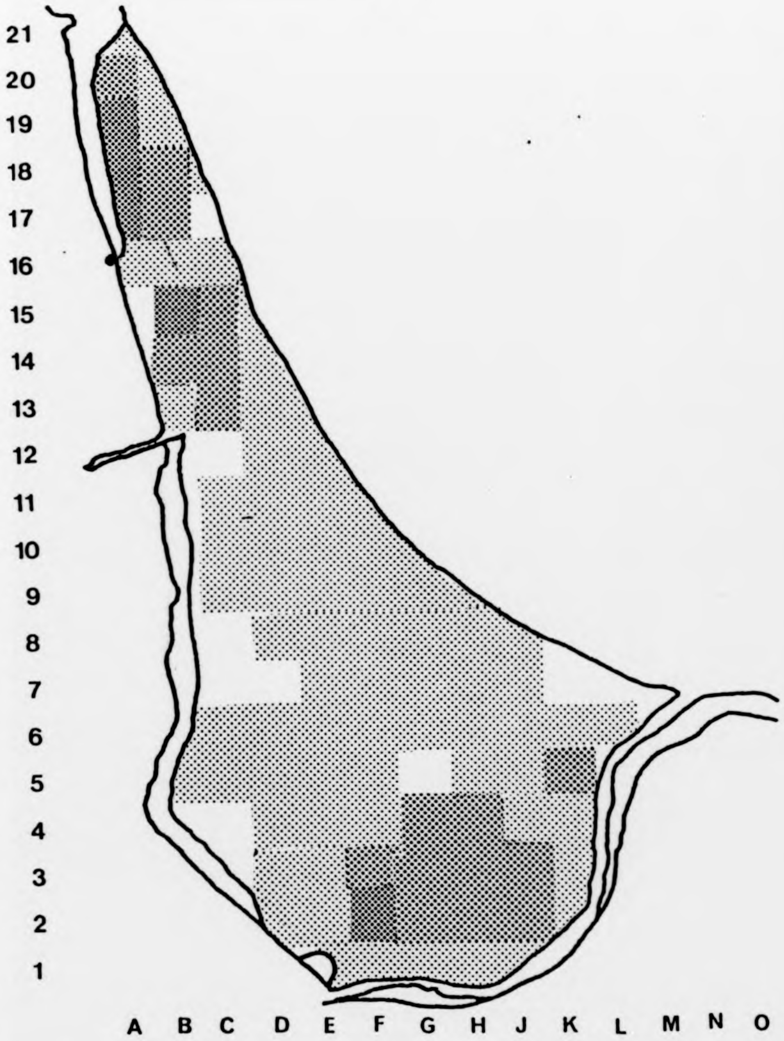
░ 0.1 - 5 birds 0.2 km^{-2}

▒ 5.1 - 10 birds 0.2 km^{-2}

▓ +10 birds 0.2 km^{-2}

(a) Neap tides n = 3

(b) Spring tides n = 5



on spring tides reflected the increased usage of this roost when Roost 1 was largely inundated by the high tide. The dispersion on both tides indicated that the majority of Redshank did not move further from the roost site than was necessary to establish adequate feeding dispersion.

The average density of feeding Redshank at Skinflats per km^{-2} at low tide was similar on neaps (85 km^{-2}, 3 - 3½ h after H.T.) and spring tides (84.25 km^{-2}, 2½ - 3 h after L.T.), indicating that the number of birds utilising the area was fairly constant over these periods.

Flow Tide:

With the advancing tide, on springs, Redshank continued to feed in dispersed flocks but an increasing proportion fed at the tide front in small, dense flocks. As the tide flowed rapidly some birds flew in stages westwards, feeding at the tide edge between flights, whilst still others flew directly to Longannet Power Station to roost on the ash-pans.

The pattern of Redshank dispersion at Skinflats consisted essentially of an expansion and contraction of the feeding flocks as they left from and returned to the roost-sites. The pattern followed the rhythmical tidal cycle and in general flying to feeding grounds was not often observed. Thus energy expenditure involved in flying to distant feeding grounds was minimised.

3.6.1 (ii) The factors influencing the low-tide feeding density of Redshank

The study of the diet of Redshank at Skinflats (Section 3.5.2) has shown that Nereis, Macoma and Hydrobia were the principal prey species. Populations of these invertebrates were found to be widely distributed in the area and data for both density and biomass collected from the ten sampling sites in November 1976 (Sections 3.3, 3.4 and Appendix 17) were used in the following analysis of Redshank feeding density .

Correlation analyses were carried out for Redshank feeding density at low water on spring tides ($\bar{n}$ 0.2 km^{-2} sp) and on neaps ($\bar{n}$ 0.2 km^{-2} sp) with invertebrate prey densities (nm^{-2}), individual and combined invertebrate prey species' biomass (gm^{-2}) and tidal height.

Further correlation analysis was carried out for Redshank feeding density at low water (springs and neaps) with the density and biomass of those size classes of invertebrate prey known from the diet study (section 3.5.2) to be exploited.

The analyses were made on raw and transformed ($\log_{10}$) data but no significant correlations could be shown. However, plots of Redshank feeding density over low water springs against Nereis and Macoma densities (Figs 3.6.5 a and b) indicated that a functional response (Holling (1959) 'Type 2') by Redshank to prey density was operating. Over the range of prey densities studied, the asymptote of both functional response curves was reached at low densities but, at stations C_1 and C_2, other factors were also operating and disturbed the response. These two sites were adjacent to Roost 3 and, as described in Section 3.6.1i, had a high feeding density compared with sites further away from the roost sites.

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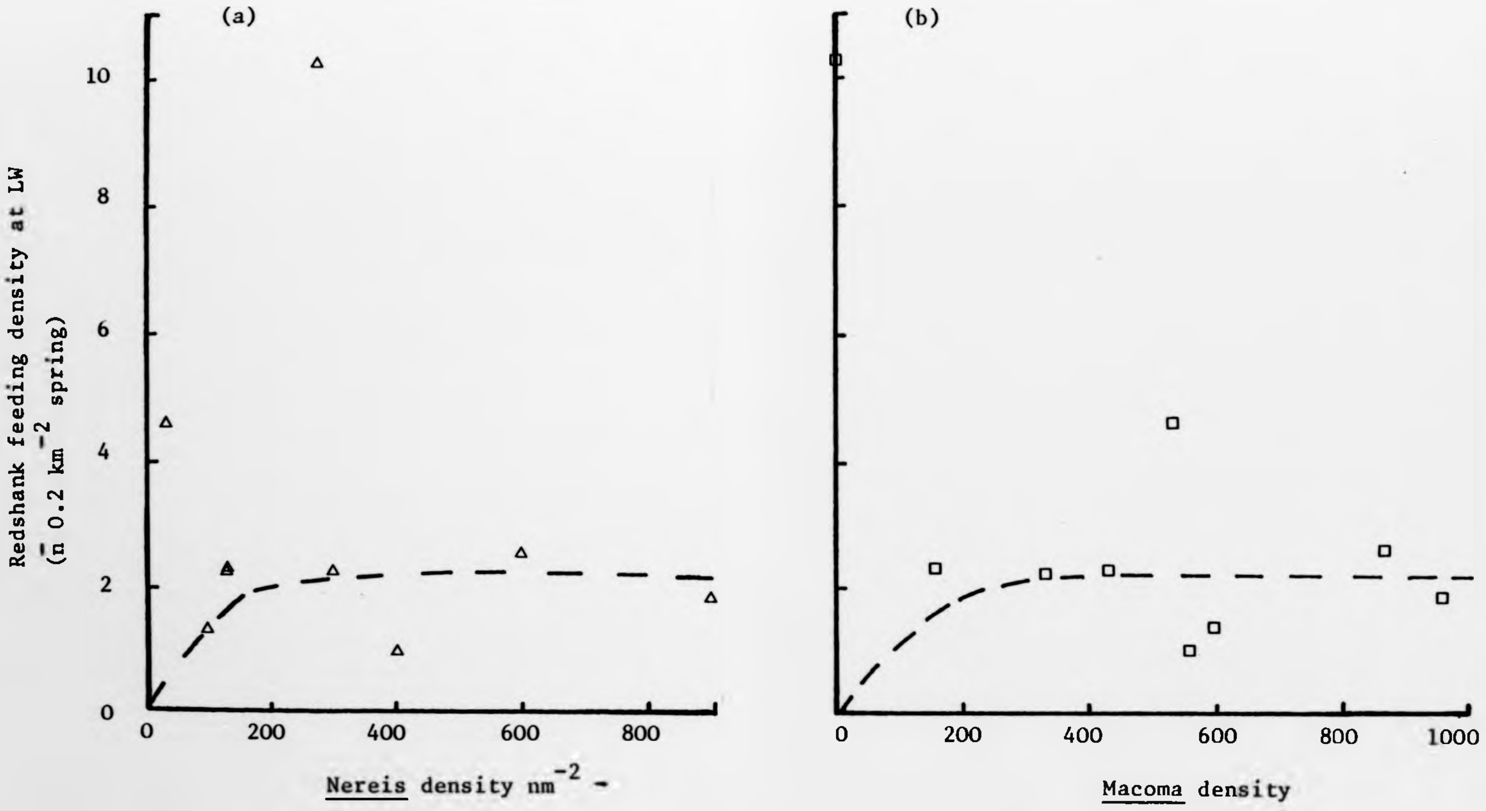


FIGURE 3.6.5: The density of feeding Redshank in relation to (a) Nereis density and (b) Macoma density

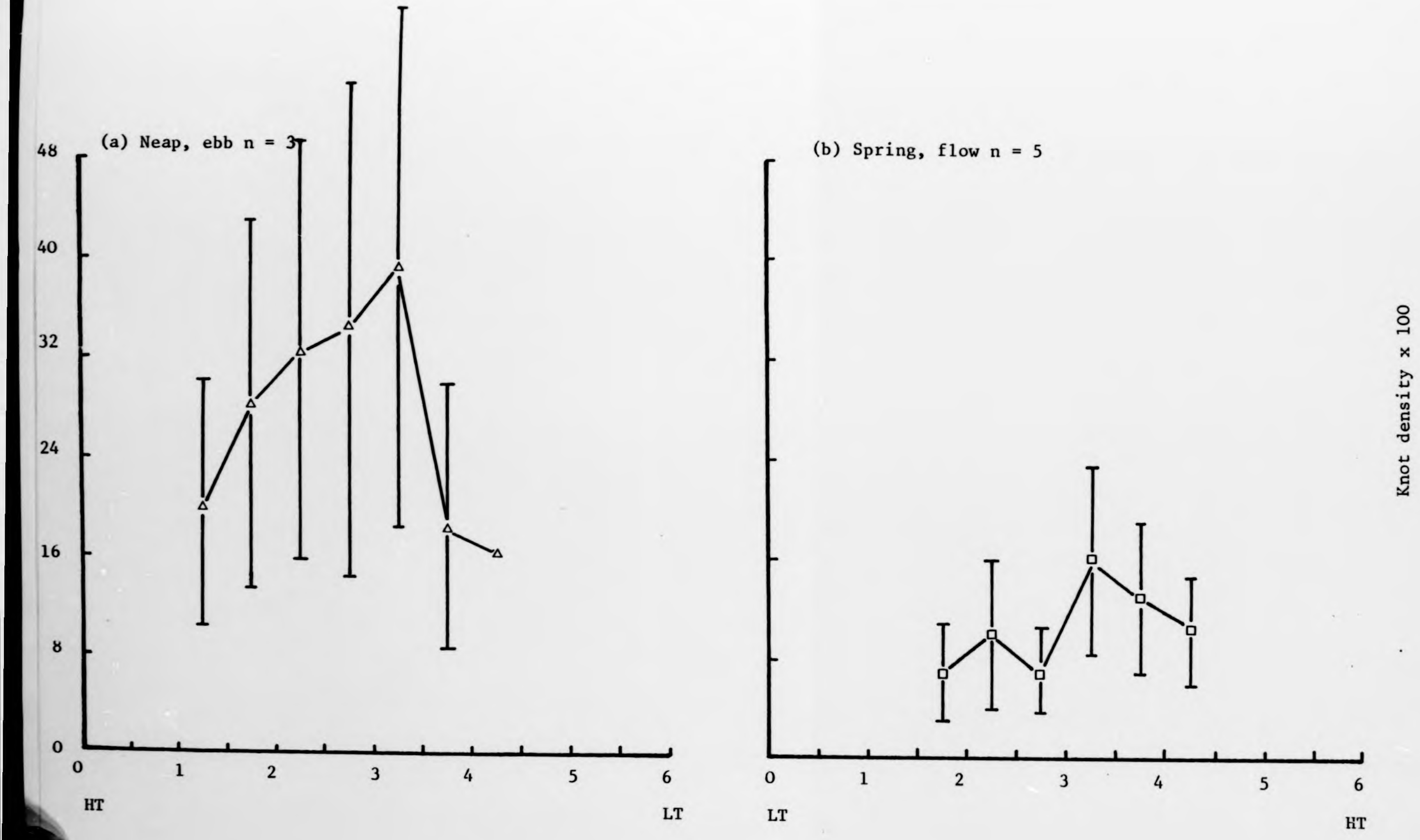
The high density of feeding Redshank in this region could not be explained in terms of increased prey density. However, it is apparent from Figs 3.6.4 and 3.6.5 that over most of Skinflats, prey density is sufficiently high for some feeding by Redshank to occur (> 1.0 birds/0.2 km^{-2}). It is also apparent that Redshank travel the minimum distance required from roost site to feeding grounds to obtain their food requirements. Thus energy expenditure for travelling further away is reduced. Upward limitations to density will be imposed by the level at which mutual interference affects feeding efficiency (Goss-Custard 1969). However, the constancy of the density pattern throughout the 1976/77 winter and between this and other winters (McLusky and Bryant 1976) indicates that prey populations are not sufficiently depleted by increased predation pressure in the areas adjacent to roost-sites to affect feeding. (See also Section 4 - Discussion). A similar upshore feeding density occurred at Kinneil (McLusky and Bryant 1976, 1978) close to the roost site in the 'Open Pan'. (Fig 1.1), indicating that this phenomenon is widespread on the Forth.

3.6.2 Knot

3.6.2 (i) Tide-related distribution and density patterns

By comparison with Redshank, Knot are gregarious, forming large highly mobile foraging flocks. Whereas the population size of Redshank varied little within or between spring and neap tides throughout mid-winter, the number of Knot feeding at Skinflats was more unpredictable (Fig 3.6.6 a and b). The highest numbers recorded occurred in late January and early February on a neap tide (max. c. 8500 feeding birds). During the other observation periods, the maximum number ranged from 850 - 4050/

FIGURE 3.6.6: The mean number of Knot recorded over (a) ebb neap tides and (b) flow spring tides during the study period


(a) Neap, ebb n = 3
48
40
32
24
16
8
0
0
1
2
3
4
5
6
HT
LT
(b) Spring, flow n = 5
0
1
2
3
4
5
6
LT
HT
Knot density x 100

4050 feeding birds.

High Tide

The major roost-site of Knot was the ICI pipeline (site 2) (Fig 3.6.1) which was only above the H.W. level on neap tides. The saltmarsh at Kincardine Bridge (site 3) was used as a roost on spring-tides to a varying degree, Longannet ash-pans providing an alternative and more frequently used roost-site.

Ebb Tide

Observations of feeding Knot on the ebb-tide of neaps (Fig 3.6.7a) suggested that, in mild winter conditions, Knot would begin to feed about one hour after predicted H.T., as soon as mud became exposed. However, on one observation period when snow and ice lay above the H.T. line, feeding commenced 0.5 hr after H.T. Regardless of the environmental conditions, during the three observation periods over the ebb tide, small flocks of up to 200 feeding birds spread along the tide-line. Once the area around and beyond sampling stations A_4 and A_5 was exposed, these small flocks congegrated there, many (500 - 2500) remaining to feed over low-tide (Fig 3.6.8a). Others flew eastwards to alternative feeding sites, principally at Kinneil.

Low Tide

On spring tides small scattered flocks fed at Skinflats over at low water, moving frequently to different areas (Fig 3.6.8b). This contrasted markedly to the large neap-tide flocks which also moved frequently but only within a small area (Fig 3.6.8a).

FIGURE 3.6.7: Fluctuations in the density of feeding Knot on (a) ebb neap tides and (b) flow spring tides during the 8 observation periods.

(a)
● 1 - 3.11.76,
■ 29.11 - 1.12.76,
▲ 28.1 - 1.2.77

(b)
● 7 - 9.11.76,
■ 23 - 26.11.76,
▲ 7 - 10.12.76
○ 20 - 22.1.77,
□ 8 - 11.3.77

ensity of
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.76,
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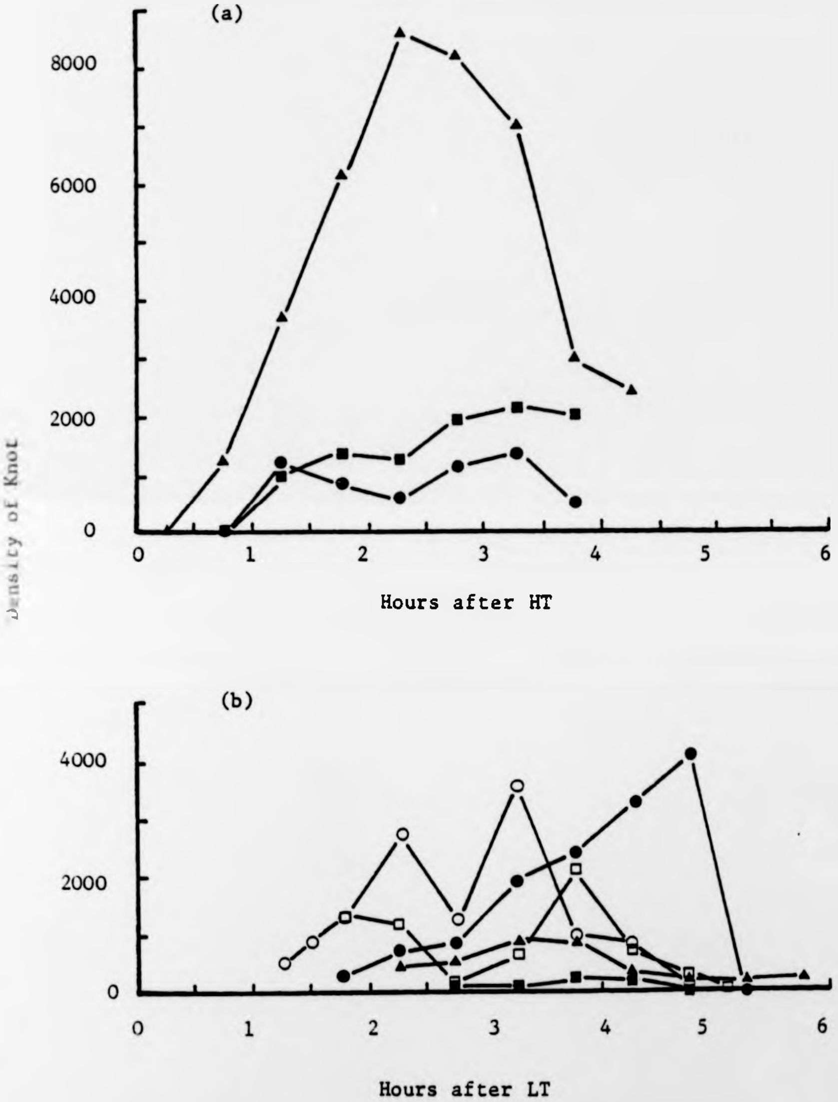


FIGURE 3.6.8: Mean LT Knot feeding densities on (a) neap tides (3 - 3.5 h after HT) and (b) spring tides (2.5 - 3 h after LT) during the winter

░ 1 - 100

▒ 101 - 500

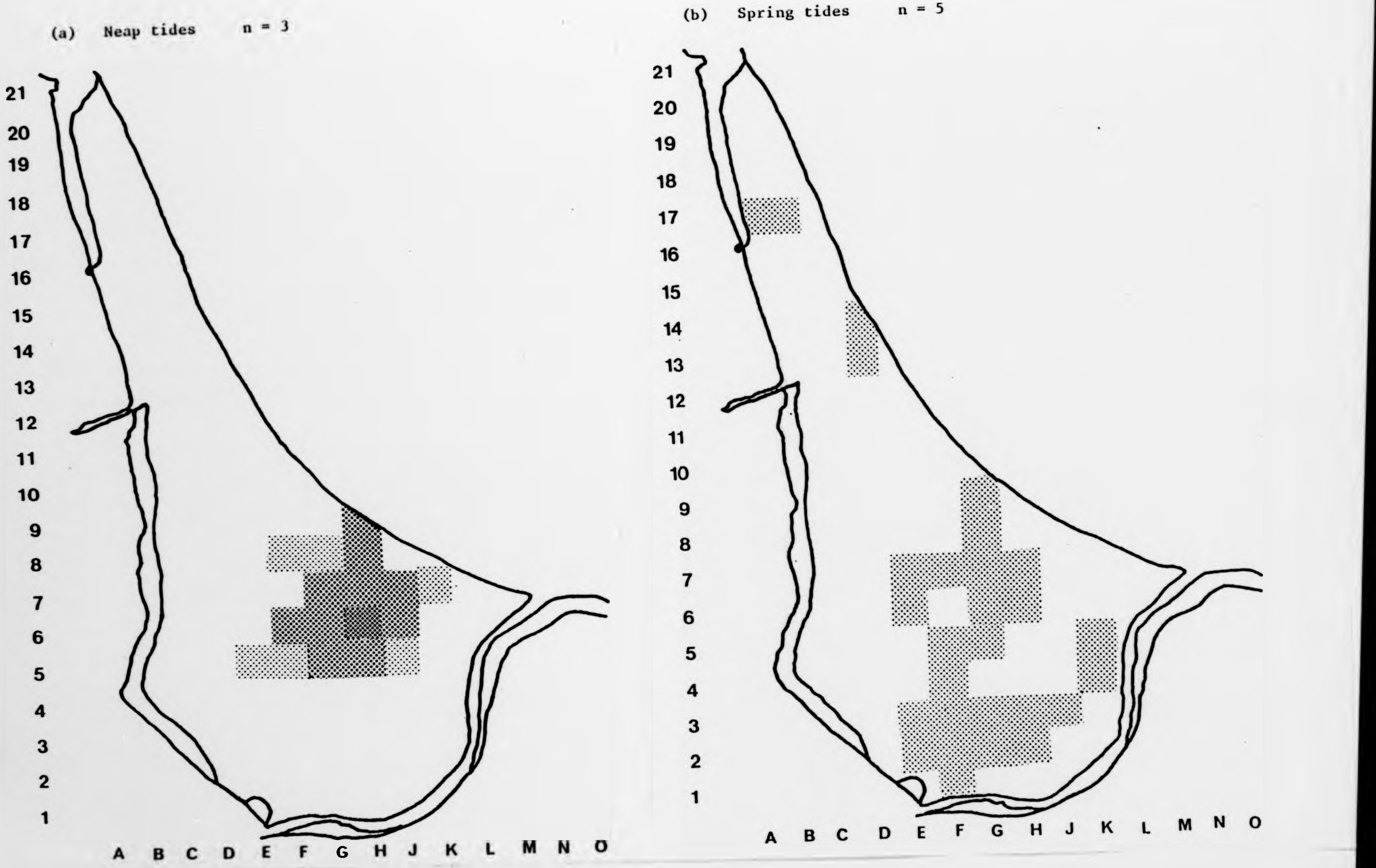
▓ +500

FIGURE 3.6.8: Mean LT Knot feeding densities on (a) neap tides (3 - 3.5 h after HT) and (b) spring tides (2.5 - 3 h after LT) during the winter

░ 1 - 100

▒ 101 - 500

▓ +500


(a) Neap tides n = 3

(b) Spring tides n = 5

Flow Tide

On spring flow tides, the number of Knot feeding at Skinflats varied widely between observation periods (200 - 4000 feeding birds) (Fig 3.6.8b). With the exception of observations in the late autumn, most Knot deserted Skinflats before the mudflat was totally inundated, maximum feeding numbers occurring at varying stages of tidal flow. Departing birds flew in large flocks mainly in the direction of Longannet ash-pans to roost.

3.6.1 (ii) The factors influencing the low-tide feeding density of Knot

During the study period of 1976/77, on neap tides, large flocks of Knot fed during the L.T. period in a well defined area although, on spring tides, only small scattered flocks occurred. In the following winter Hydrobia and Macoma were found in pellets and the hypothesis that the abundance of these molluscs influenced the choice of feeding site and the density of Knot was tested. Additionally, since in 1976/77 the abundance of 0+ year class Cardium was high but was virtually absent in the following year when the pellets were collected, the possible influence of Cardium on feeding density was investigated. Cardium are known to be a favoured food of the Knot (Section 3.5.3).

A correlation analysis proceeded to determine relationships between L.T. feeding density of Knot on (a) neap tides and (b) spring tides at the 10 sampling sites. The variables included were as follows: tidal height above OD (m), exposure time (h), estimates of the density (nm^{-2}) and biomass (gm^{-2}) of the total and 'preferred size-class' populations of each prey/

prey species and estimates of the total mollusc density at each site.

Preferred size classes (ie sizes found in pellets) included:

Hydrobia $\geqslant$ 1.8 mm shell height
Macoma 4 - 10 mm shell height
Cardium $\leqslant$ 14 mm (Goss-Custard, Jones & Newbery 1977)

These were determined from the measurements of fragments taken from pellets.

There were no significant relationships during spring tide conditions between Knot feeding density and any factors investigated (Appendix 19) but the relationships between the feeding density on neap tides and various factors (Table 3.6.1) show that Knot fed at the lower tidal levels where the preferred size-classes of Hydrobia were abundant, Cardium present and the total biomass of the molluscan fauna was high. Intercorrelations between these factors made interpretation difficult but Stepwise Multiple Regression analysis indicated that the density of the preferred size-classes of Hydrobia was the most important factor determining the low-tide density of Knot on neap tides at Skinflats (Table 3.6.2). This factor accounted for 94% of the total variation in Knot density.

Within the high-density Hydrobia area, Macoma were common and in the 1976/77 winter, first-year Cardium were abundant (Section 3.4.3). Thus, although the density of Hydrobia primarily appears to have attracted Knot, these other invertebrates would have been encountered and undoubtedly exploited./

TABLE 3.6.1: Correlation analysis of LT feeding intensity of Knot and several factors

	Tidal height (m)	Density (nm^{-2}) Knot-sized Hydrobia	Biomass (gm^{-2}) Knot-sized Hydrobia	Biomass (gm^{-2}) Knot-sized Macoma and Hydrobia	Density (nm^{-2}) Cardium	Biomass (gm^{-2}) Knot-sized Macoma Cardium and Hydrobia	Biomass (gm^{-2}) Hydrobia and Macoma
Low-tide feeding intensity - neaps (3 - 3½ h after HT)	-0.6932 *	0.9704 ***	0.8249 **	0.8556 ***	0.6251 *	0.8026 **	0.8506 ***

TABLE 3.6.2: Regression analysis of LT feeding density of Knot

Factor	B	β	F	Sig	r^2 x 100	Constant
density of knot-sized Hydrobia (nm^{-2})	0.655 ± 0.58	0.97	128.96	***	94.16	-40.19

TABLE 3.6.3: Biomass data of Knot prey species at Skinflats in two successive winters

		Hydrobia (knot-sized)	Macoma "available" (knot-sized)	Cardium (knot-sized)
Av. biomass gm^{-2} over flats	Nov.'76	3.9 ± 2.8	0.88 ± 0.75	0.22 ± 0.59
	Dec.'77	2.1 ± 1.79	0.26 ± 0.23	0
Av. biomass gm^{-2} A_4 and A_5	Nov.'76	8.35	1.00	1.08
	Dec.'77	2.22	0.43 ± 0.23	0

exploited.

In the 1977/78 winter, few Knot fed at Skinflats (McLusky and Bryant 1978) and there was also a 46.2% reduction in the mean biomass (gm^{-2}) of the size-classes of Hydrobia preferred by Knot. In the area exploited by Knot in the 1976/77 winter (Stations A_4 and A_5) the reduction was 73.4% (Table 3.6.3). The overall decrease in food stocks was also likely to have influenced the usage of Skinflats by Knot since the Cardium population was absent and the Macoma population reduced. Thus, whereas in November 1976, a mean biomass of 5.0 gm^{-2} was available, only 2.64 gm^{-2} was available in December 1977; a reduction of 53%.

Wader counts from 1969 (Bryant unpubl.), feeding density studies (McLusky and Bryant 1976, 1978) and the present study have provided evidence to suggest that Skinflats and Kinneil constitute a single mudflat unit separated only visually by Grangemouth Docks. During the study years, the majority of Knot fed at Kinneil over low water utilising Skinflats mainly on the ebb and flow of neap tides. On spring tides the majority flew direct from their low water feeding grounds to roost, as Skinflats is inundated rapidly by the tide and does not provide feeding for a long period on the ebb or flow. Thus, in winters when food supplies at Skinflats are low, as is indicated for the 1977/78 winter, it may not be worthwhile for Knot to feed there at all. During the 1977/78 winter, feeding at Kinneil was indeed high (McLusky and Bryant 1978) at low tide and the majority flew direct to Culross Ash-Pans to roost during the study period in January 1978. This was a winter when Hydrobia and Macoma densities at Skinflats were low and Cardium was absent (Table 3.6.3), suggesting that

visits/

visits to this site on flow tides were not worthwhile.

3.6.3 Dunlin

3.6.3 (i) Tide-related distribution and density patterns

High Tide

The principal Dunlin roost sites were located at Kincardine Bridge (Roost 3) and, on neap tides, the ICI pipeline track (Roost 2). Smaller roosts occurred on the saltings, mainly between Orchardhead and Pocknave.

Ebb Tide

Within an hour of high tide, Dunlin began to feed on the mud behind the receding tide, maximum numbers being attained by 2.5 h after H.T. (Fig 3.6.9a). Following this, many birds flew to Kinneil to continue feeding behind the falling tide-line at that site. Those remaining at Skinflats either fed at the tide edge in dense flocks or dispersed more widely over the exposed mudflat.

Low Tide

On both spring and neap tides, Dunlin were widely distributed over Skinflats at low tide, although feeding density was higher on the outer areas, particularly on neap tides (Fig 3.6.10). The up-shore areas were used more extensively on spring tides but on both tides, the highest density occurred in the vicinity of square G9.

Flow Tide

On the flow tide Dunlin returned from Kinneil to feed at Skinflats; a reversal of the movements on the ebb tide (Fig 3.6.9 a and b) (see also Bryant 1978). The largest movements occurred between 3 and 3.5 h after low tide and the birds

FIGURE 3.6.9: Fluctuations in the density of feeding Dunlin on (a) ebb neap tides and (b) & (c) on flow spring tides during the winter

(a) ● 1-3.11.76,
■ 29.11 - 1.12.76,
▲ 28.1 - 1.2.77

(b) ○ 7 - 9.11.76,
△ 23 - 26.11.76,
□ 7 - 10.12.76

(c) ● 20 - 22.1.77,
■ 8 - 11.3.77

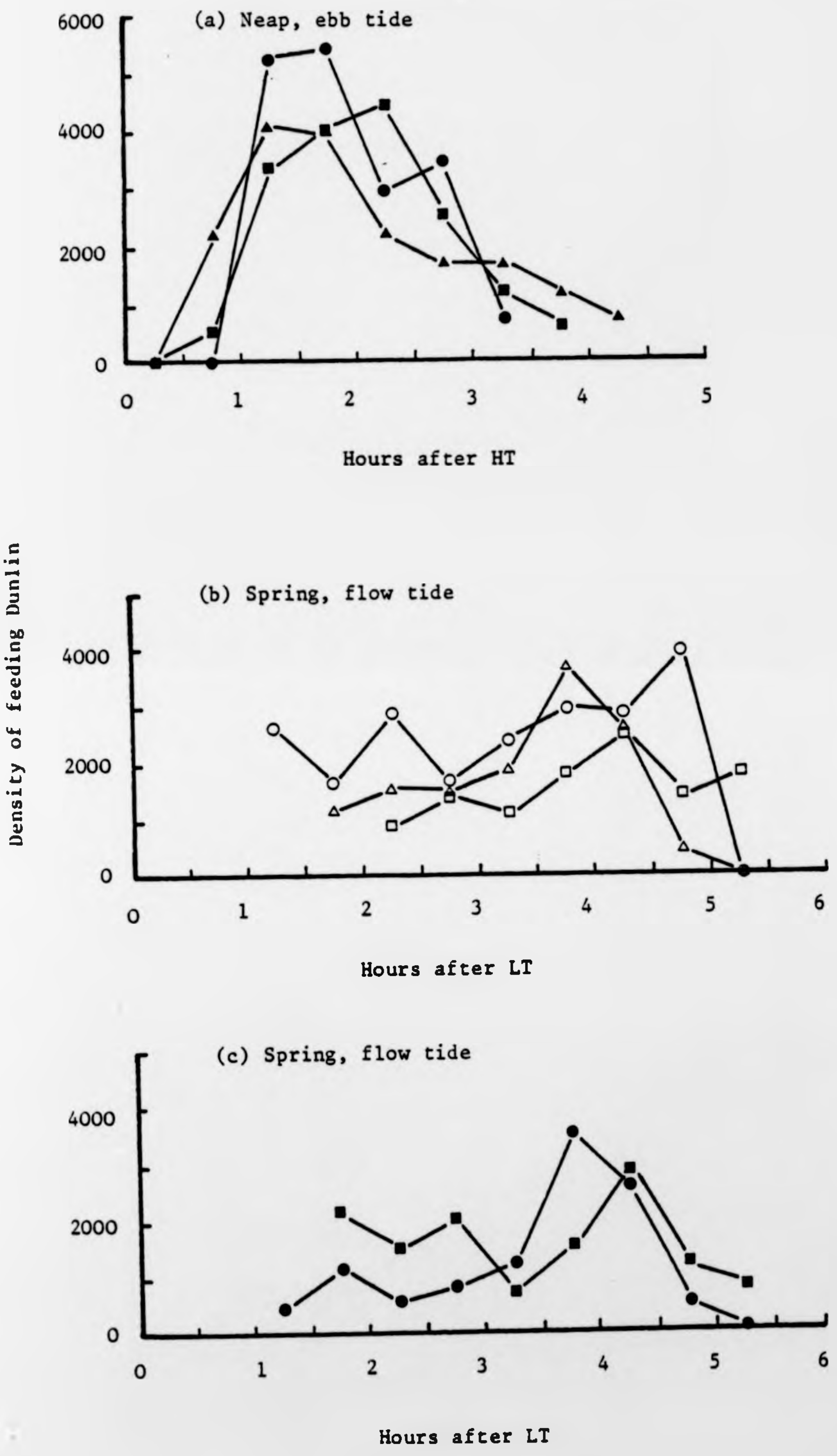

(a) Neap, ebb tide
6000
4000
2000
0
0
1
2
3
4
5
Hours after HT
Density of feeding Dunlin
(b) Spring, flow tide
4000
2000
0
0
1
2
3
4
5
6
Hours after LT
(c) Spring, flow tide
4000
2000
0
0
1
2
3
4
5
6
Hours after LT

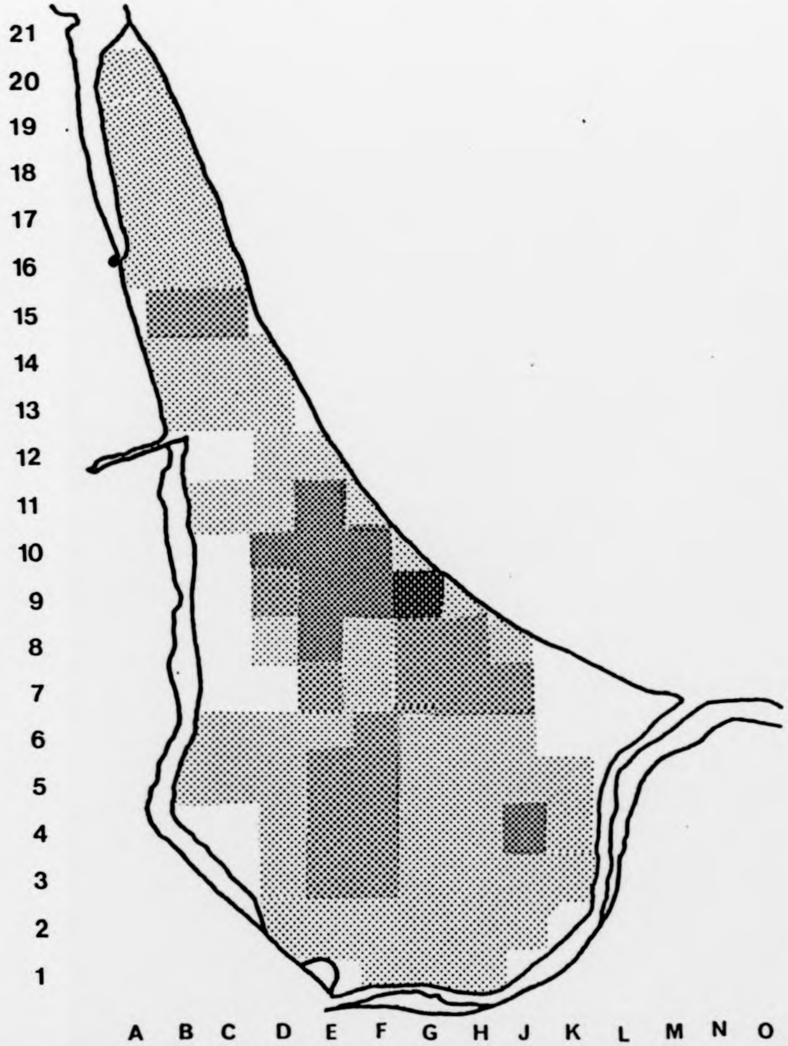
FIGURE 3.6.10: The mean LT Dunlin feeding densities on (a) neap tides (3 - 3.5 h after HT) and (b) spring tides (2.5 - 3 h after LT) during the winter

Key:- birds 0.2 km^{-2}

□	0
░	0.1 - 50
▒	50.1 - 100
▓	100.1 - 500
█	+500

(a) Neap tides

(b) Spring tides



followed the advancing tide, feeding in dense flocks until the whole area was inundated.

The movements of Dunlin between Skinflats and Kinneil involved similar numbers of birds on each tide (Fig 3.6.9) indicating that the two flats act as one unit over a tidal cycle as with Knot. Additionally, colour marking of Dunlin at Skinflats indicated a high degree of site specificity (Bryant and Fleming in prep., Fleming and Warnes 1979, M.Davies unpubl.).

3.6.3 (ii) The factors influencing the low-tide feeding density of Dunlin

During the low-tide period between 600 and 800 Dunlin remained at Skinflats on neap tides (n = 3) and between 450 and 2650 on springs (n = 5) (Fig 3.6.11 a and b).

In the diet study (Section 3.5.4), Nereis and Hydrobia were found to be the most important prey species. Oligochaetes were also included in the diet but their importance was not determined. Correlation analyses were carried out (Pearson and Spearman Rank analyses) for Dunlin feeding density at low water on spring tides ($\bar{n}$ 0.2 km^{-2} sp)and neap tides ($\bar{n}$ 0.2 km^{-2} np) (Appendix 18) with invertebrate prey densities (nm^{-2}) and biomass (gm^{-2}), the densities and biomass of the size-classes of prey taken by Dunlin (Section 3.5.4), total biomass of prey and tidal height. The results are shown in Appendix 19.

On spring tides, Dunlin feeding density was negatively correlated with tidal height ($p < 0.05$); on neap tides, in addition to a negative correlation with tidal height ($p < 0.001$ ***), feeding density was positively correlated with the

total/

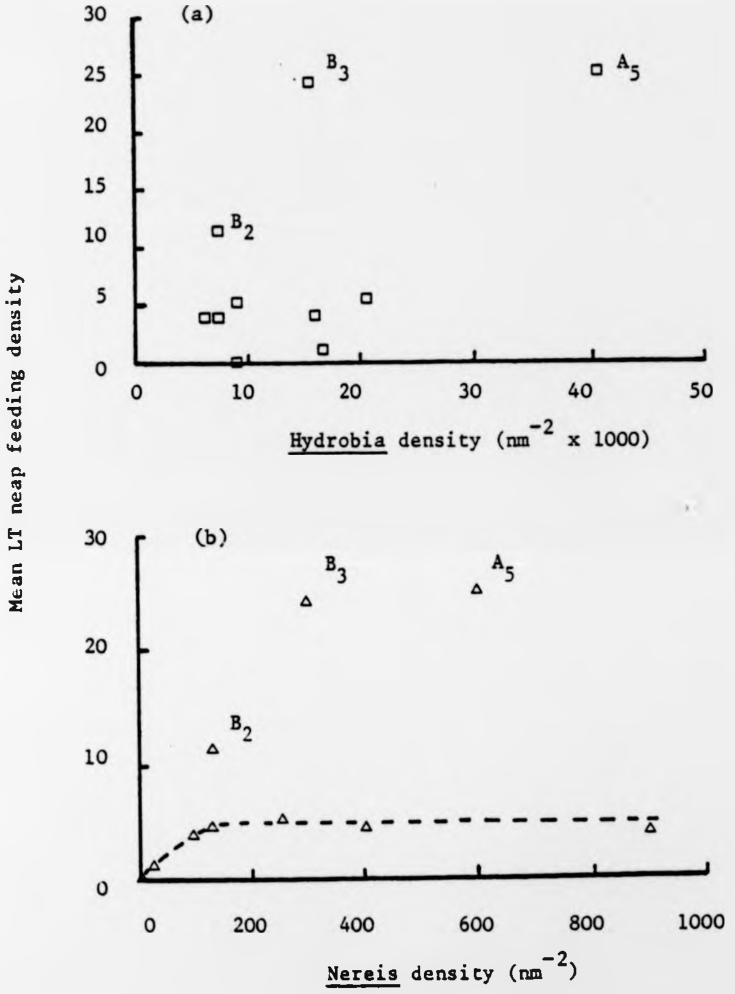


FIGURE 3.6.11: The relationship between the LT feeding density of Dunlin and (a) *Hydrobia*, (b) *Nereis* at Skinflats

TABLE 3.6.4: Multiple Regression Analysis of factors affecting LT feeding intensity of Dunlin on neap and spring tides

FACTOR		B	β	F	SIG	r^2 x 100	CONSTANT
NEAP	Tidal Height (m)	-22.21 ± 4.64	-0.867	22.87	0.001 ***	74.1	101.203
SPRING	Tidal Height (m)	-16.314 ± 5.6	-0.716	8.415	0.02 *	51.0	80.811

total density of Hydrobia ($p < 0.05^*$) and the density of the 'preferred size-classes' of Hydrobia. Intercorrelation between Hydrobia density and tidal height ($p < 0.01^{**}$), however, made interpretation of these results difficult.

Stepwise Multiple Regression Analysis was then carried out to investigate the relative importance of tidal height and the various invertebrate factors on Dunlin feeding density. Tidal height was the only significant factor in the analysis, accounting for 74% of the variation in feeding density on neap tides and 51% on springs (Table 3.6.4). Thus a considerable amount of variation remained unexplained.

Although no significant linear relationship was found between Dunlin feeding density and Nereis density, a functional response by Dunlin to this prey species was indicated (Fig 3.6.11b). However, other factors such as tidal height were involved at B_2, B_3 and A_5 to disturb the response. The positive correlation between feeding density and Hydrobia largely resulted from the high density of Hydrobia at low tidal levels around Station A_5 and no functional response to Hydrobia density was indicated (Fig 3.6.11a).

3.6.4 Shelduck

3.6.4 (i) Tide-related distribution and density patterns

The feeding methods and behaviour of Shelduck in relation to the tide at Skinflats were investigated in detail during the construction of the ICI industrial effluent pipeline (Bryant and Leng 1975). The present study was conducted to compare the distribution and density after completion of the pipeline. The behaviour of Shelduck was not studied in detail./

detail.

The low-tide distribution of Shelduck was more widespread and the density higher on spring tides compared to neaps (Fig 3.6.12). However, on both tides, Shelduck avoided the up-shore areas between Orchardhead and the ICI pipeline track.

3.6.4 (ii) The factors influencing the low-tide feeding density of Shelduck

Gut analysis of four birds from Kinneil show that the diet of Shelduck included not only Hydrobia but also Macoma, oligochaetes, Manayunkia and other small worms (Section 3.5.9). Bryant and Leng (1975), however, concluded from their behavioural study at Skinflats, that Hydrobia was the most important prey at this site.

Correlation analysis was carried out on the basis of this information for low water feeding density of Shelduck at Skinflats on spring and neap tides. Factors included in the analysis were: Hydrobia, oligochaete and Manayunkia densities and biomass m^{-2}, the combined Hydrobia and oligochaete biomass m^{-2}, the combined biomass of Hydrobia, oligchaetes, Macoma, Manayunkia and Nereis m^{-2}, percentage water in the sediment, percentage silt and clay in the sediment and tidal height. The sediment characteristics were included to investigate the influence of the sediment type on feeding, since feeding methods vary depending on different substrate types on the Forth estuary (Warnes et al 1980).

The results (Appendix 19) show a negative correlation

on/

FIGURE 3.6.12: The mean LT Shelduck feeding densities on (a) neap tides (3 - 3.5 h after HT) and (b) spring tides (2.5 - 3 h after LT) during the winter

Key:- birds 0.2 km^{-2}

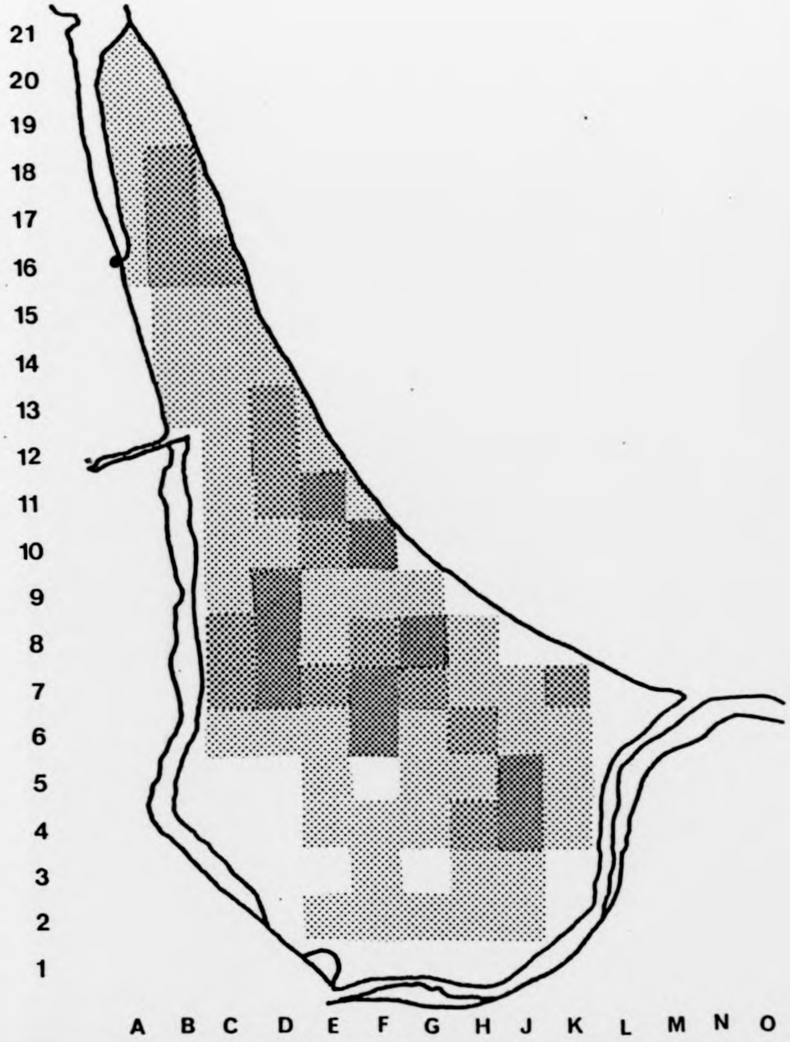
░ 1 - 5

▒ 6 - 10

▓ 11+

(a) Neap tides

(b) Spring tides



on both spring and neap tides between low-tide feeding density of Shelduck and tidal height ($p \leqslant 0.01$** neaps $p \leqslant 0.001$ *** springs). There was also a positive correlation between feeding density on spring tides and Hydrobia density ($p \leqslant 0.05$*), although as previously stated, tidal height and Hydrobia density are themselves correlated. However, a functional response resembling Holling's (1959) Type 2 is indicated from the relationship between low-tide Shelduck feeding density and Hydrobia density (Fig 3.6.13). This suggests that density dependent factors were acting to prevent a linear response to prey density.

The relationship between feeding density and Hydrobia is further evidence that Hydrobia is the most important food of Shelduck at Skinflats (Bryant and Leng 1975) and that the abundance of this prey influences the feeding density of the birds. Both the distribution patterns and density of Shelduck were similar to those during the previous 1972/73 and 1976 studies (Bryant and Leng 1975, McLusky and Bryant 1976) even though the construction of the ICI pipeline took place during the earlier investigation. Thus, concentration of feeding efforts where Hydrobia are most abundant is indicated by all studies.

3.6.5 Discussion

The use of similar methods in estimating the feeding density of shorebirds had the advantage of standardising results but also had disadvantages. Species forming dense flocks could accurately be located on field maps since the flock boundaries were well defined. However, boundaries of the widely dispersed Redshank flocks had to be drawn arbitrarily and subtle changes in density within them were not/

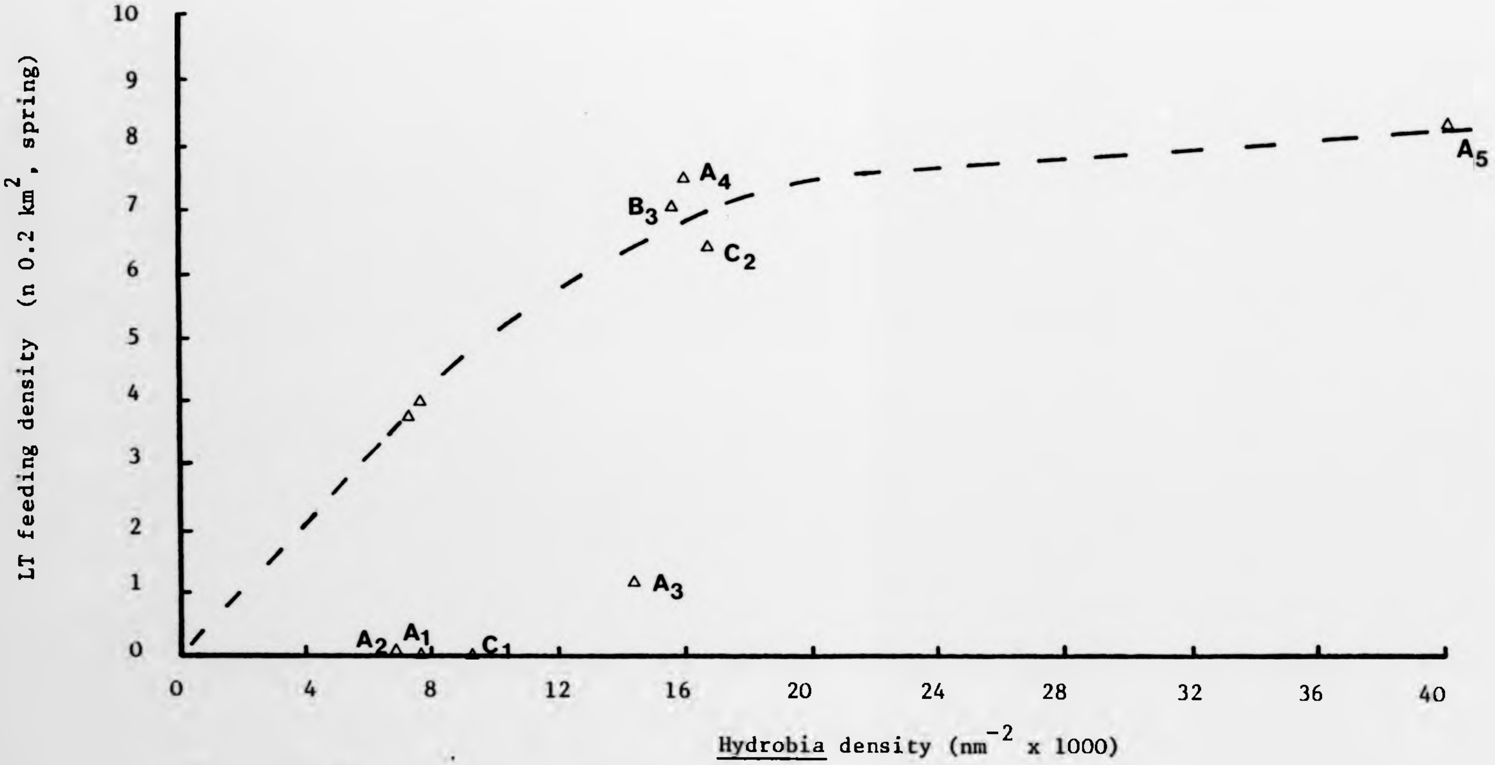


FIGURE 3.6.13: The relationship between the LT feeding density of Shelduck on spring tides and the density of *Hydrobia* at Skinflats

not recorded. A more elaborate method would be required to achieve this but, over the large study area, was not feasible. Nevertheless, the methods were considered adequate to compare the distribution and density of shorebirds feeding at Skinflats.

In general, the low-tide feeding densities of Redshank, Knot, Dunlin and Shelduck increased in response to increasing prey abundance but environmental and behavioural factors also influenced density. Knot responded most significantly to prey density by feeding in large, compact flocks almost exclusively in the area where *Hydrobia* was most abundant and bivalve molluscs were common. By also feeding where large *Hydrobia* occurred, they thus concentrated their feeding efforts in the most profitable parts of the habitat as predicted for predators by Royama (1971).

Redshank, however, fed in scattered flocks with the highest densities occurring close to the roost-sites where prey density was low. Only in areas further away from the roosts did they show a functional response to *Nereis* and *Macoma* density. There, feeding numbers increased to 0.2 birds per 0.2 km^{-2} at around 200 *Macoma* and at a similar density of *Nereis*, remaining at this level at higher prey densities (Fig 3.6.6). Since it is apparent that the areas adjacent to the roosts are the favoured feeding areas, it would seem prudent for all birds to remain there. However, it has been proposed by Zwartz (1974, 1976) that birds will occupy a preferred area until density reaches a threshold, beyond which a spread over the less-preferred areas occurs. This has been further indicated from studies on Redshank on the Ythan (Joffe 1978). The density of Redshank at Skinflats was not studied outwith the winter period but if this is a general principal, it would explain the low, relatively even spacing of/

of Redshank away from the preferred areas.

Dunlin and Shelduck also showed a functional response to prey density, although as with Redshank, other factors disturbed the relationship. Dunlin generally followed the tide as it ebbed and those remaining over low tide tended to disperse along the outer edge where the substrate would remain wet. This preference by several shorebird species for wet areas of mud has been demonstrated elsewhere (Burger et al 1977, Evans et al) and may result from an increase in prey availability and most likely accounted for the higher feeding density at A_5, B_2 and B_3 (see Fig 3.6.12). The increase in density elsewhere levelled at 5 birds per 0.2 km^{-2}, around 200 Nereis m^{-2} and did not increase at higher prey densities.

The functional response by Shelduck to Hydrobia density (Fig 3.6.13) was also disturbed since upshore areas were little used despite relatively high prey densities. Two factors probably influenced feeding there. Wildfowlers frequent the area causing Shelduck to be very wary close inshore (Bryant and Leng 1975) and, the sediment may not have been suitable for 'scything' since it dries out on neap tides and is also liable to freezing in winter.

Behavioural differences and habitat preferences of the four common species of shorebird at Skinflats resulted in no two species favouring the same feeding zone and with only a small degree of overlap, the mudflat and its resources were thus partitioned. Two species, Redshank and Knot, which both preferred the same size classes of Hydrobia and Macoma differed not only in the proportion of each prey taken (Section 3.5.6) but also in feeding zone and thus were not observed in direct competition. Similarly, Shelduck and Knot were potential competitors for Hydrobia at Skinflats but it was noticeable

on/

on neaps, when Knot were present in the areas of large Hydrobia abundance, that Shelduck fed at a lower density in comparison to spring tides (Fig 3.6.12).

Since competition is rarely observed in the field, the cause of habitat partitioning is difficult to assess. However, there is some evidence of interspecific competition between shorebirds. Dense flocks of Dunlin are known to displace Redshank (Monmontzi 1977) and increased feeding densities of gulls and Curlew led to a decrease in the number of Avocets feeding in an intertidal zone in the Waddensea (Zwartz 1978). Thus the mid-winter segregation of shorebirds at Skinflats may have resulted not only in habitat selection but also from interspecific competition and further research is required to investigate this possibility.

4 GENERAL DISCUSSION

4.1 Energy Balance and Winter Survival of Shorebirds

A major factor contributing to the winter survival of a shorebird will be its ability to balance energy intake and expenditure (Evans 1976). Measurements of energy intake can readily be made over a range of environmental conditions (eg Smith 1975, this study) but expenditure is not easily quantified. Factors which increase the daily energy requirements include low temperatures, wind, precipitation and increased costs of food gathering caused, for example, by scarcity of prey, type of sediment, increased wave action and strong winds (Evans 1976). Food gathered per day may not be sufficient to satisfy these energy demands in winter and energy saving measures then become important. Whitlock (1979) found that the metabolic rates of Oystercatcher and Dunlin increased at low temperatures and in strong winds illustrating some of the ways in which energy requirements will vary throughout the winter according to the prevailing conditions. By making increased use of shelter in roosting, however, energy savings of up to 20% can be made during harsh conditions (Whitlock 1979) which will be important if food intake is reduced due to bad conditions (Evans 1976). Furthermore, experiments with laboratory rats show that, when starving, energy expenditure is reduced and basal metabolic rate is lowered (Westerterp 1976). Although the relevance to normal, everyday experience is probably not great, this does further illustrate how animals may adapt to survive extreme environmental conditions.

With increased demands on energy requirements during the winter it might be expected that shorebirds would feed at a higher rate or for a longer period. There is, however, no supportive evidence that feeding rates increase as the day-length decreases or cold increases (eg Pienkowski 1973, Goss-Custard 1977c) but most shorebirds do feed

for/

for a longer period and many feed at night (eg Goss-Custard, Jenyon et al 1977, Pienkowski 1973).

In general, shorebirds deposit fat reserves with the advancing winter and the associated weight changes follow a similar pattern each year. Two hypotheses have been proposed to account for this (Pienkowski 1973). The first suggests that fat reserves which are built up during the early winter when prey abundance and availability are high, are depleted rapidly in late winter through food shortage, resulting from a decrease in the abundance, condition and availability of prey. The second hypothesis proposes that the weight peak, occurring in November or December is a form of insurance against the likelihood of severe weather later in the winter and that weight is allowed to fall as the probability of inclement weather decreases. A third possibility is that fat is stored for overnight survival on roost-sites, ie a short-term insurance, during the longest nights.

Evidence for the first 'insurance hypothesis' comes from studies of Dunlin (Pienkowski et al 1979). During a period of cold weather the weights of Dunlin on the Wash fell but rose soon after mild conditions were resumed. A similar pattern was found in Grey Plover after a spell of severe weather (Davidson in prep.) suggesting that food is plentiful and can be readily exploited to replace energy losses. Furthermore, evidence provided by Dunlin weights shows that birds wintering in areas of low mean winter temperatures were heavier than those in milder regions in Britain. These higher weights were maintained throughout the winter.

The following discussion centres around Redshank and possible ways in which its energy balance is achieved. Data drawn from published data/

data supplement observations from this study, and differences in survival strategies of various species of shorebirds are proposed.

Three steps were included in the procedure for determining the daily energy intake:

(a) The determination of Basal Metabolic Rate (BMR)

(b) The time available for feeding on an average day each month

(c) Determination of energy intake and its relationship to estimates of BMR

(a) <u>The determination of BMR</u>

BMR (the metabolic rate of birds resting in a thermoneutral environment) is strongly weight dependent and several methods have been used to estimate its value for birds.

(1) Lasiewski and Dawson (1967)

$$\mathrm{BMR}_{(\mathrm{Kcal\ h^{-1}\ bird^{-1}})} = 0.0317 \times w^{0.726} \quad \text{..... equation (1)}$$

(2) Aschoff and Pohl (1970) (simplified)

$$\mathrm{BMR}_{(\mathrm{Kcal\ h^{-1}\ bird^{-1}})} = 3.6 \times w^{0.734} \quad \text{..... equation (2)}$$

(3) Kendeigh (1974)

$$\mathrm{BMR}_{(\mathrm{Kcal\ h^{-1}\ bird^{-1}})} = 0.5224 \times w^{0.7347} \quad \text{..... equation (3)}$$

(where w = body weight on g)

Since the BMR estimates of Aschoff and Pohl (1970) and Kendeigh are similar, equations (1) and (3) are used in the following calculations to give a range of possible values. Data from studies on the Wash (Minton 1975) provide values of monthly weight changes for many shorebirds and BMR (L & D, and K) was calculated from these. These weight data are especially appropriate given similar winter temperatures (Pienkowski <u>et al</u> 1979). Total weight was used in equations (1) and (3) in preference to lean weight since the original determinations/

determinations of BMR were made on total weight.

(b) Determination of the time available for feeding

An analysis of the predicted period (h) each day throughout the year when sandbank heights between 0.5 and 6.1 m OD were exposed in 1978 during daylight, darkness and moonlight at Grangemouth, was carried out by M.Davies in conjunction with the University of Stirling Computer Unit (unpublished material). Mudflat (sandbank) heights at Skinflats were obtained from Admiralty Charts and from this, it was possible to calculate the number of hours per day, and thus per month, that Skinflats was exposed and thus the time available for intertidal feeding in daylight and at night. An average day each month was used in all calculations.

(c) Determination of energy intake

Food intake (number of items per day) was calculated by multiplying feeding rates on the various prey items at each stage in the tidal cycle by the number of hours in either daylight or darkness available for feeding.

Obtaining a measure of the energy ingested involved multiplying the number of each species ingested per day by the biomass (gAFDW) of the mean prey size ingested and by the energy value of each prey (Kcal g^{-1} AFDW).

It has been assumed that between 70% and 90% of the energy ingested is assimilated, depending on the type of prey eaten. Prey such as *Macoma* and *Hydrobia*, having shells will take more energy to process in the gut than soft-bodied animals such as *Nereis* and flesh may be ejected in faeces or pellets, together with shell fragments. Thus the assimilation efficiency will vary with the prey eaten.

Assimilated/

Assimilated energy is expressed as multiples of BMR (= Factor x BMR).

The calorific equivalents used were:

Nereis	4.36 kcals (18.25 kJ) g^{-1} AFDW (Chambers & Milne 1975b)
Macoma	4.77 kcals (19.97 kJ) g^{-1} AFDW (Elliott 1979)
Hydrobia	4.8 kcals (20.09 kJ) g^{-1} AFDW (estimate)
Small worms	- assumed the same as Nereis
Cardium	- assumed the same as Macoma
Corophium	- assumed the same as Nereis

In darkness, the feeding rates of waders were based on 'touch-feeding methods' measured in daylight since no night observations were made.

Daily energy expenditure has not been measured in free-living wading birds. A value of 3.3 x BMR was used in the present study; the mean value derived from various studies on passerine and non-passerine and summarised in King (1974), excluding hummingbirds. This provided a basis for comparing energy intake by waders at Skinflats to the theoretical energy expenditure. It is stressed that this is only an average value as the actual DEE will vary between species depending on activity.

4.1.1 Redshank

Basal Metabolic Rate (BMR) and Daily Energy Expenditure (DEE)

The monthly estimates of BMR from equations (1) and (3) are shown in Table 4.1.

Time available for feeding

On the ebb and flow tides the proportion of Redshank feeding by sight or touch at Skinflats varied between 100% sight-feeding over/

TABLE 4.1: Mean body weights and estimated BMR of Redshank

MONTH	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Total mean body weight (g)	159.5	147.5	142.5	151.5	138.5	130.5	146.5	144	145	158.5	164.5	164.2
BMR (k cal day^{-1}) Lasiewski and Dawson (1)	30.2	28.6	27.9	30.3	27.3	26.1	28.4	28.1	28.2	30.1	30.9	30.9
BMR (k cal day^{-1}) Kendeigh (3)	21.7	20.5	19.97	20.9	19.6	18.7	20.4	20.1	20.2	21.6	22.2	22.2

over low-tide and 100% touch-feeding 1½ - 2 hrs either side of high-water (Fig 4.1) (see also section 3.6.1). The total intake also varied over a tidal cycle since the prey species and ingestion rates differed with the foraging method.

The ebb and flow periods were divided into arbitrary zones according to the proportion of the population sight- and touch-feeding (Fig 4.2). These zones corresponded to certain heights above OD.. The time available for feeding in each zone per month and on an average day per month could be calculated from the computer analysis of exposure times at the arbitrary boundaries.

Thus:

(a) below 3.1 m, all birds were assumed to be sight-feeding (zone A)

(b) between 3.1 and 4.4 m, 77% were assumed to be sight-feeding and 23% touch-feeding (zone B)

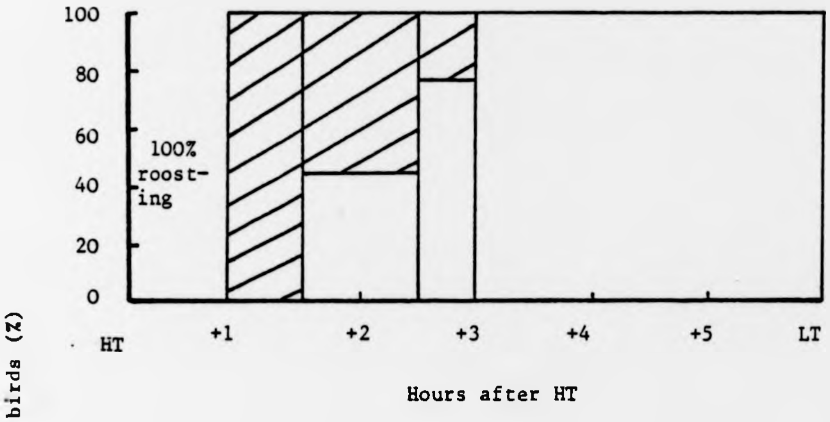
(c) between 4.4 and 4.7 m, 45% were assumed to be sight-feeding and 55% touch-feeding (zone C)

(d) between 4.7 and 5.0 m, all birds were assumed to be touch-feeding (zone D)

Determination of energy intake

The energy intake of sight- and of touch-feeding Redshank was calculated from the product of the mean ingestion rates (Carron Mouth and Powfoulis estimates pooled) and the biomass of the mean size of each prey species taken (Table 4.3). It is assumed that birds feeding at night touch-fed at the rates observed in daylight and that night feeding occurred between October and March as on the Ythan/

(a) Neap tides : ebb n = 3 observations



(b) Spring tides : flow n = 5 observations

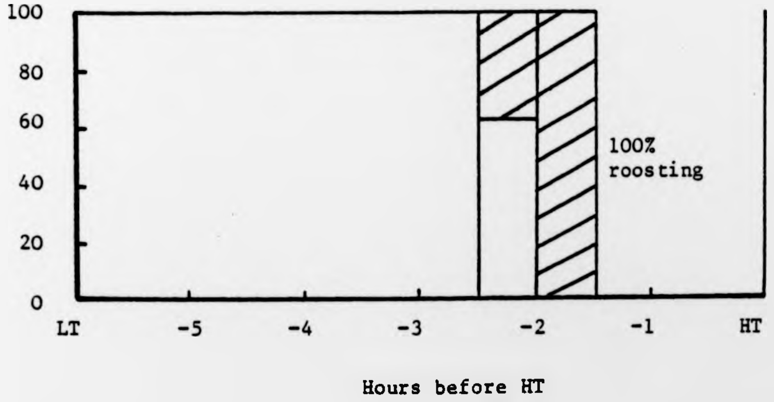


FIGURE 4.1: The proportion of Redshank using sight (unshaded) and touch (shaded) methods of prey detection in relation to tidal cycle on (a) ebb neap tides and (b) flow spring tides

FIGURE 4.2: Map showing Redshank feeding zones, delimited by tidal heights of 3.1 m, 4.4 m and 4.7 m on ebb and flow tides.

A = 100% of birds sight-feeding;

B = 77% sight-feeding, 23% touch-feeding;

C = 45% sight-feeding, 55% touch-feeding;

D = 100% touch-feeding

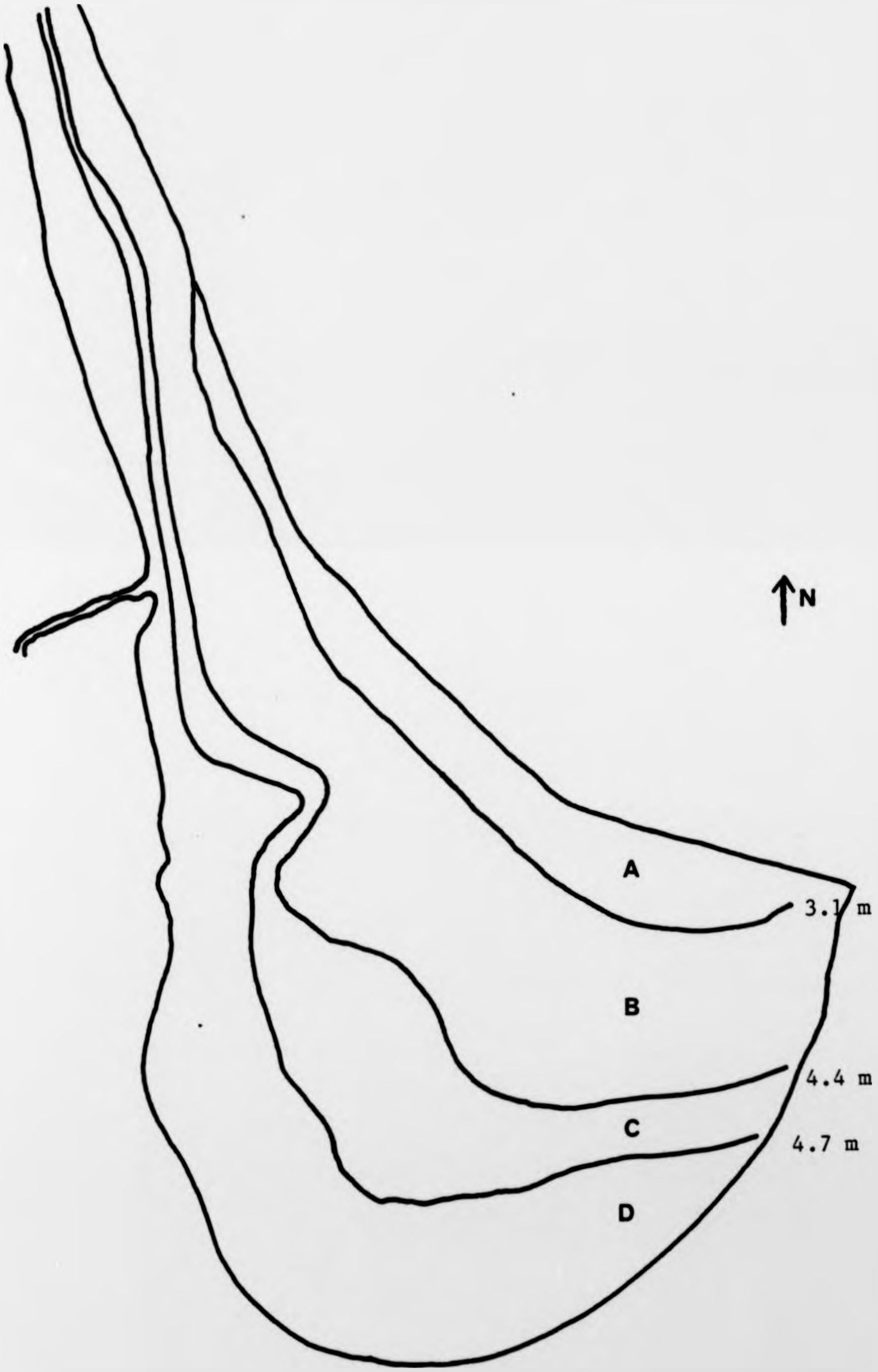

N
A
3.1 m
B
4.4 m
C
4.7 m
D

TABLE 4.2: Summary of the average daily energy intake (Kcals) of Redshank throughout the year

	DAYLIGHT								DARKNESS						DAYLIGHT AND DARKNESS							
	ZONE				Total energy (kcal) assimilated	Total energy (kJ) assimilated	Factor x BMR (Kendeigh)	Factor x BMR (Lasiewski & Dawson)	ZONE				Total energy (kcal) assimilated	Total energy (kJ) assimilated	ZONE				Total energy (kcal) assimilated day^{-1}	Total energy (kJ) assimilated day^{-1}	Factor x BMR (Kendeigh)	Factor x BMR (Lasiewski & Dawson)
	A	B	C	D					A	B	C	D			A	B	C	D				
Jan	23.47	11.00	2.41	1.98	38.86	162.7	1.8	1.3	19.34	7.58	4.39	3.03	34.34	143.8	42.81	18.58	6.80	5.01	73.20	306.5	3.4	2.4
Feb	27.86	12.01	3.09	1.94	44.90	188.0	2.2	1.6	17.22	7.63	2.29	1.95	29.01	121.5	45.08	19.64	5.38	3.89	73.99	309.8	3.6	2.6
Mar	33.68	14.14	3.71	2.6	54.13	226.6	2.7	1.9	4.66	3.16	0.61	0.65	9.08	38.0	38.34	17.30	4.32	3.25	63.21	264.6	3.2	1.9
Apr	39.78	17.18	4.02	2.9	63.88	267.5	3.1	2.1	-	-	-	-	-	-	39.78	17.18	4.02	2.90	68.88	288.4	3.3	2.3
May	44.07	19.43	4.32	3.58	71.40	298.9	3.6	2.6	-	-	-	-	-	-	44.07	19.43	4.32	3.58	71.40	298.9	3.6	2.6
Jun	48.62	19.67	6.13	4.02	78.44	328.4	4.2	3.0	-	-	-	-	-	-	48.62	19.67	6.13	4.02	78.44	328.4	4.2	3.0
Jul	47.68	18.53	6.86	4.36	77.43	324.2	3.8	2.7	-	-	-	-	-	-	47.68	18.53	6.86	4.36	77.43	324.2	3.8	2.7
Aug	43.1	16.94	5.35	3.41	68.8	288.1	3.4	2.4	-	-	-	-	-	-	43.10	16.94	5.35	3.41	68.80	288.1	3.4	2.5
Sep	36.86	15.02	3.90	2.81	58.59	245.3	2.9	2.1	-	-	-	-	-	-	36.86	15.02	3.90	2.81	58.59	245.3	2.9	2.1
Oct	30.60	12.65	3.06	2.49	48.80	204.3	2.3	1.6	5.06	2.55	1.00	0.99	9.6	40.2	35.66	15.20	4.06	3.48	58.40	244.5	2.7	1.9
Nov	24.99	10.38	2.36	1.98	39.71	166.3	1.8	1.3	18.58	8.55	2.58	1.58	31.29	131.0	43.57	18.93	4.94	3.56	71.00	297.3	3.2	2.3
Dec	22.11	8.94	2.09	2.08	35.20	147.4	1.6	1.1	20.08	8.63	3.50	1.66	33.87	141.8	42.19	17.58	5.59	3.74	69.07	289.2	3.1	2.2

Table 4.3: Mean biomass and ingestion rates of each prey species of Redshank

	Mean biomass (mg AFDW) ingested per individual	Number of each species ingested per hour	
		sight-feeding birds	touch-feeding birds
Hydrobia	0.48	380	1428
Nereis	5.57	163	-
Macoma	3.2	83	-

Ythan estuary, Aberdeenshire (Goss-Custard 1967). There, in addition, night-feeding in October and March only occurred on moonlight nights and a similar pattern is assumed at Skinflats.

The total assimilated daily energy, ie, energy incorporated in body tissues and respiration throughout the year, is summarised in Table 4.2. This was derived from the feeding rate data (Section 3.5.2) and assumes an 80% assimilation efficiency since the diet consists of shelled and soft-bodied animals. A full computation is given in Appendix 20.

The time available for feeding in daylight decreases in the winter months so that in December, energy assimilation is only 1.6 x BMR (1.1 x BMR Lasiewski and Dawson) whereas, by feeding at the same rate in June, intake is 4.2 x BMR (3.0 x BMR). Assuming an energy expenditure of 3.3 x BMR (see above), feeding at night must therefore take place to maintain the energy balance in winter. At the level suggested, night feeding increases the energy intake to

3.1/

3.1 x BMR (2.2 x BMR) in December which is still below the theoretical DEE of 3.3 suggested above. However, energy conservation measures may save up to 20% of energy expenditure (Whitlock 1979) which could offset this apparent deficit.

The effects of harsh conditions on energy intake

In winter at low temperatures and in high winds, Redshank are unable to feed by sight and adopt touch-feeding methods even in daylight (section 3.5.2, Goss Custard 1976). Assuming continuous feeding when the mudflats are exposed under such conditions, the energy intake in December is reduced by 20.7% (Table 4.4) and by larger amounts in January (21.7%) and February (25.0%).

The winter survival strategy of Redshank at Skinflats

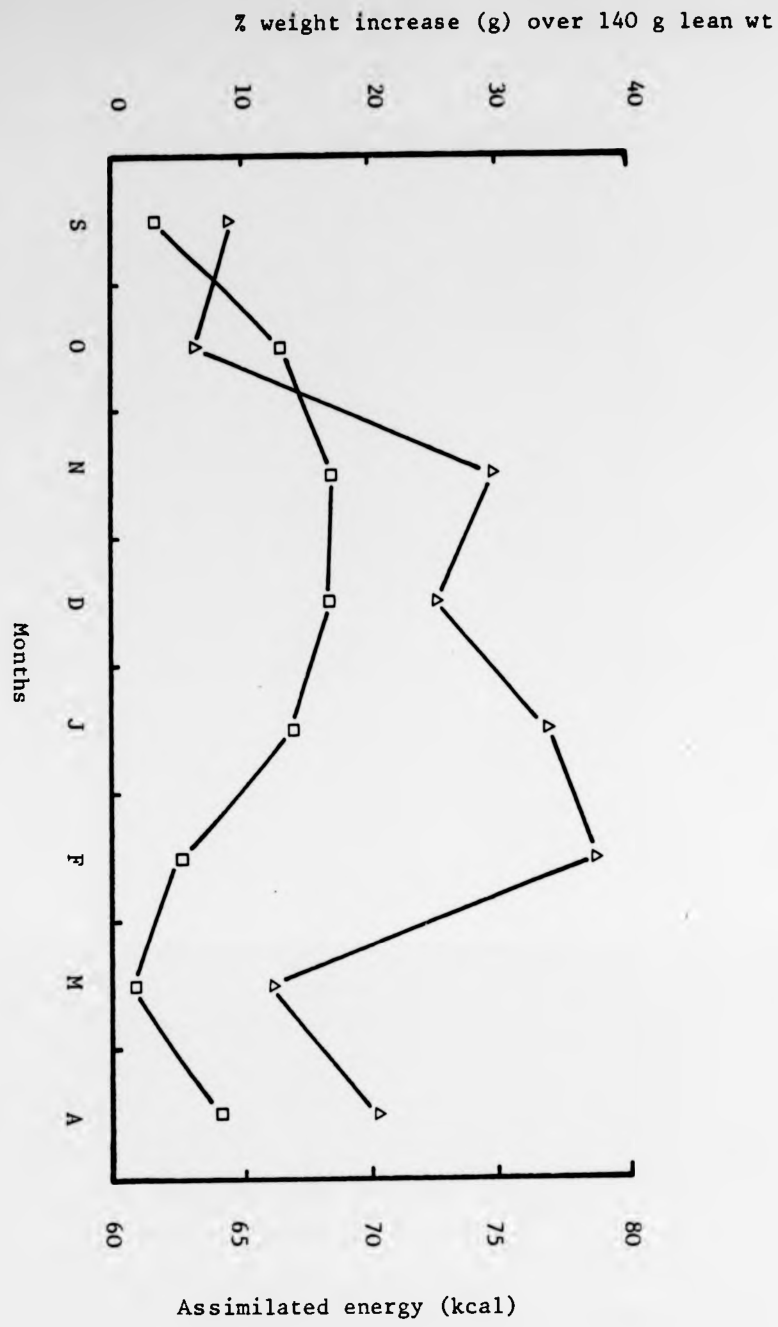
The potential daily energy intake of Redshank during the winter months at Skinflats and the mean monthly weight increase, expressed as a percentage of lean weight (140 g) of birds from the Wash (Minton 1975), are shown in Fig 4.3. Weights of small samples of birds from the Forth indicate that the monthly means from the two sites are similar (Davies unpublished). Between September and November, the fat content increases from c. 3.5% to c. 17% and declines thereafter. The rate of this decrease is slow between November and January but rapid between then and March when only c. 2% fat remains. During March and April pre-migratory fat is rapidly laid down.

The similarity in this pattern between years (N. Davidson pers. comm) indicates that the weight fluctuations represent a strategy for surviving the winter. During the period of weight loss, energy intake in mild conditions is potentially higher than in the early winter/

TABLE 4.4: Maximal daily energy intake by Redshank at temperatures below 4°C at Skinflats

	Time (h) available for daylight feeding	Total energy (kcals) assimilated in daylight	Total energy (kJ) assimilated in daylight	Total energy (kcals) assimilated in darkness	Total energy (kJ) assimilated in darkness	Total energy (kcals) assimilated in daylight and darkness	Total energy (kJ) assimilated in daylight and darkness	Factor x BMR (Kendeigh)	Factor x BMR (Laziewski and Dawson)
Oct	10.96	28.85	120.8	9.60	40.2	38.45	161.0	1.8	1.3
Nov	8.90	23.42	98.1	31.29	131.0	54.71	229.1	2.5	1.8
Dec	7.94	20.90	87.5	33.87	141.8	54.77	229.3	2.5	1.8
Jan	8.74	23.00	96.3	34.34	143.8	57.34	240.1	2.6	1.9
Feb	10.05	26.45	110.7	29.01	121.5	55.46	232.2	2.7	1.9
Mar	12.15	31.98	133.9	9.08	38.0	41.06	171.9	2.1	1.5

FIGURE 4.3: Weight changes (-□-) and predicted average daily assimilated energy (-△-) of Redshank during the winter. (Weight data from the Wash - Minton 1975)


% weight increase (g) over 140 g lean wt
0
10
20
30
40
S
O
N
D
J
F
M
A
Months
60
65
70
75
80
Assimilated energy (kcal)

winter (Fig 4.3) and, unless conditions are severe for long periods, obtaining sufficient food to meet energy requirements should not present a problem to a Redshank. Data collected on invertebrate populations at Skinflats (Sections 3.3, 3.4) indicates, in addition, that food supplies are adequate throughout the winter.

Assuming that energy stores are built up to enable a bird to survive short spells of cold and/or windy conditions, the energetic cost of carrying these reserves must be taken into account. Such reserves are not only energetically expensive to build up but also costly to maintain, thus increasing the total metabolism of the animal. Depending on the metabolite and the amount stored, between 5 and 25% of the energy content of food ingested by laboratory rats was required in the conversion to fat reserves (Westerterp 1976). Assuming similarly high levels in a shorebird, there must be an important advantage to having a fat store, most likely an insurance against harsh winter conditions (Pienkowski et al 1979). In harsh conditions, energy intake can be forcibly reduced by 20.7 - 25%, although switching to a less expensive feeding method may compensate for some of this loss (Evans 1979, Goss-Custard 1976). Providing the mudflats are not frozen, a bird will have to decide whether feeding or roosting is the best strategy. In cold conditions at Skinflats, Redshank feed for longer on neap tides (Section 3.6.1), suggesting the energy gain equals or exceeds energy expenditure at this time. Under more severe temperature conditions or when winds are strong, energy expenditure may exceed intake and roosting may be the best strategy to adopt. On spring tides, feeding for longer on the mudflats is not possible and unless feeding grounds inland are available, roosting/

roosting is enforced.

Although the way in which energy is conserved and fat reserves used during roosting by shorebirds has not been quantified, the savings are likely to be large. In laboratory rats, for example, energy expenditure is known to decrease by more than 60% during food deprivation due largely to decreases in activity and BMR (Westerterp 1976). Thus, in harsh conditions when food is unavailable or energetically very expensive to collect, wading birds such as Redshank may be able to reduce energy expenditure by similar means. Also, at low temperatures and at high wind speed, Redshank seek "mutual" and "environmental" shelter and could save at least 5% and possible 17.5% of the potential metabolic rate under full exposure to the same conditions (Whitlock 1979). Furthermore, since 11 - 15% of total energy intake of laboratory rats is used in food processing (Westerterp 1976), by switching to the use of fat reserves a Redshank would not only reduce metabolic costs of maintaining the energy store but also save on food processing costs. Thus, the possible ways of saving energy in harsh conditions are several and further investigations are required to quantify them.

Assuming that a fat-store is built up as an insurance against harsh weather and that it is allowed to fall as winter progresses, a model of survival strategy can be proposed (Fig 4.4). In early winter the need to build up fat levels may trigger night-feeding so that intake is boosted. In mild conditions the energy obtained will not only balance the daily maintenance requirements but some will also be utilised in the build-up and maintenance of the energy store. In/

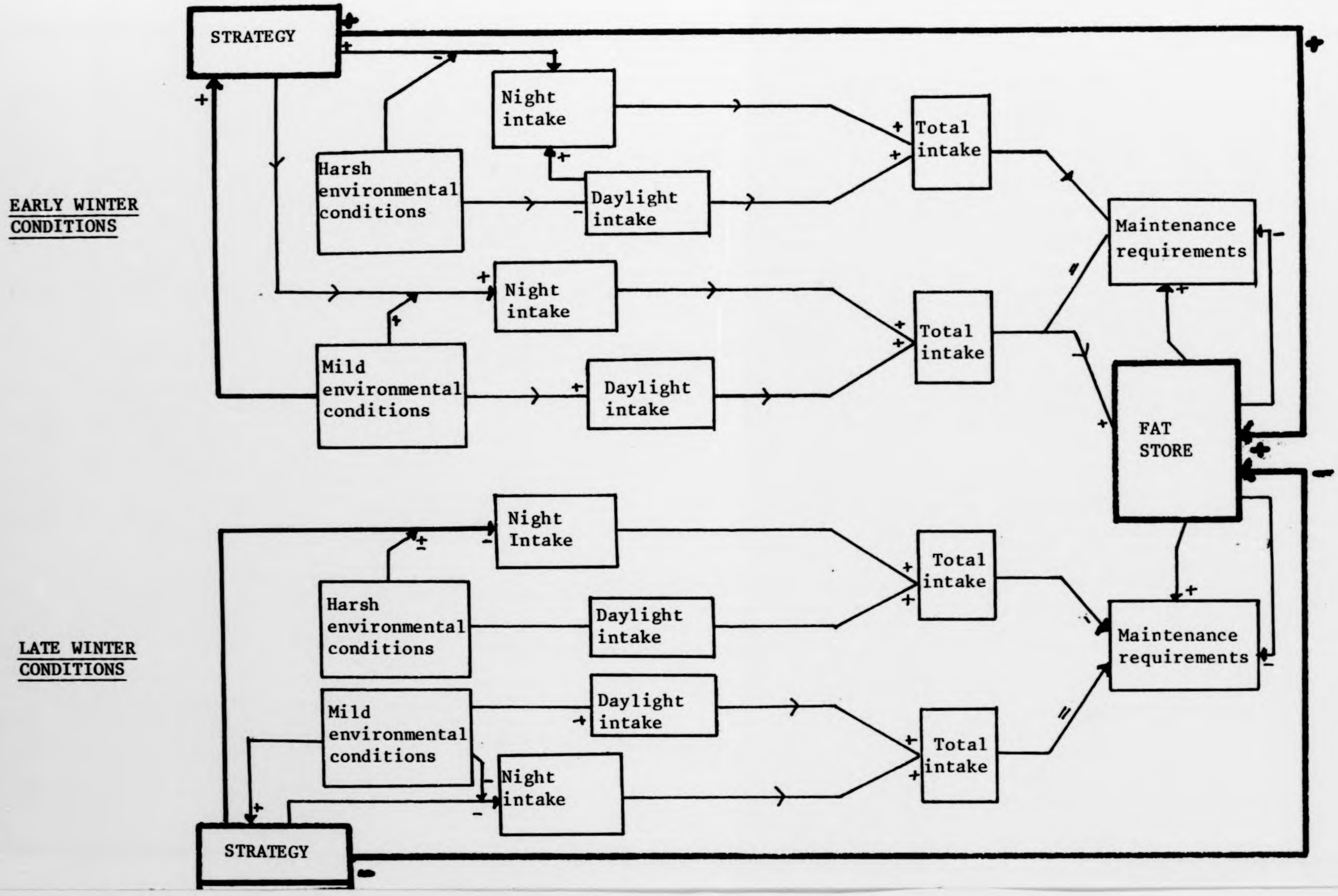
In harsh conditions, if daylight intake is reduced, night feeding will be further re-inforced, unless conditions are so severe that it is prevented. Then all energy will be directed to maintenance and it may be necessary to draw upon the reserves. However, since in early winter the likelihood of prolonged harsh conditions is unlikely, a fat store should be laid down in preparation for later bad conditions.

Since in late winter the potential daily energy intake increases (Fig 4.3), the reduction of the fat store appears to be a positive strategy by Redshank. Weather conditions may be more severe than earlier in the winter but the time available to collect energy is progressively increasing (Fig 4.3). Thus losses of reserves can readily be repleted after a cold or very windy period. It has been shown that Dunlin and Grey Plover can regain weight to "normal" levels very rapidly (Davidson in press) after exposure to severe conditions and therefore it is likely that Redshank also can increase body weight rapidly.

The strategy in late winter is thus to reduce the fat store to save the cost of carrying it. This may be achieved in mild weather by decreasing night feeding, relying more heavily on the fat store and thus expending less energy (as discussed above). In harsh weather, however, if the mudflats are not frozen, night-feeding may be continued, supplemented by the fat store to balance maintenance requirements. Under prolonged severe conditions, this strategy may fail since the longer the period of food deprivation continues, the more susceptible the birds will become to exposure and disease. Having allowed the fat reserves to fall to levels below that of

Knot/

FIGURE 4.4: Model of the Winter Survival of Redshank


EARLY WINTER CONDITIONS
STRATEGY
Night intake
Harsh environmental conditions
Daylight intake
Total intake
Night intake
Mild environmental conditions
Daylight intake
Total intake
Maintenance requirements
FAT STORE
LATE WINTER CONDITIONS
Night Intake
Harsh environmental conditions
Daylight intake
Total intake
Mild environmental conditions
Daylight intake
Night intake
Total intake
Maintenance requirements
STRATEGY
+
-
=

Knot and Dunlin at the same time of year (see below) a prolonged cold spell may in part account for the high mortality in hard winters (eg Baillie 1980, Dobinson and Richards 1974, Goss-Custard, Jenyon _et al_ 1977), in comparison to the other two species. More research is clearly required to quantify energy balance and the effects of severe weather on the survival strategy of Redshank and such a study was outwith the scope of this project.

4.1.2 Knot

Basal Metabolic Rate (BMR) and Daily Energy Expenditure (DEE)

The monthly estimates of BMR from equation (1) and (2) are shown in Table 4.5.

Time spent feeding

Unlike Redshank, Knot did not spend all the available time feeding in daylight (Section 3.6.2). On flow spring tides, they flew across the estuary to their roost sites before complete tidal inundation; although on neap tides, when they roosted at Skinflats, they commenced feeding activity soon after the mud below HW level was exposed. The time spent feeding in daylight was thus assumed to be the period when the mudflat below 4.7 m was exposed (Fig 4.2).

Energy intake

With the exception of observations on Knot at Torry Bay (Section 3.5.3), no feeding rate measurements were available from the present study. However, on Morecambe Bay, Knot fed on _Hydrobia_ at a rate of 50 min^{-1} two hours either side of high water and on _Macoma_ at a rate of 1.87 min^{-1} over low water (Prater 1970). Assuming a similar rate of feeding on _Hydrobia_ throughout the tidal cycle at Skinflats and on _Macoma_ over low water, the daily energy intake could be estimated. The mean biomass of a knot-sized _Hydrobia_

was/

TABLE 4.5: Mean body weights, BMR and predicted DEE of Knot

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Mean body wt. (g)	150.5	136.5	135.5	140.5	176.5	-	135	133	135	136	154.5	159
BMR kcal. day^{-1} (Lasiewski and Dawson)	29	27	26.9	27.6	32.5	-	26.8	26.5	26.8	26.9	29.5	30.2
BMR kcal day^{-1} Kendeigh	20.8	19.4	19.2	19.8	23.4	-	19.2	19.0	19.2	19.3	21.2	21.6

was 0.99 mg and that of Macoma 1.57 mg, calculated from the mean sizes taken from pellets (Section 3.5.3). A 70% assimilation efficiency was assumed since both prey species have a high proportion of shell, making the assimilation of flesh more difficult. Feeding rates on Hydrobia were similar on the Ribble, although higher (3.2 min^{-1} in January) for Macoma (Greenhalgh 1975).

The estimated daily energy intake of Knot at Skinflats in daylight feeding only on Hydrobia is shown in Table 4.6a. The energy intake from Macoma over low water is given for comparison (Table 4.6b). By feeding in daylight only, the assimilated energy from a Hydrobia diet exceeds that assimilated by Redshank feeding in daylight and darkness (Section 4.1.1) and exceeds the estimated DEE of 3.3 x BMR described earlier in this section. However, if Macoma were the principal prey over low water (Table 4.6b), the intake would be considerably lower. Thus, if Knot are maximising their energy intake, they should concentrate their foraging efforts on Hydrobia as indicated by the results in Sections 3.5.3 and 3.6.2.

The effect of severe weather on energy intake

Since Knot feed by touch, a reduction in temperature should not affect their feeding success unless the mudflats are frozen. Freezing is very infrequent at mid-tidal levels where feeding is most intense (Section 3.6.2) and yet feeding rate is reduced at low temperatures (Goss-Custard, Jenyon et al 1977). This may be an energy saving behaviour to reduce energy expenditure in harsh weather but no data are available to substantiate this.

The winter survival of Knot

It is apparent that if Knot feed in daylight, principally on Hydrobia/

TABLE 4.6: Summary of the estimated daily energy intake of Knot feeding on (a) *Hydrobia* over the whole tidal cycle and (b) *Macoma* over low-tide in daylight only

	LOW TIDE (tide below Zone A)				EBB AND FLOW TIDES (Zones B and C)							
	Time (h) available for feeding	Biomass (g) ingested bird^{-1}	Assimilated energy kcal bird^{-1}	Assimilated energy kJ bird^{-1}	Time (h) available for feeding	Biomass (g) ingested bird^{-1}	Assimilated energy kcal bird^{-1}	Assimilated energy kJ bird^{-1}	Total assimilated energy (kcal bird^{-1})	Total assimilated energy (kJ bird^{-1})	Factor x BMR (Kendeigh)	Factor x BMR (Lasiewski and Dawson)
Jan	4.81	14.29	48.00	200.97	3.18	9.45	31.70	132.72	79.70	333.69	3.83	2.75
Feb	5.71	16.96	57.00	238.65	3.60	10.69	35.93	150.43	92.93	389.08	4.79	3.44
Mar	6.90	20.49	68.90	289.47	4.26	12.65	42.51	177.98	111.41	466.45	5.80	4.14
Apr	8.15	24.21	81.30	340.39	5.04	14.97	50.30	210.60	121.60	509.11	6.14	4.41
May	9.03	26.82	90.11	377.27	5.64	16.75	56.28	235.63	146.39	612.91	6.89	4.50
Jun	9.96	29.58	99.39	416.13	6.19	18.38	61.77	258.62	161.16	674.74	-	-
Jul	9.77	29.02	97.50	408.21	5.93	17.61	59.18	247.78	156.68	655.99	8.16	5.85
Aug	8.83	26.23	88.10	368.86	5.35	15.89	53.39	223.53	141.49	592.39	7.45	5.34
Sep	7.55	22.42	75.34	315.43	4.55	13.51	45.41	190.12	120.75	505.56	6.29	4.51
Oct	6.27	18.62	62.57	261.97	3.74	11.11	37.32	156.25	99.89	418.22	5.18	3.71
Nov	5.12	15.21	51.10	213.95	3.03	9.00	30.24	126.61	81.34	340.56	3.84	2.76
Dec	4.53	13.45	45.21	189.29	2.62	7.78	26.15	109.48	71.36	298.77	3.30	2.36

(a) HYDROBIA

LOW TIDE		
Biomass (g) ingested bird^{-1}	Total assimilated energy (kcal bird^{-1})	Total assimilated energy (kJ bird^{-1})
0.85	2.83	11.85
0,63	2.12	8.88
1.22	4.06	17.00
1.56	5.22	21.86
1.59	5.31	22.23
1.75	5.86	24.53
1.72	5.75	24.07
1.56	5.19	21.73
1.33	4.44	18.59
1.10	3.69	15.45
0.90	3.01	12.60
0.80	2.66	11.14

(b) MACOMA

Hydrobia and at the rates suggested above, then by feeding at mid-tidal levels where freezing of the mud is unlikely, they should experience little difficulty in obtaining their daily energy requirements (Fig 4.5). That their predicted energy intake exceeds that of Redshank suggests that they need to balance a higher energy expenditure. Knot are certainly more mobile, seeking areas of high prey density (Section 3.6.2) and at least sometimes flying long distances from feeding grounds to roost-sites (Pienkowski 1979). For example, the flight from Skinflats to Cramond Island, a known roost-site, is a distance of 26.5 km and would require an energy expenditure of about 8 kcals (83.5 kJ) (Tucker 1970) which is equivalent to approximately 10% of estimated daily energy intake. Without more work on time budgeting in various weather conditions, the energy expenditure cannot be judged but it is likely to be higher than that of Redshank which are more site-specific (Minton 1975) and do not appear to be so mobile (pers. obs).

The pattern of weight changes over the winter in Knot (Fig 4.5) is similar to that of Redshank although the levels of fat laid down are higher (cf. Fig 4.3). Since the cost of maintenance and transport of fat reserves is high, the benefits of laying down the reserves must be significant. As yet no time budgeting or other energetic studies have been undertaken to look at the effects of varying environmental conditions on energy requirements. However, it seems likely that the energy required to travel to the most profitable feeding areas increases in periods of adverse weather and that fat reserves will be required either to meet these costs or to supplement energy gained from feeding in less profitable areas during harsh conditions. They may also be required during the longer roosting/

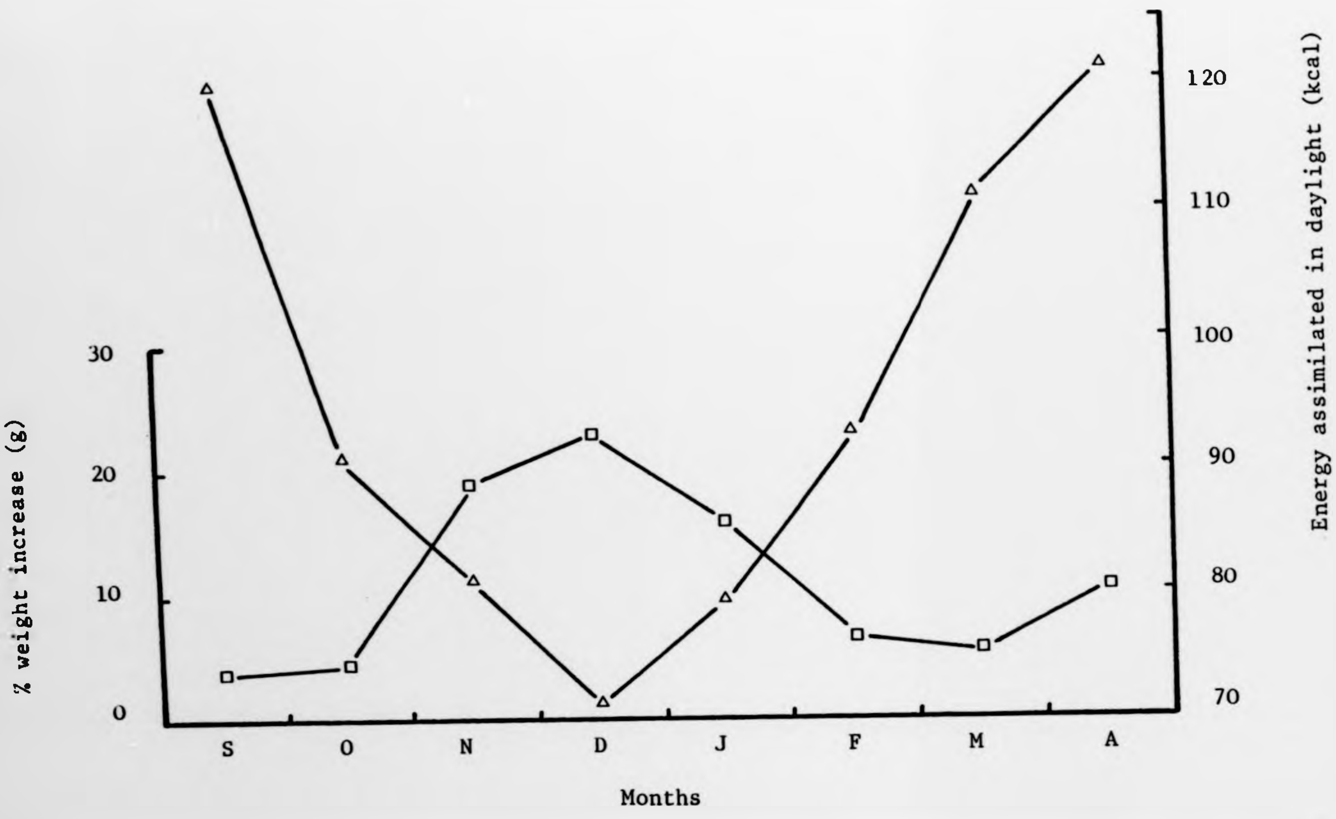


FIGURE 4.5: Weight changes (–□–) and predicted average daily assimilated energy (–△–) of Knot feeding in daylight in winter (weight data from the Wash – Minton 1975)

roosting period (compared with Redshank or Dunlin) on more distant roost-sites and thus have a short-term importance.

4.1.3 Dunlin

Basal Metabolic Rate (BMR) and Daily Energy Expenditure (DEE)

The monthly estimates of BMR from equations (1) and (3) are shown in Table 4.7.

Time spent Feeding

Dunlin spent most of the daylight hours available in winter actively feeding (Section 3.6.3). They fed at night (D.M.Bryant pers.comm) although the extent of night-feeding was not known. It was assumed that they fed for the same time period as Redshank since both species fed over HW neaps in cold weather (D.Waugh pers.comm, personal observation).

Energy Intake

No data were available concerning feeding rates of Dunlin or the proportion of each prey species taken.

Feeding rates on Nereis on the Ribble were estimated to be 4.7 min^{-1} (Greenhalgh 1975). When feeding on Hydrobia there was a high peck rate ($74.2 \pm 4.0 \text{ min}^{-1}$) and high success rate (80%) gave a capture rate of 59 Hydrobia min^{-1}. In the following calculations of energy intake a conservative intake rate of 30 min^{-1} was used at Skinflats, an estimate which may prove to be innaccurate.

There are no published data on the feeding rates of Dunlin on Macoma but these bivalves were not considered to be as important as Nereis and Hydrobia at Skinflats (Section 3.5.4).

The biomass of an average Hydrobia taken by Dunlin was 0.356 mg and/

TABLE 4.7. Mean body weights of Dunlin from the Firth of Forth

(after Pienkowski *et al* 1979)

MONTH	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Mean total wt(g)	55.3	54.0	55.5	-	-	-	-	-	50	52.5	56.7	59.5
BMR kcal day^{-1} (L & D)	14.01	13.77	14.05	-	-	-	-	-	13.02	13.49	14.27	14.78
BMR kcal day^{-1} (K)	9.96	9.79	9.99	-	-	-	-	-	9.25	9.59	10.15	10.51

and of an average Nereis 2.91 mg, determined from the mean sizes taken from pellets (Section 3.5.4). An 80% assimilation efficiency was assumed in all calculations of energy intake since Hydrobia are shelled animals, Nereis soft-bodied (see earlier this section).

Since the daily intake from Nereis and Hydrobia was unknown, two estimates of total daily intake were made. In the first, it was assumed that Nereis were taken exclusively over LT (tide below 3.1 m) and that Hydrobia were taken extensively on the ebb and flow tides in daylight. In the second, it was assumed that Nereis were taken exclusively during all daylight feeding. Night feeding was estimated on the assumption that only Hydrobia were consumed and that the same feeding regime existed as for Redshank (Section 4.1.1). Whilst it is accepted that the errors on these estimates of energy intake may be large, this method enabled a measure of the impact of Dunlin on their prey population to be made (Section 4.2).

The estimated energy intake by Dunlin feeding exclusively on Nereis is about 6% higher than when feeding on a mixed diet of Nereis and Hydrobia (Table 4.8). The DEE of 3.3 x BMR predicted from King (1974) (see earlier) is not balanced in daylight during the winter months. However, by feeding at night on Hydrobia (Table 4.9), the total predicted energy intake exceeds this estimate in all months except December, when day length is short.

The winter survival of Dunlin

The mean monthly weights of Dunlin on the Firth of Forth (Fig 4.6) are larger than those from areas with higher mean winter temperatures (Pienkowski et al 1979). The pattern of weight change is similar to that found on the Wash (Minton 1975) but the higher weights are maintained for longer on the Forth, suggesting that/

TABLE 8.2: The estimated energy intakes of Dunlin in daylight

	LOW TIDE (tide below zone A) NEREIS				EBB and FLOW TIDES (Zones B-D) - Alternative Prey								NEREIS (LT) + HYDROBIA (EBB AND FLOW)				NEREIS ONLY			
					(a) HYDROBIA				(b) NEREIS											
	Time (h) available for feeding	Biomass (g) ingested bird^{-1}	Assimilated energy kcal bird^{-1}	Assimilated energy kJ bird^{-1}	Time (h) available for feeding	Biomass (g) ingested bird^{-1}	Assimilated energy kcal bird^{-1}	Assimilated energy kJ bird^{-1}	Time (h) available for feeding	Biomass (g) ingested bird^{-1}	Assimilated energy kcal bird^{-1}	Assimilated energy kJ bird^{-1}	Total assimilated energy (kcal bird^{-1})	Total assimilated energy (kJ bird^{-1})	Factor x BMR (Kendeigh)	Factor x BMR (Lasiewski & Dawson)	Total assimilated energy (kcal bird^{-1})	Total assimilated energy (kJ bird^{-1})	Factor x BMR (Kendeigh)	Factor x BMR (Lasiewski & Dawson)
SEP	7.55	6.19	21.60	90.42	5.62	3.60	13.83	57.89	5.62	4.61	16.09	67.35	35.43	148.31	3.83	2.72	37.69	157.77	4.07	2.89
OCT	6.27	5.15	17.90	74.93	4.69	3.01	11.54	48.31	4.69	3.85	13.43	56.22	29.44	123.24	3.07	2.18	31.33	131.15	3.27	2.32
NOV	5.12	4.20	14.70	61.53	3.78	2.42	9.30	38.93	3.78	3.10	10.82	45.29	24.00	100.46	2.36	1.68	25.52	106.83	2.51	1.79
DEC	4.53	3.72	13.00	54.42	3.41	2.19	8.39	35.12	3.41	2.80	9.76	40.86	21.39	89.54	2.04	1.45	22.76	95.27	2.17	1.54
JAN	4.81	3.95	13.77	57.64	3.93	2.52	9.67	40.48	3.93	3.23	11.25	47.09	23.44	98.12	2.35	1.67	25.02	104.73	2.51	1.79
FEB	5.71	4.69	16.34	68.40	4.34	2.78	10.68	44.71	4.34	3.56	12.42	51.99	27.02	113.11	2.51	1.96	28.76	120.39	2.94	2.09
MAR	6.90	5.66	19.75	82.67	5.25	3.36	12.92	54.08	5.25	4.31	15.03	62.92	32.67	136.76	3.27	2.33	34.78	145.59	3.48	2.48

TABLE 4.9: The estimated energy intake of Dunlin (a) at night and the estimated total daily intake (b) if feeding on <u>Nereis</u> and <u>Hydrobia</u> in daylight and (c) if feeding on <u>Nereis</u> only in daylight

(a)

	NIGHT FEEDING - HYDROBIA			
	Time (h) available for night feeding	Biomass ingested bird^{-1}	Assimilated energy kcal bird^{-1}	Assimilated energy kJ bird^{-1}
OCT	1.92	1.23	4.73	19.80
NOV	7.06	4.52	17.38	72.75
DEC	7.63	4.89	18.78	78.61
JAN	7.35	4.71	18.08	75.68
FEB	6.54	4.19	16.10	67.39
MAR	1.77	1.13	4.35	18.21

(b)

DAY FEEDING ON NEREIS AND HYDROBIA + NIGHT FEEDING			
Assimilated energy kcal bird^{-1} day + night	Assimilated energy kJ bird^{-1} day + night	Factor x BMR (Kendeigh)	Factor x BMR (Lasiewski & Dawson)
34.17	143.04	3.56	2.53
41.38	173.22	4.08	2.90
40.17	168.15	3.82	2.72
41.52	173.80	4.17	2.96
43.12	180.50	4.40	3.13
37.02	154.97	3.71	2.63

(c)

DAY FEEDING ON NEREIS ONLY + NIGHT FEEDING			
Assimilated energy kcal bird^{-1} day + night	Assimilated energy kJ bird^{-1} day + night	Factor x BMR (Kendeigh)	Factor x BMR (Lasiewski & Dawson)
36.06	150.95	3.76	2.67
42.90	179.58	4.23	3.01
41.54	173.89	3.95	3.95
43.10	180.42	4.33	3.08
44.86	187.78	4.58	3.26
39.13	163.80	3.92	2.79

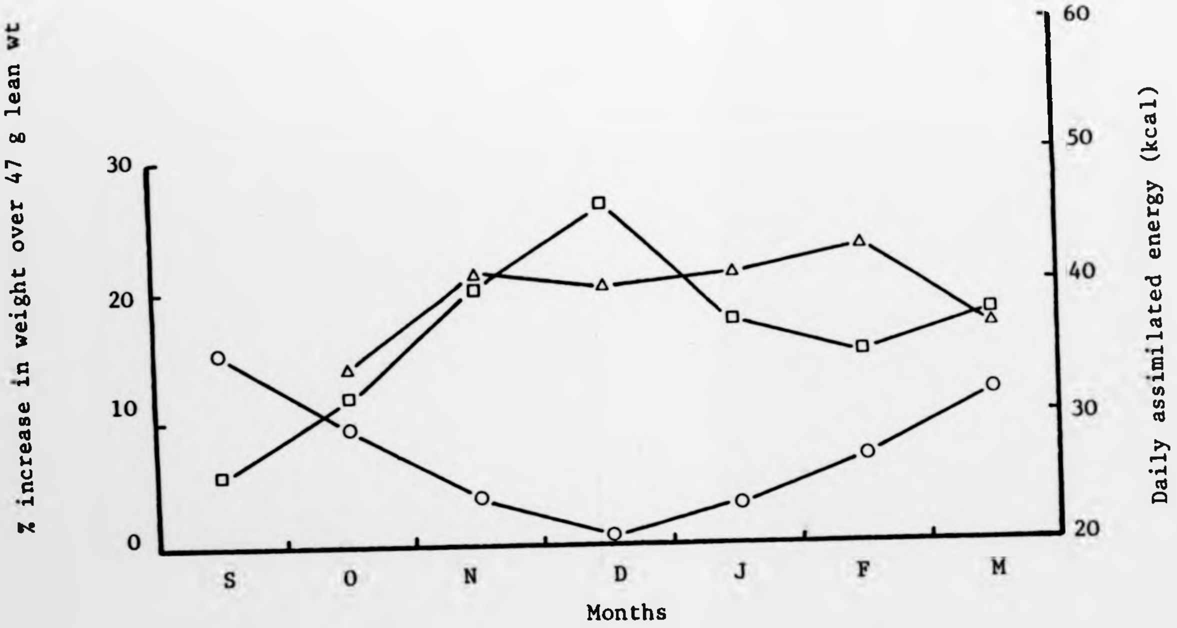


FIGURE 4.6: Weight changes (□) and predicted average daily assimilated energy of Dunlin feeding in daylight on *Nereis* and *Hydrobia* (○) and in both daylight and darkness (△)

that the fat reserves are required as an insurance for a longer period. The potential daily energy intake, including night feeding, similarly remains high (Fig 4.6) unlike the energy intake for Redshank which falls considerably between February and March (Fig 4.3). The probability of Dunlin being found dead on the Wash was found to be lower than for Redshank (Goss-Custard, Jenyon et al 1977c) and on the Forth the ratio of the % total population of Redshank: Dunlin found dead increased from a mean of 0.77 during 1976/77 and 1977/78 winters to 3.51 in the severe winter of 1978/79 (D.M. Bryant pers. comm). Thus, there is indirect evidence that Dunlin are better adapted to surviving adverse conditions. Assuming that Hydrobia only are eaten by both species in severe weather in December, Dunlin would only suffer a decrease of 9% of their daylight energy intake, compared to mild conditions, whereas Redshank would suffer a 20.7% reduction (Section 4.1). In late winter, when Dunlin weights are high and Redshank weights are declining, this could be a serious reduction, particularly if Redshank are unable to employ energy saving behaviours.

4.1.4 Curlew

Basal Metabolic Rate (BMR) and Daily Energy Expenditure (DEE)

The monthly estimated of BMR from equations (1) and (3) are shown in Table 4.10.

Time spent feeding

Since Curlew feed mainly by day in both intertidal and inland habitats (Burton 1974), it was assumed that, at Skinflats, feeding took place when the tide was below 4.7 m (Zone C) in daylight only.

Energy intake

Sight-feeding/

TABLE 4.10: Mean body weights of Curlew from the Wash (Minton 1975) and estimated BMR

MONTH	NOV	DEC	JAN	FEB	MAR
mean total monthly body wt (g)	832	860	840	830	923
BMR (L & D) k cal day^{-1}	100.3	102.73	101.0	100.12	108.2
BMR (K) k cal day^{-1}	73.02	74.81	73.53	72.89	78.8

Sight-feeding Curlew at Skinflats took, on average, 2.6 items min^{-1} (Section 3.5.5). All prey items taken were assumed to be Nereis to simplify the following calculations.

Nereis virens has not been recorded from Skinflats and so the mean biomass of N. diversicolor taken at Skinflats was assumed to be similar to that estimated from the gizzard contents of a Curlew collected at Kinneil ($\bar{x}$ = 30 mg) (Section 3.5.5). A 90% assimilation efficiency was assumed since worms are soft-bodied.

The estimated energy intake in daylight was equivalent to 1.76 x BMR (Kendeigh) in December and 2.6 x BMR in March from feeding only on the mudflats (Table 4.11a). During the winter months, however, fewer than 20% of the population at Skinflats feed on the mudflats (Moffat 1975), the majority feeding on the adjacent fields. Even those birds on the mudflat fed only during the period 3 to 1 h before HT on springs and 1½ - 5 h after HT on neaps. Feeding on earthworms on the fields would appear to be more profitable and the low intake from the mudflats could account for the increased usage of the fields.

Curlew feeding at a similar rate in the more marine parts of the estuary on N. virens would be able to obtain their energy requirements from the estuary alone (Table 4.11b), assuming a DEE of 3.3 x BMR , although studies on the Tees Estuary (D. Townshead in press) suggest that only female Curlew, with their long bills, can exploit these large Nereis. If male Curlew are unable to feed on N. virens and cannot achieve an energy balance from feeding on N. diversicolor, this would account for the extensive use of inland fields by the males.

TABLE 4.11: Estimated energy intake of Curlew in daylight if feeding on (a) <u>Nereis diversicolor</u> and (b) <u>Nereis virens</u> in bays further down the Forth estuary

	LOW TIDE (TIDE BELOW 3.1m)				EBB and FLOW TIDES (Tide between 3.1 and 4.7m)				Total energy assimilated in daylight kcal bird^{-1}	Total energy assimilated in daylight kJ bird^{-1}	Factor x BMR (Kendeigh)	Factor x BMR (Lasiewski & Dawson)
	Time (h) available for feeding	Biomass (g) ingested bird^{-1}	Assimilated energy kcal bird^{-1}	Assimilated energy kJ bird^{-1}	Time (h) available for feeding	Biomass (g) ingested bird^{-1}	Assimilated energy kcal bird^{-1}	Assimilated energy kJ bird^{-1}				
Jan	4.81	22.51	88.34	396.8	3.18	14.88	58.40	244.4	146.74	641.2	2.06	1.45
Feb	5.71	26.72	104.85	438.9	3.6	16.85	66.11	276.7	170.96	715.6	2.35	1.71
Mar	6.90	32.29	126.72	530.4	4.26	19.94	78.23	327.5	204.95	857.9	2.60	1.89
Apr	8.15	38.14	149.67	626.5	5.04	23.59	92.56	387.4	242.23	1014.0	3.25	-
May	9.03	42.26	165.87	694.3	5.64	26.40	103.57	433.6	269.44	1127.9	3.61	-
Jun	9.96	46.61	182.88	765.5	6.19	28.97	113.67	475.8	296.55	1241.4	3.97	-
Jul	9.77	45.72	179.46	751.2	5.93	27.75	108.89	455.9	288.35	1207.0	3.86	-
Aug	8.83	41.32	162.18	678.9	5.35	25.04	98.25	411.3	260.43	1090.2	3.49	-
Sep	7.55	35.33	138.69	580.6	4.55	21.30	83.17	348.1	221.86	928.7	2.97	-
Oct	6.27	29.34	115.2	482.2	3.74	17.50	68.68	287.5	183.88	769.7	2.46	-
Nov	5.12	23.96	94.05	393.7	3.03	14.18	55.64	232.9	149.69	626.6	2.05	1.49
Dec	4.53	21.20	83.16	348.1	2.62	12.26	48.12	201.4	131.28	549.5	1.76	1.28

(a)

Assimilated energy from N virens over LW kcals bird^{-1}	Assimilated energy from N virens over LW kJ bird^{-1}	Factor x BMR (Kendeigh)	Factor x BMR (Lasiewski & Dawson)
431.84	1807.7	5.87	4.27
512.64	2144.4	7.03	5.12
619.48	2593.2	7.86	5.73
731.71	3063	-	-
810.71	3394	-	-
894.20	3743.2	-	-
877.15	3671.8	-	-
792.76	3318.5	-	-
677.84	2837.4	-	-
562.92	2356.3	-	-
459.70	1924.2	6.30	4.5
406.70	1702.5	5.44	3.96

(b)

4.2 The Impact of Waders and Shelduck on the Production Ecology of Invertebrates at Skinflats

Since 1969, when the Birds of Estuaries Enquiry was launched by the BTO and RSPB, monthly spring high-tide numbers of waders and wildfowl have been recorded at all sites on the Forth estuary (D.M.Bryant unpubl.). The mean highest monthly counts of the regular visitors between 1969 and 1976 (Table 4.12) show that Shelduck, Redshank, Knot and Dunlin are the most numerous. The numbers refer to roosting birds and do not necessarily represent those feeding at Skinflats. Curlew, for example, feed mainly on the fields adjacent to the mudflat (Moffat 1975) and Dunlin largely feed at Kinneil mudflat over the low-water period (Bryant 1976, 1978). The presence of a small number of Oystercatchers throughout the year indicates that these may be juvenile non-breeding individuals. Redshank, Knot and Dunlin are present in large numbers during the autumn and spring passages and in winter but few occur at Skinflats in the summer.

Grey and Golden Plover generally feed on the mud at Skinflats only when the surrounding fields are frozen. The number present from 1969 - 1976, therefore, fluctuated considerably in winter, presumably depending on local environmental conditions. The populations of Redshank, Shelduck, and Dunlin remained fairly constant from year to year, however, with only a small increase in Shelduck and a decrease in Dunlin numbers, but the occurrence of Knot was less predictable (D.M.Bryant unpubl.). Between 1970 and 1979 large flocks were generally found at Skinflats during the winter but in 1976 - 1977 numbers were low. In the mild winter of 1979 - 80 few visited Skinflats, although the total population of the Firth of Forth was similar to previous years (Bryant 1980). The impact of individual bird species on the invertebrate fauna will/

TABLE 4.12: Average monthly populations of waders at Skinflats, 1969-76 . (BOE enquiry data)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Shelduck	1028	650	288	208	74	19	6	13	121	300	351	1176
Redshank	1039	864	909	741	72	58	84	886	1055	765	625	1163
Knot	16667	1347	1633	568	14	0	18	21	39	130	3283	11166
Dunlin	5612	4990	2562	1932	940	13	81	867	1279	2038	1257	5142
Curlew	225	317	186	63	21	0.5	170	109	410	183	210	267
Oystercatcher	15	11	38	17	40	18	11	27	45	16	55	26
Grey Plover	6	33	13	0.3	2	0	0	0.7	67	85	5	14
Golden Plover	313	866	162	15	0	0	48	517	1667	1304	189	127
Bar-tailed Godwit	8	0	7	8	7	0	0	9	41	25	3	29

will thus vary between years.

Gut and pellet analyses (Section 3.5) indicate that *Hydrobia*, *Nereis* and *Macoma* are the most important prey of overwintering birds at Skinflats. Birds such as Oystercatcher with a preference for *Cardium* and *Mytilus*, and Turnstone with their principal diet of *Littorina* and *Gammarus* were more common at other sites on the Forth (Bryant 1976). Curlew were more numerous at Torry Bay where the range of prey species was wider (Section 3.5.5) and Bar-tailed Godwit were more common at sites where they could feed at the edge of the tide below mid-tidal levels. At Skinflats this was not possible as most of the area lies above mid tide.

It was outwith the scope of the present study to assess the impact of overwintering birds on the invertebrates in different areas of Skinflats. However, the areas of highest feeding intensity of Redshank, Knot, Dunlin and Shelduck on an average 12.5 h tide (Mean of 8 observation periods) show where predation pressure is highest (Figs 4.7 - 4.10). The increase in feeding intensity upshore results from many birds feeding in a small area around high tide but the habitat partitioning seen over low tide (Section 3.6) is still evident. Redshank feeding intensity is concentrated upshore, Knot and Shelduck downshore, with Dunlin feeding intensity more evenly spread over the area.

Of the principal prey species taken at Skinflats, *Hydrobia* is the most widespread and numerous. Excluding oligochaetes, small polychaetes and the patchily distributed *Corophium*, it is also the most productive species, producing 3.9 gm^{-2} yr^{-1} from a $\bar{B}$. of 3.32 gm^{-2} (Section 3.3.5). The size classes taken by Redshank and Knot overlap considerably but the spatial separation of the two species ensures that the predation pressure on these 1+ age class individuals is not concentrated in only one/

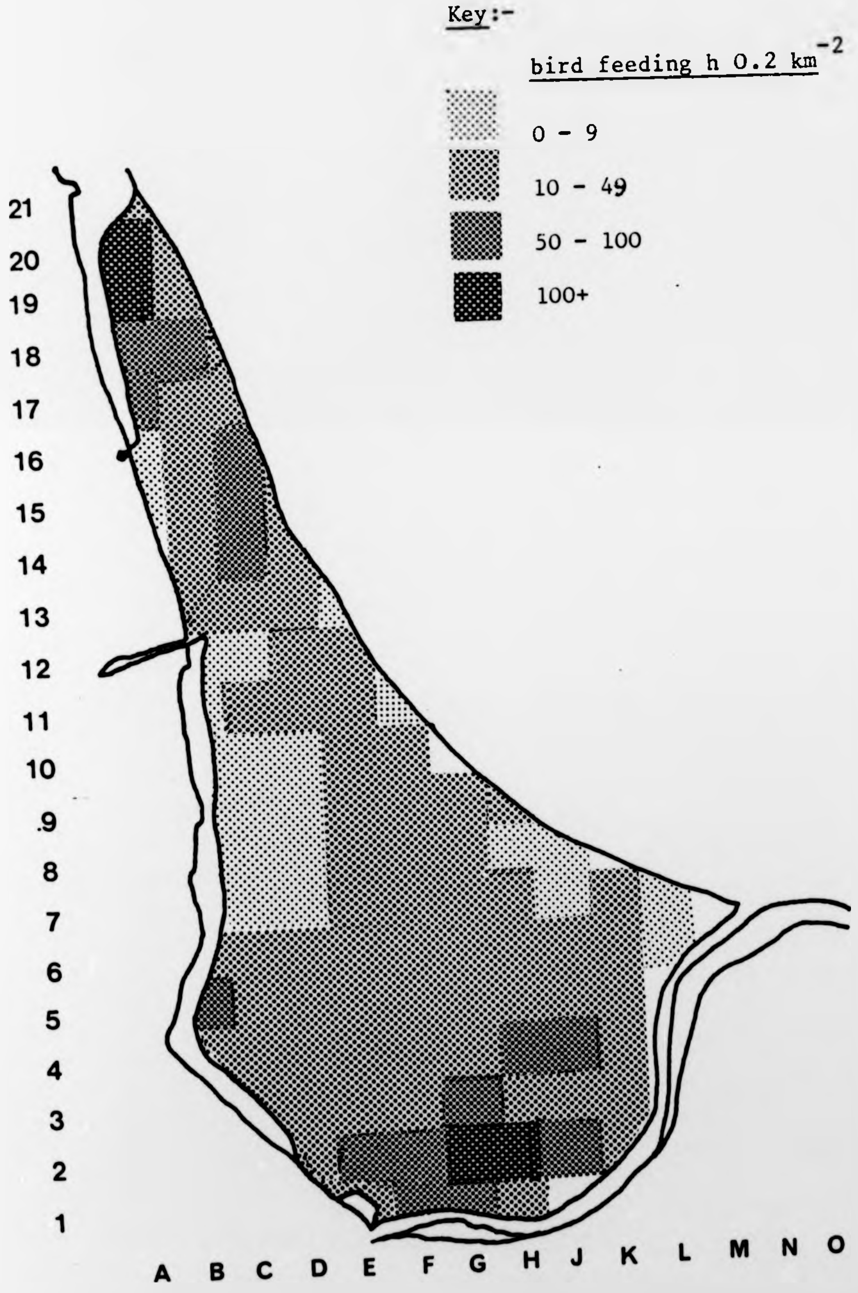


FIGURE 4.7: The average number of Redshank feeding hours per tidal cycle during the 1976/77 winter at Skinflats

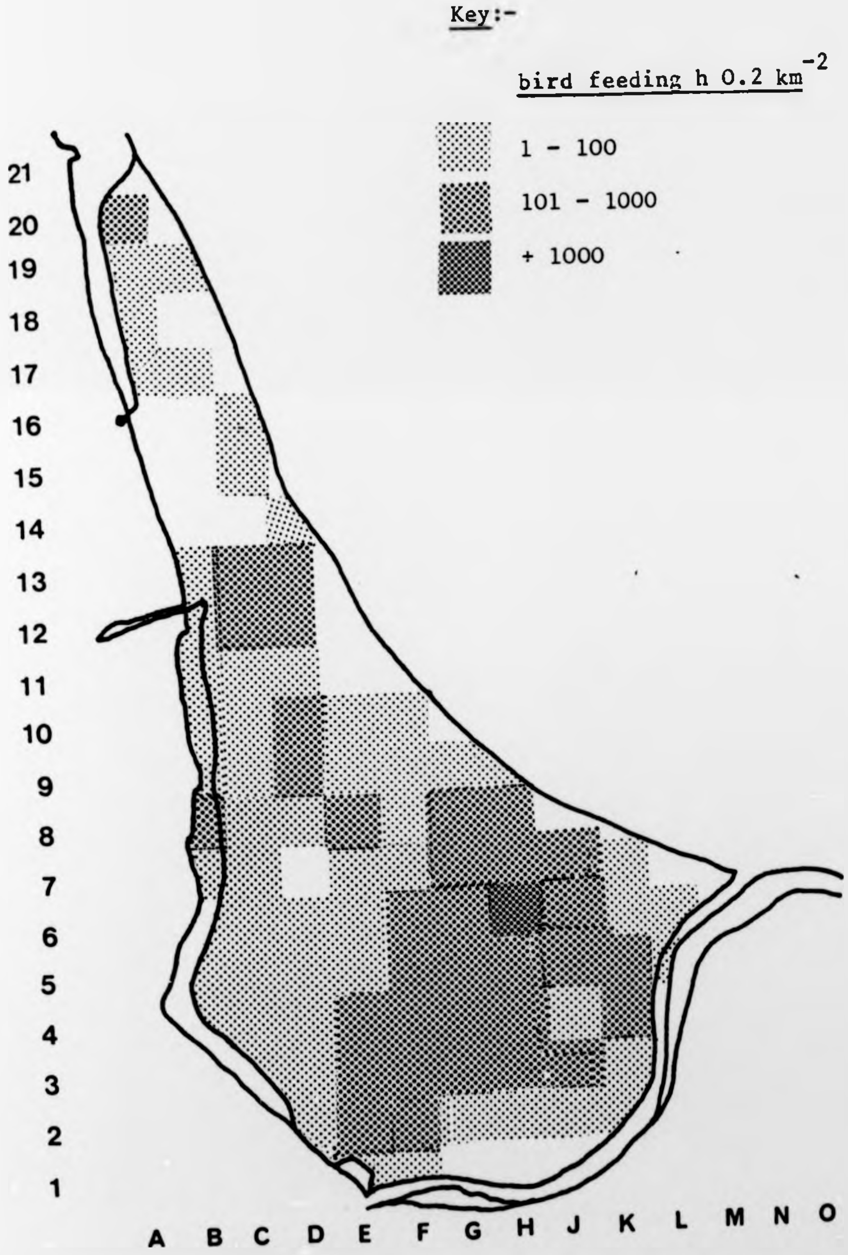


FIGURE 4.8: The average number of Knot feeding hours per tidal cycle during the 1976/77 winter at Skinflats

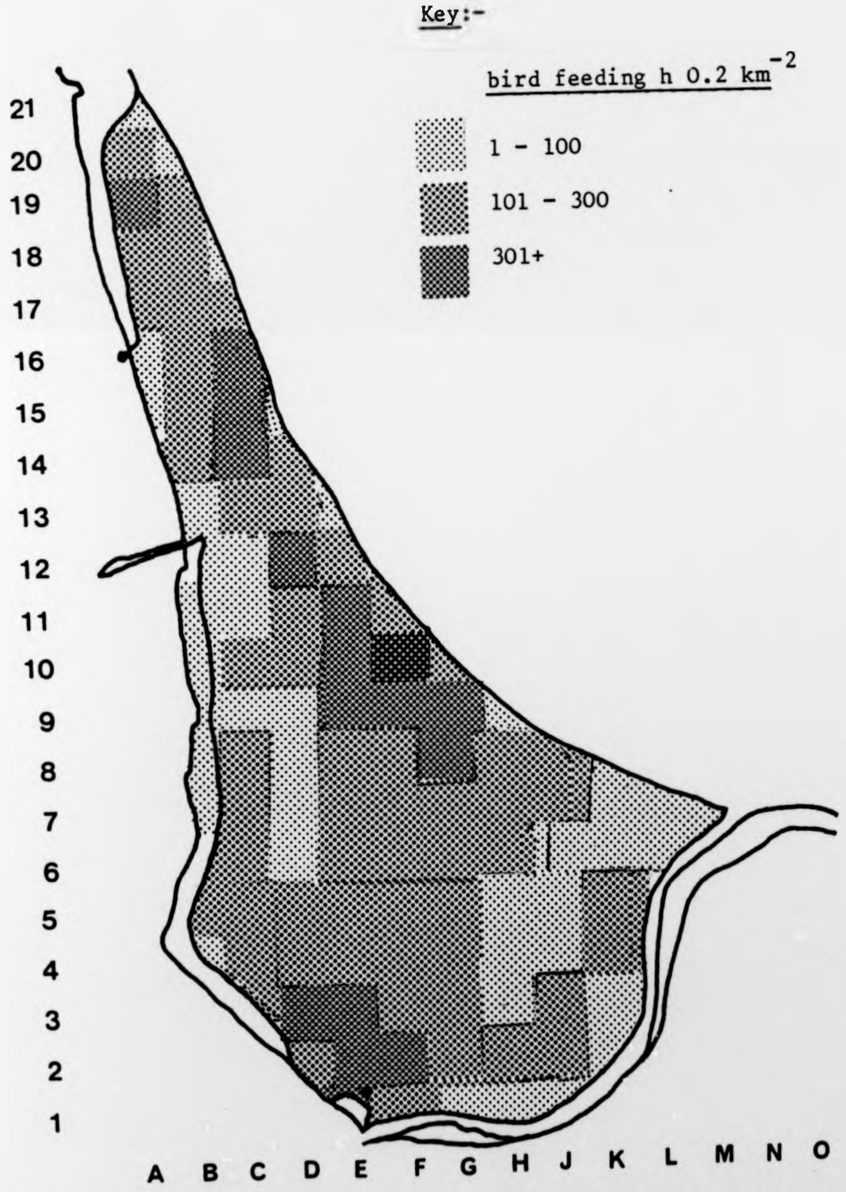


FIGURE 4.9: The average number of Dunlin feeding hours per tidal cycle during the 1976/77 winter at Skinflats

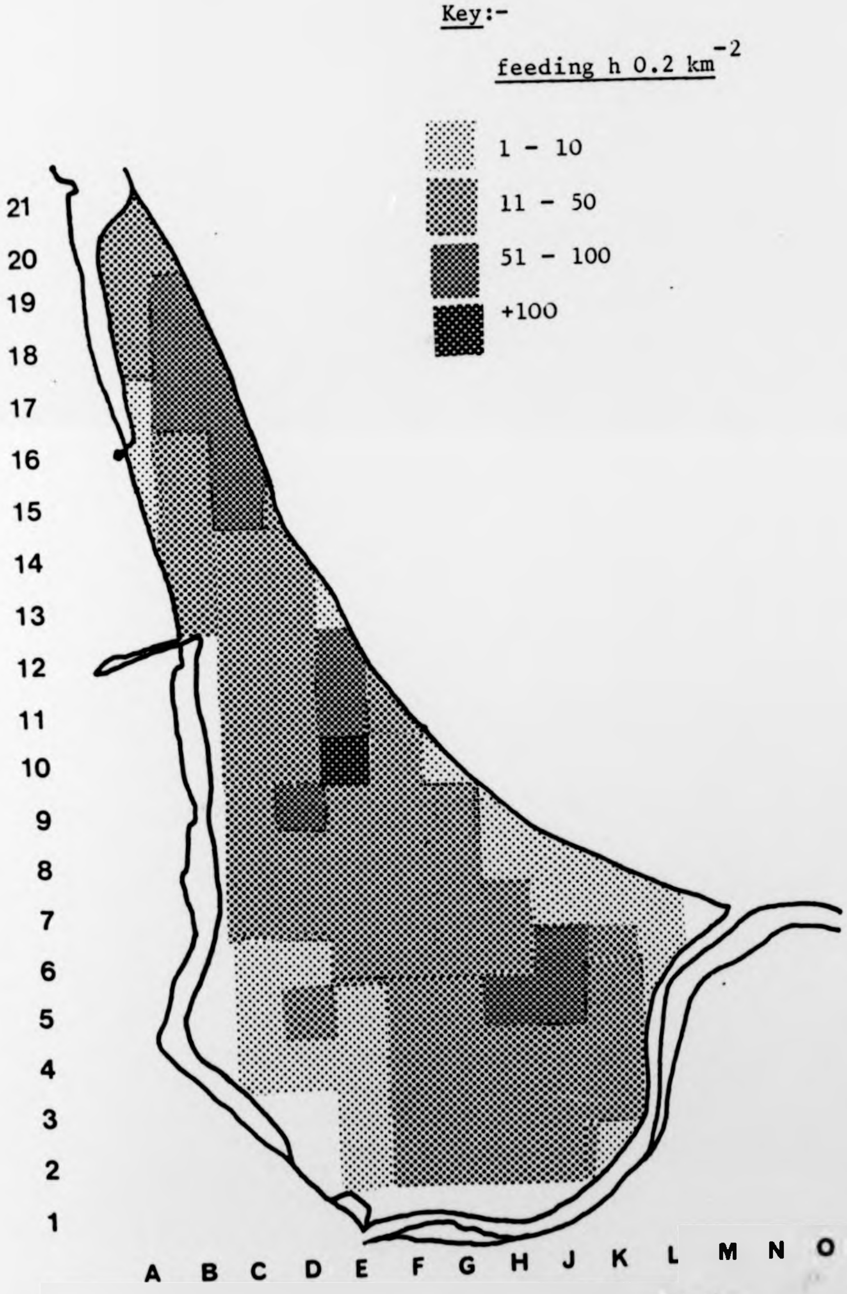


FIGURE 4.10: The average number of Shelduck feeding hours per tidal cycle during the 1976/77 winter.

one area (Section 3.6). Dunlin take smaller items and thus are not in competition when feeding in areas frequented by either Knot or Redshank.

That Hydrobia are common to the diets of all four bird species may in part reflect its availability. The snails are all found within the top 4 cm and most occur in the top 2 cm (Vader 1964). At low temperatures they appear to be the only prey available to Redshank (Section 3.5.2 iii) and are thus an important resource in all environmental conditions. There is also no evidence that the condition of Hydrobia decreases in winter (Section 3.3.4) with the result that the biomass ingested per individual snail will not vary with season. In contrast, a decrease in biomass of 40 - 50% occurs in individual Macoma from spring to winter (Elliott 1979) which will influence the amount of food ingested per bivalve by a bird predator.

The impact of Redshank predation on their prey

Throughout the present investigation, Redshank and Hydrobia have been studied in most detail. The impact of Redshank predation on the population of Hydrobia at Skinflats is thus treated fully in the following discussion to illustrate how such relationships may be explored. The impact of Redshank on Macoma and Nereis together with the impact of the other bird predators on their prey populations is modelled on this method but is treated in less detail.

The preferred sizes of Hydrobia taken by Redshank were of the 1+ age class. This cohort produced 1.421 g AFDW m^{-2} y^{-1} from a mean annual biomass of 2.436 gm^{-2} and was thus less productive than the 0+ age class (Section 3.3.5). The proportion of the Redshank diet consisting of Hydrobia varied with tidal state and environmental conditions/

conditions (Section 3.5.2), although in the following analysis it is assumed, for simplicity, that all days were milder than 4°C.

The proportion of the total annual mortality (Section 3.3.4d) of Hydrobia attributable to Redshank predation (Table 4.13) was calculated on a monthly basis. The feeding population out of the study period (Nov - Mar) was estimated from counts made by D.M.Bryant (unpubl.) and from BOE data. The annual predation pressure was calculated by summing the product of the monthly population density and the energy obtained from Hydrobia per bird each month (Section 4.1) Of the 20.05 kcals (83.93 kJ)m^{-2} removed annually from the 1+ age class of Hydrobia at Skinflats, 1.48 kcals (6.2 kJ)m^{-2} were taken by the Redshank population (7.4%). The highest proportion of the monthly mortality estimates taken by Redshank was in September (41%) and October (33%), when migrant passage birds were feeding at Skinflats (Table 4.13). The contribution by Redshank to the total Hydrobia mortality during the winter months was small.

The production of all age classes of Hydrobia at Skinflats (3.9 g AFDW m^{-2}) was equivalent to 18.72 kcals (78.36 kJ) m^{-2} and thus 7.9% was accounted for in terms of predation by Redshank. In terms of the standing crop (annual $\bar{B}$ = 3.32 gm^{-2} = 15.9 kcals), this is equivalent to 9.3%.

The production of Macoma and of Nereis was calculated over a thirteen month period. During this time the Macoma population produced 0.748 gm^{-2} (3.57 kcal, 14.9 kJ) from a $\bar{B}$ of 1.29 gm^{-2} (6.19 kcals, 25.9 kJ), the Nereis population 1.07 gm^{-2} (4.67 kcals, 19.53 kJ) from a $\bar{B}$ of 0.355 gm^{-2} (1.55 kcals, 6.48 kJ). The amount of energy required annually from Macoma by the Redshank population was 0.541 kcals (2.26 kJ) m^{-2} and 1.69 kcals (7.07 kJ)m^{-2} from Nereis (Table 4.13). Thus,

Redshank/

TABLE 4.13: Annual impact of Redshank predation on Hydrobia Macoma and Nereis populations

	Feeding population of Redshank at Skinflats	Energy in kcal m^{-2} (kJm^{-2}) obtained from Hydrobia	Total energy kcal m^{-2} (kJm^{-2}) lost from 1+ age class of Hydrobia population	Proportion (%) of Hydrobia mortality due to Redshank predation	Energy in kcal m^{-2} (kJm^{-2}) obtained from Macoma	Energy in kcal m^{-2} ($kJ\ m^{-2}$) obtained from Nereis
Jul ^{o}	84	0.02 (0.08)	-	-	0.01 (0.04)	0.04 (0.17)
Aug ^{1}	455	0.08 (0.33)	-0.72 (- 3.01)	11.0	0.06 (0.25)	0.18 (0.75)
Sep ^{1}	1000	0.14 (0.59)	-0.34 (- 1.23)	41.0	0.11 (0.46)	0.33 (1.38)
Oct ^{1}	1000	0.22 (0.92)	-0.65 (- 2.72)	33.0	0.09 (0.38)	0.29 (1.21)
Nov *	571	0.23 (0.96)	-4.16 (-17.41)	5.5	0.04 (0.17)	0.13 (0.54)
Dec *	343	0.15 (0.63)	+2.43 (+10.17)	-	0.02 (0.08)	0.07 (0.29)
Jan *	532	0.24 (1.00)	-8.37 (-35.04)	2.8	0.04 (0.17)	0.12 (0.50)
Feb *	342	0.21 (0.88)	-3.07 (-12.85)	6.8	0.03 (0.13)	0.08 (0.33)
Mar *	389	0.07 (0.29)	-0.65 (- 2.72)	10.8	0.04 (0.17)	0.12 (0.50)
Apr ^{o}	741	0.11 (0.46)	-3.54 (-14.82)	3.1	0.09 (0.38)	0.27 (1.13)
May ^{1}	10	0.002 (0.008)	+0.61 (+ 2.55)	-	0.001 (0.004)	0.03 (0.13)
Jun ^{o}	58	0.01 (0.04)	-1.59 (- 6.66)	0.6	0.01 (0.04)	0.03 (0.13)
TOTAL		1.482 (6.20)	-20.05 (-83.93)	Mean 7.4%	0.541 (2.26)	1.69 (7.07)

* Mean number of feeding birds counted in the present study

^{o} BOE enquiry HT counts

^{1} Feeding bird counts - D M Bryant

Redshank predation accounted for approximately 16% of the annual *Macoma* production and 9.5% of the annual $\bar{B}$. Of the *Nereis* population 39% was predated by Redshank, 23% of the annual $\bar{B}$. This impact on the *Nereis* population was most likely an overestimation since large *Nereis* dwelling deeper than 10 cm were taken by Redshank but were not adequately sampled (Section 3.4.2).

Although most of the size classes of *Nereis* taken by Redshank were only available when present in the upper portions of their burrows (Section 3.4.4v), 81 - 88% of the *Macoma* population was potentially available to Redshank in the top 4 cm (Section 3.4.2v). However, at low temperatures very few *Macoma* were taken, indicating that their activity and hence availability decreases in these conditions.

The impact of Redshank predation on the other prey species such as *Carcinus*, *Cardium* and small worms (Section 3.5.2) remained unknown.

The impact of Knot predation on their prey

As the relative contribution of *Hydrobia* and *Macoma* to the diet of Knot was not known, it was assumed, for simplicity, that *Hydrobia* was the only prey taken at Skinflats. Although undoubtedly erroneous, this enabled a maximum predation pressure estimate of Knot on *Hydrobia* to be made by two methods: (a) Assuming the same feeding rates as described in Section 4.1, a total of 5.19 kcals (21.73 kJ)m^{-2} would be removed annually from the 1+ age class of *Hydrobia* (Table 4.14);
(b) The daily energy requirement of a Knot is taken to be the same as that of Redshank, ie average 3.36 x BMR, then 3.99 kcals (16.70 kJ)m^{-2} would be removed. Taking the latter estimate, the predation pressure was highest between February and March (Table 4.14) and depending on method of/

TABLE 4.14: Annual energy requirements of Knot at Skinflats and impact of predation on Hydrobia

	Feeding population of Knot at Skinflats	Bird days per month (neap tides)	Estimate from feeding rate data		Estimate from daily energy requirement data		
			Total energy intake bird^{-1} (kcal) 70% assimilation efficiency	Energy (kcals) removed m^{-2} from the mudflat	Energy required bird^{-1} assuming D = 3.36 x BMR (Kendeigh)	Energy removed m^{-2} by population	The proportion of the 1+ age class Hydrobia mortality predated
Jul^{o}	18	279	223.83	0.02	92.16	0.007	-
Aug^{1}	3	46	202.13	0.002	91.20	0.001	0.1
Sep^{1}	1	15	172.50	negligible	92.16	0.0004	0.1
Oct^{1}	250	3875	142.70	0.14	92.64	0.094	14.5
Nov*	1077	16155	116.20	0.49	101.76	0.430	10.3
Dec*	1129	17500	101.94	0.47	103.68	0.475	-
Jan*	3252	50406	113.86	1.50	99.84	1.317	15.7
Feb*	3252	45528	132.76	1.58	93.12	1.110	36.1
Mar*	929	14400	159.16	0.60	92.16	0.347	53.3
Apr^{o}	568	8520	173.71	0.39	95.04	0.212	6.0
May^{1}	0	0	-	0	-	0	0
Jun^{o}	0	0	-	0	-	0	0
			Total	5.19 kcals m^{-2} (21.73 kJ)		3.99 kcals m^{-2} (16.72 kJ)	

* Mean number of feeding birds counted in the present study

o BOE enquiry HT counts

1 Feeding bird counts - D.M.Bryant

of calculation, could annually remove between 21% and 28% of the production of Hydrobia, 25 - 33% of the annual $\bar{B}$. This is most likely to be an overestimate since Macoma will undoubtedly be taken when encountered, particularly over the low-water period.

Knot feeding intensity per tidal cycle was concentrated in the area around stations A_4 and A_5 (Fig 4.8) and thus predation pressure would have been high in this area, where the abundance of Hydrobia was also high (Section 3.6.2). During the winter of 1976-77, Knot regularly visited Skinflats but few fed there in 1977-78 winter. The biomass of Hydrobia had decreased from 8.35 gm^{-2} to 2.22 gm^{-2} in these comparable periods and it has been suggested (Section 3.6.2) that the low density of Hydrobia in 1977-78 contributed to the scarcity of Knot at Skinflats. The high predation pressure by Knot in comparison to Redshank further indicates that the low biomass of Hydrobia over the whole mudflat, and around A_4 and A_5 in particular, could have been insufficient to attract the dense feeding flocks of Knot in the 1977-78 winter.

The impact of Dunlin predation on their prey

Pellet and gut analysis (Section 3.5.4) indicate that Dunlin take a variety of prey but predominantly Nereis and Hydrobia. The extent to which oligochaetes and other small worms contribute to the diet could not be estimated. Assuming an energy requirement of 3.36 x BMR per bird per day, the amount taken by Dunlin was estimated at 4.93 kcals (20.64 kJ)m^{-2} yr^{-1} (Table 4.15). The entire production of Nereis occurring in the top 10 cm of sediment over thirteen months was only 4.67 kcals (19.53 kJ)m^{-2}, the annual $\bar{B}$ 1.43 kcals m^{-2}. However, many Dunlin feeding at Skinflats will also have spent some of the tidal cycle at Kinneil (Section 3.6.3) and thus the amount of food required from/

TABLE 4.15: Annual energy requirements of Dunlin at Skinflats

	Feeding population of Dunlin at Skinflats	Bird days per month	Total energy (kcal) required by the population x 10^3 Assuming an 80% assimilation efficiency	Energy (kcal) required m^{-2} by Dunlin population
Jul	81[o]	2511	97.6	0.03
Aug	230[1]	7130	277.0	0.007
Sep	1000[1]	30000	1165.5	0.31
Oct	1750[1]	54250	2185.1	0.57
Nov	3061*	91830	3914.7	1.02
Dec	1368*	42408	1872.0	0.49
Jan	2050*	63550	2658.4	0.69
Feb	2050*	57400	2360.2	0.62
Mar	1626*	50406	2114.9	0.55
Apr	1932[o]	57960	2251.7	0.59
May	150[1]	4650	180.7	0.05
Jun	13[o]	390	15.2	0.004

Total 4.931

* Mean number of feeding birds counted in the present study

[o] BOE enquiry HT counts

[1] Feeding bird counts - D M Bryant

from Skinflats may be an overestimate. Taking the production of Hydrobia and Nereis together, Dunlin could account for a maximum of 21% of their combined annual production.

The impact of Curlew predation on their prey

Of the total roosting population at Skinflats (Table 4.16) only a maximum of 20% fed on the mudflats (Moffat 1975), the remainder feeding on the fields adjacent to the mudflat. The energy taken during mudflat feeding (Section 4.1) was estimated to be 0.732 kcal (3.06 kJ)m^{-2} y^{-1} (Table 4.16) which, if derived entirely from the Nereis population (Section 3.3.5) was equivalent to 17% of the production or 47% of the annual $\bar{B}$, large worms excluded.

The impact of Oystercatcher predation on their prey

The small population of Oystercatcher at Skinflats (Table 4.12) fed almost entirely on the developing mussel bed where, in addition to Mytilus, Cerastoderma and Littorina were present. These populations were not studied but feeding observations at Kinneil and gut analysis (Section 3.5.7) show these to be the most likely prey. The impact of predation has not been assessed but is not unlikely to be significant with such a small population of birds.

The impact of Shelduck predation on their prey

At Kinneil gut analysis revealed that Hydrobia, oligochaetes, small polychaetes and Macoma were commonly taken as prey (Section 3.5.9). Here, the predominant feeding method was scything (Warnes et al 1980) whereas, at Skinflats, the most common methods were upending and head-dipping, on the ebb and flow tides (Bryant and Leng 1975, Warnes et al 1980). Hydrobia were probably the most important prey at this site, although Macoma and small worms will have been taken to a lesser extent. Assuming a daily energy requirement of 2.18 x BMR as for Barnacle Geese/

TABLE 4.16: Annual energy requirements by Curlew at Skinflats

	Mean monthly population of Curlew at Skinflats	Feeding population at Skinflats (20% of total population)	Bird days per month spent feeding at Skinflats	Energy intake (kcal $bird^{-1}$) (from feeding rate data) assuming a 90% assimilation efficiency	Energy (kcal m^{-2}) removed by population from Skinflats
Jul	170	34	1054	320.39	0.088
Aug	109	23	713	289.37	0.054
Sep	410	82	2460	246.51	0.159
Oct	183	37	1147	204.31	0.061
Nov	210	42	1260	166.32	0.055
Dec	267	53	1643	145.87	0.063
Jan	225	45	1395	163.04	0.060
Feb	317	63	1764	190.00	0.088
Mar	186	37	1147	227.72	0.068
Apr	63	13	390	269.14	0.027
May	21	4	124	299.38	0.009
Jun	1	0	0	296.55	-

Total 0.732 kcals m^{-2} (3.06 kJ)

TABLE 4.17: Annual energy requirements of Shelduck and the impact of predation on invertebrates at Skinflats

	Population of Shelduck at Skinflats	Bird days per month	Approx body weights (g)	BMR (Kendeigh) kcals	BMR x 2.18	Energy (kcals) required by population x 10^3	Energy (kcals m^{-2}) required by population
Jul	6	186	1060	87.2	190.1	35.4	0.01
Aug	13	403	1060	87.2	190.1	76.6	0.02
Sep	121	3630	997	83.4	181.8	659.9	0.17
Oct	300	9300	997	83.4	181.8	1690.7	0.44
Nov	351	10530	997	83.4	181.8	1914.4	0.50
Dec	1176	36456	997	83.4	181.8	6627.7	1.74
Jan	1028	31868	997	83.4	181.8	5793.6	1.52
Feb	650	18200	997	83.4	181.8	3308.8	0.87
Mar	288	8928	997	83.4	181.8	1623.1	0.42
Apr	208	6240	1152	92.8	202.3	1262.4	0.33
May	74	2294	1152	92.8	202.3	464.1	0.12
Jun	19	570	1060	87.2	190.1	108.4	0.03

Total 6.17 kcals (25.83 kJ) m

Geese (Ebbinge et al 1975), the feeding population at Skinflats would take 6.17 kcals (25.83 kJ)m^{-2} y^{-1} (Table 4.17). If feeding entirely on Hydrobia this is equivalent to 51% of the total production. As this figure is so high, it is suggested that at least some of the energy requirements of Shelduck are derived from oligochaetes, small polychaetes and Macoma, as found on the Tees (Evans et al 1979). The production of all these invertebrates together amounts to 81.43 kcals (340.86 kJ) m^{-2} and Shelduck predation would thus account for 11.7% of their combined production. The annual $\bar{B}$ of these animals amounts to 40.04 kcals (167.6 kJ) and thus 15.4% of the standing crop could be predated by Shelduck.

The total annual production by the invertebrates studied at Skinflats was 108.17 kcals (452.8 kJ)m^{-2}. Of this, an estimated 21.735 kcals (95.68 kJ)m^{-2} was accounted for in terms of predation by the overwintering birds studied. Thus only 23.5% of the total annual production flowed into the avian portion of the next trophic level (Fig 4.11). Taking the annual $\bar{B}$ of 10.29 gm^{-2} (46.6 kcals, 195 kJ)m 49% of the standing crop was predated. Predators not considered included fish and various carnivorous invertebrates. Of the fish, the flounder (Platichthys flesus) is thought to be common (local fishermen pers. comm.) and these flatfish are known to take Hydrobia, Corophium, Nereis and Macoma siphons (eg Summers 1974). On the Ythan Summers (1974) found that 97% of the Corophium and 50% of the Nereis production was predated by flounders. Invertebrate predators included shorecrabs (Carcinus maenas) and Retusa obtusa, an opisthobranch which feeds on Hydrobia. The role of these animals in the estuarine food web needs further investigation on the Forth.

Possible implications of proposed reclamation schemes on the shorebirds of the Forth estuary

Although/

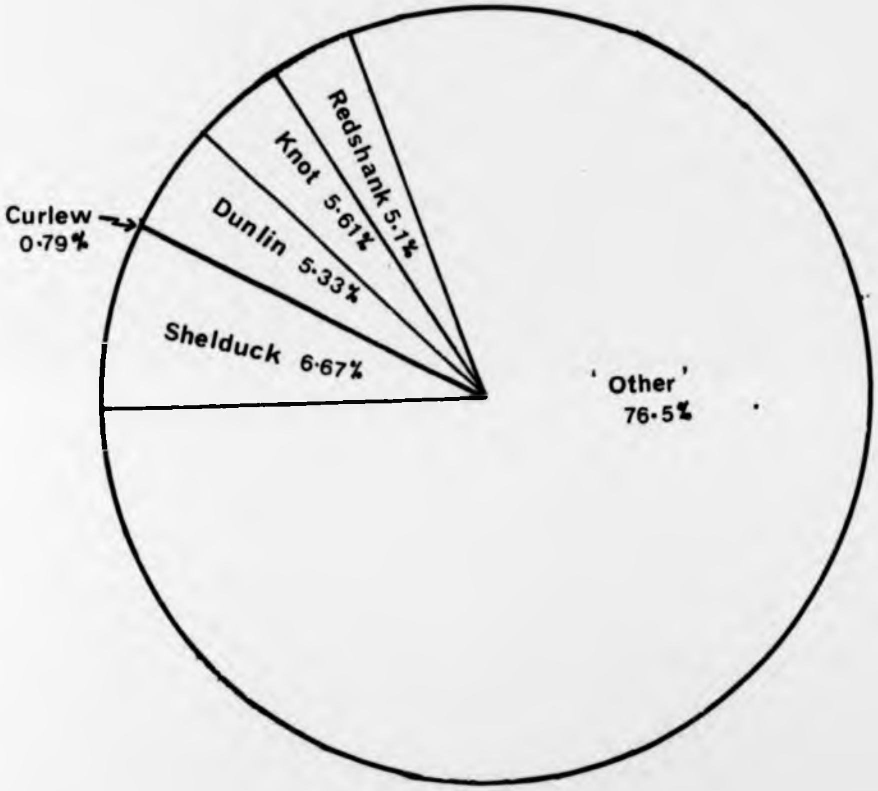


FIGURE 4.11: Fate of the total annual production of invertebrates studied at Skinflats

Although Skinflats is under lease to the Royal Society for the Protection of Birds and, as such, is unlikely to be reclaimed for industrial purposes, the future of Kinneil mudflat is less secure. Areas of Torry Bay, an important refuge for wintering wildfowl and waders, have recently been reclaimed (1979) for waste fly-ash dumping and there are plans for reclaiming large portions of Kinneil. The effects of reducing the intertidal area of Torry Bay have been monitored (Bryant 1980) and although the effects of this piecemeal reclamation appear to be slight, the consequences for the waders and wildfowl if an entire major feeding area is reclaimed may be serious. Loss of Kinneil could result in the entire feeding population of Dunlin attempting to feed at Skinflats. Unless they rely heavily on the small polychaete and oligochaete populations, some of which are themselves subject to severe density fluctuations (Sections 3.4.5 - 3.4.7) the <u>Nereis</u> and <u>Hydrobia</u> populations could not support such high numbers (see earlier in this section). Additionally, as with all waders, Dunlin require a certain social space in which to feed (Bryant 1979, Goss-Custard 1970b) and this may act to prevent an area being overpredated and food becoming scarce in late winter. Intra-specific and interspecific competition may thus result from an increase in the density of Dunlin, as in other waders (Zwartz 1976, in press, Goss-Custard 1977a, and in press), so that many would be forced to seek feeding areas elsewhere. This would only be possible if other areas have below their carrying capacity of waders. More research into this area of wader ecology is required before such predictions can be verified but it seems certain that Skinflats could not support large populations of Dunlin feeding over the whole tidal cycle.

Another species likely to decrease in number if reclamation proposals are implemented is the Redshank. This species is relatively site/

site specific (Minton 1975) and requires a larger individual feeding area than Dunlin to maintain feeding efficiency (Bryant 1979, Goss-Custard 1970b). The extent to which density could be increased if displaced birds from Kinneil fed at Skinflats would thus depend on social space and also on the density of other species which may interfere with Redshank feeding efficiency. Dense flocks of Dunlin, for example, are known to displace Redshank (Moumontzi 1977) and, in addition, Redshank and Knot populations are largely concentrated in different areas of Skinflats (Section 3.6) so that competition between the two species was not evident.

Knot feed at Kinneil in large numbers in a localised area (Bryant 1976-80) and as discussed earlier in this section (and Section 3.6), the density of Hydrobia at Skinflats would not be high enough to support displaced birds. Reclamation would undoubtedly result in Knot frequenting feeding areas in the outer Forth. In mild winters they, anyway, often remain in the outer estuary, as in 1979-80 (pers. obs., Symmonds in prep.) and research is currently being undertaken to investigate the movements of Knot, both within and between estuaries. It is thus not possible to predict the impact of reclamation on such a mobile species.

Since the commonly taken foods of Oystercatcher and Curlew are not abundant at Skinflats, reclamation of Kinneil would be unlikely to increase the number of these species at Skinflats. Curlew may feed to an increased extent on inland pastures but since the north shore of the Forth is important for Oystercatcher, loss of intertidal mudflat at Kinneil would be unlikely to greatly affect the density of Oystercatcher on the inner Forth. Reclamation of either Culross Bay (Fig 1.1) or Torry Bay would affect this species to a greater extent.

The moulting flock of Shelduck at Kinneil has increased dramatically in the last few years (Bryant 1978b) and there is a large overwintering flock at Kinneil and Skinflats (Bryant 1980). At Kinneil, they feed mainly on oligochaetes, small polychaetes, Hydrobia and Macoma (Section 3.5.9). Increased effluent output at this site could seriously affect the moulting and overwintering flocks if the grossly-polluted area (McLusky 1979b) is allowed to extend and total reclamation could also have larger implications. Kinneil is the only large known moulting ground in Britain, apart from Bridgewater Bay in Somerset and care should therefore be taken to conserve this important site.

In conclusion, maintaining the integrity of both Skinflats and Kinneil is likely to be an essential factor in the maintenance of populations of several overwintering species on the Forth estuary. Unfortunately, until further research into the ways in which overwintering waders and wildfowl choose feeding areas and the extent to which they move between estuaries during a winter is complete, the possible effects of reclamation proposals cannot be predicted in detail.

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APPENDIX 1

Sediment pipette analysis: recalculated settling velocities (SV) and time taken to settle 20 cm (62.5 um) or 10 cm (all other particle sizes)

	PARTICLE SIZE (um)									
	62.5		31.5		15.6		7.8		3.9	
TEMP °C	SV	settling time (min : s)	SV	settling time (min : s)	SV	settling time (min : s)	SV	settling time (min : s)	SV	settling time (hr : min : s)
20	0.35	0:57	0.0876	1:54	0.0218	7:39	0.00545	30:35	0.00136	2:02:33
21	0.36	0:56	0.0898	1:51	0.0224	7:26	0.00559	29:49	0.00140	1:59:03
22	0.37	0:54	0.0920	1:49	0.0229	7:17	0.00573	29:05	0.00143	1:56:33
23	0.38	0:53	0.0942	1:46	0.0235	7:06	0.00586	28:27	0.00147	1:53:23
24	0.39	0:51	0.0963	1:44	0.0240	6:57	0.00600	27:47	0.00150	1:51:07
25	0.40	0:50	0.0986	1:41	0.0246	6:47	0.00614	27:09	0.00154	1:48:14

APPENDIX 2

Percentages of grain sizes from sediment particle-size analysis

ϕ	mm	A_1	A_2	A_3	A_4	A_5	B_1	B_2	B_3	C_1	C_2
-1	> 2.0	-	-	-	0.146	0.189	0.268	-	-	-	-
0	1.0-2.0	0.019	-	0.008	0.028	0.054	0.057	0.033	-	-	0.025
1	0.5-1.0	0.155	0.025	0.046	0.191	0.165	0.083	0.201	0.014	0.033	0.042
2	0.25-0.5	0.447	0.330	0.911	0.513	1.944	0.364	2.888	0.440	5.303	1.171
3	0.125-0.25	1.283	1.844	6.449	2.764	0.236	1.629	3.585	5.553	5.805	3.407
4	0.063-0.125	3.529	9.834	22.135	7.670	21.935	8.897	15.487	21.859	9.963	16.017
5	0.031-0.063	80.059	70.637	64.722	36.330	60.118	19.360	23.945	65.514	10.677	29.304
6	0.016-0.031	7.636	8.639	2.780	46.530	12.845	63.244	44.949	3.832	61.780	37.936
7	0.008-0.016	4.597	5.945	1.897	3.846	1.777	3.381	6.180	2.189	4.061	8.967
8	0.004-0.008	2.275	2.746	1.053	2.126	0.736	2.721	2.732	0.599	1.917	3.155

APPENDIX 3

Analysis of Carbon and Nitrogen content of sediments at Skinflats
(a) % N, (b) % C, (c) C : N ratio

1976

(a)

	JAN	FEB	MAR	APR	MAY	JUN
A_1	0.189	0.155	0.226	0.299	0.153	0.147
A_2	0.167	0.135	0.263	0.247	0.316	0.105
A_3	0.124	0.122	0.205	0.160	0.169	0.205
A_4	0.114	0.139	0.140	0.131	0.135	0.103
A_5	0.161	0.144	0.165	0.239	0.238	0.187
B_1	0.180	0.182	0.249	0.303	0.281	0.223
B_2	0.139	0.191	0.320	0.211	0.211	0.156
B_3	0.161	0.140	0.132	0.205	0.163	0.126
C_1	0.272	0.269	0.187	0.191	0.379	0.230
C_2	0.195	0.170	0.165	0.157	0.197	0.126

(b)

A_1	4.028	3.426	3.685	4.828	3.632	2.953
A_2	4.765	3.395	4.365	4.290	4.323	2.440
A_3	2.671	2.282	2.564	2.580	2.842	2.315
A_4	2.250	1.926	2.460	2.609	2.431	1.691
A_5	3.678	2.890	3.147	2.600	4.577	3.430
B_1	2.841	2.960	3.646	4.181	5.420	4.047
B_2	1.842	3.109	4.587	3.328	3.334	3.270
B_3	3.565	2.260	2.270	2.925	3.129	2.258
C_1	4.843	4.276	3.332	3.342	6.594	4.341
C_2	2.765	3.364	2.739	3.033	3.858	2.564

(c)

A_1	21.31	22.10	16.31	16.15	23.74	20.09
A_2	28.53	25.15	16.60	17.37	13.68	23.24
A_3	21.54	18.70	12.51	16.13	16.82	11.29
A_4	19.74	13.86	17.57	19.92	18.01	16.42
A_5	22.84	20.07	19.07	10.88	19.23	18.34
B_1	15.78	16.26	14.64	13.80	19.29	18.15
B_2	13.25	16.28	14.33	15.77	15.80	20.96
B_3	22.14	16.14	17.20	14.27	19.20	17.92
C_1	17.81	15.90	17.82	17.50	17.40	18.87
C_2	14.18	19.79	16.60	19.30	19.58	20.35

APPENDIX 4

Density of <u>Hydrobia ulvae</u> at each sampling station throughout the study period (x 100)

	DEC 75	JAN 76	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
A_1	72	20	76	60	84	52	52	80	108	104	104	76	20
A_2	392	112	88	84	84	116	80	108	160	200	132	68	64
A_3	108	216	100	168	232	144	156	156	152	140	108	144	120
A_4	108	216	192	176	168	132	208	236	196	200	124	160	156
A_5	80	32	108	72	32	32	76	28	172	220	348	412	276
B_1	244	184	68	108	44	72	52	12	352	104	172	92	88
B_2	108	56	48	96	152	128	120	56	148	140	204	76	68
B_3	32	44	28	52	20	28	16	948	280	164	200	156	100
C_1	116	152	68	72	76	68	64	124	96	328	84	92	76
C_2	192	76	104	128	84	204	112	284	204	144	364	168	76
$\bar{X}$	145.2	110.8	88	101.6	97.6	97.6	93.6	203.2	186.8	174.4	184	144.4	104.4
SD	105.56	76.2	44.42	43.42	66.83	56.45	56.64	275.67	77.79	66.91	99.21	101.78	70.19

	JAN 77	FEB	MAR	APR	MAY	JUN	JUL	SEP	DEC	MAR 78	$\bar{X}$ ± ISD
A_1	48	52	28	20	32	28	80	120	88	44	63 ± 30.6
A_2	64	40	24	4	32	40	60	136	8	24	92.17 ± 81.9
A_3	68	64	20	48	32	24	64	120	128	48	111.3 ± 58.2
A_4	132	60	64	16	108	148	64	160	88	140	141.4 ± 56.7
A_5	96	84	64	56	76	164	44	292	56	72	125.7 ± 109.9
B_1	28	36	12	28	28	12	44	108	60	36	86.3 ± 83.0
B_2	44	28	64	12	32	8	72	28	88	56	79.7 ± 50.4
B_3	40	56	36	116	32	8	16	104	28	32	110.3 ± 195.4
C_1	8	4	8	0	24	0	8	88	60	40	72 ± 70.3
C_2	36	40	52	16	36	92	88	224	48	68	123.5 ± 88
$\bar{X}$	56.4	46.4	37.2	31.6	43.2	52.4	54	138	65.2	56	
SD	35.80	27.01	22.16	34.59	26.98	60.59	26.14	73.71	34.31	33.20	

APPENDIX 5

Mean number of eggs per capsule at each station during two breeding seasons of *Hydrobia*

		STATION									
		TRANSECT A					TRANSECT B			TRANSECT C	
		1	2	3	4	5	1	2	3	1	2
1976	MAR	17	0	16	12.5	7	0	0	0	0	0
	APR	16.5	13.8	14.2	17.4	15	19	14.1	6	14.3	12.7
	MAY	13.3	12.09	14.9	15.5	20.5	0	14.3	13.3	13	7.8
	JUN	0	0	12.6	12.9	17.5	0	0	20	0	0
	JUL	5	0	10.2	9.5	19.5	0	0	0	0	0
1977	MAR	0	10	0	6.5	7.5	0	16	0	0	0
	APR	0	0	11.5	13.45	11.1	0	14.5	14	0	0
	MAY	18.6	15.7	13.4	17	13.3	18.3	22.3	18.1	40.7	17
	JUN	17.3	10.4	14	15	18.7	0	0	18	0	14.9
	JUL	0	11	11.3	0	0	0	9	0	0	0

APPENDIX 6

Computation of production of 1976 cohort (0+ age class) of HYDROBIA July '76 - June '77

	MIW $\bar{w}$ (µg)	Population density (Nm^{-2})	Biomass $N\bar{w}$ (g)	$\bar{N}$ over period $\frac{1}{2}(Nt + Nt + \Delta t)$	$\bar{w}$ over period µg	$-\Delta N$	$\Delta\bar{w}$	P ($\bar{N}\Delta\bar{w}$) mg	M ($\bar{w}\Delta N$) mg
JUL	43.68 ± 28.06	12600	0.550	-	-	-	-	-	-
AUG	66.69 ± 60.36	11120	0.742	11860	55.19	-1480	+ 23.01	+272.9	- 81.681
SEP	94.54 ± 88.02	10160	0.961	10640	80.62	- 960	+ 27.85	+296.3	- 77.39
OCT	100.76 ± 89.42	11360	1.145	10760	97.65	+1200	+ 6.22	+ 66.9	+117.18
NOV	125.85 ± 92.8	8920	1.123	10140	113.31	-2400	+ 25.09	+254.4	-276.5
DEC	184.05 ± 98.95	4840	0.891	6880	154.95	-4080	+ 58.2	+400.4	-632.2
JAN	132.51 ± 82.14	2720	0.360	3780	158.28	-2120	- 51.54	-194.8	-335.6
FEB	158.31 ± 83.13	2720	0.431	2720	145.41	0	+ 25.8	+ 70.1	0
MAR	161 ± 94.58	2000	0.322	2360	159.66	- 720	+ 2.69	+ 6.35	-114.96
APR	159.31 ± 96.1	2480	0.395	2240	160.16	+ 480	- 1.69	- 3.79	+ 76.88
MAY	307.05 ± 138.55	3480	1.069	2980	233.18	+1000	+147.74	+440.3	+233.18
JUN	507.68 ± 170.14	4680	2.376	4080	407.36	+1200	+200.63	+818.6	+488.8

APPENDIX 6 (cont'd)

Computation of production of 1975 cohort (1+ age class) of HYDROBIA July '76 - June '77

	MIW $\bar{w}$ (ug)	Population density (Nm^{-2})	Biomass $N\bar{w}$ (g)	$\bar{N}$ over period	$\bar{w}$ over period	$-\Delta N$	$\Delta\bar{w}$ ug	$\Delta\underline{P}$ ($\bar{N}\Delta\bar{w}$) mg	$\Delta\underline{M}$ ($\bar{w}\Delta N$) mg
JUL	478.36 ± 161.7	7680	3.674	-	-	-	-	-	-
AUG	598.8 ± 173.9	7400	4.431	7540	538.58	- 280	+120.44	+908.12	- 150.8
SEP	592.6 ± 177.4	7280	4.314	7340	595.7	- 120	- 6.2	- 45.51	- 71.48
OCT	538.03 ± 179.3	7040	3.788	7160	565.32	- 240	- 54.57	-390.72	- 135.68
NOV	600.98 ± 244.3	5520	3.317	6280	569.51	-1520	+ 62.95	+395.33	- 865.65
DEC	663.86 ± 180.77	5600	3.718	5560	632.42	+ 80	+ 62.88	+349.61	+ 505.9
JAN	636.79 ± 284.6	2920	1.859	4260	650.33	-2680	- 27.07	-115.32	-1742.9
FEB	641.21 ± 177.6	1920	1.231	2420	639.0	-1000	+ 4.42	+ 10.70	- 639.0
MAR	707.18 ± 192.6	1720	1.216	1820	674.20	- 200	+ 65.97	+120.07	- 134.8
APR	710.16 ± 196.5	680	0.483	1200	708.67	-1040	+ 2.98	+ 3.56	- 737.02
MAY	875.2 ± 224.7	840	0.735	760	792.68	+ 160	+165.04	+125.43	+ 126.83
JUN	966.0 ± 81.85	480	0.464	660	920.6	- 360	+ 90.8	+ 59.93	- 331.42

APPENDIX 6 (cont'd)

Computation of (a) 1974 cohort (2+ age class) of Hydrobia
and (b) 1977 cohort (-1 age class)

(a)

1974	MIW $\bar{w}$ (mg)	Population density (Nm^{-2})	Biomass $N\bar{w}$ (g)	$\bar{N}$ over period	$\bar{w}$ over period	$-\Delta N$	$\Delta\bar{w}$ ug	ΔP ($N\Delta\bar{w}$) mg	ΔM ($\bar{w}\Delta N$)
JULY	964.5 -	40	0.039	-	-	-	-	-	-
AUGUST	1465.5 ± 240.6	160	0.234	100	1215	+120	+501	50.1	121.5
		$\bar{x}$ =	0.137 ± 0.138				Total	0.05 g	

(b)

JUNE 1977	33.45 ± 41.8	80	0.003	-	-	-	-	2.676 mg	
							Total	0.0027 g	

APPENDIX 7

Species recorded (R) from small samples throughout the study period but not studied in detail

	DEC '75	JAN '76	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN '77	FEB	MAR	APR	MAY	JUN	JUL	SEP	DEC	MAR '78	
RETUSA retusa	R				R	R	R	R		R			R					R	R	R			R	
DIPTERAN larvae	R	R						R		R			R	R	R						R	R	R	
CARDIUM edule	R							R	R	R	R	R	R	R							R			
NEPTHYS hombergii		R				R			R				R		R	R			R	R	R			
MYA arenaria				R				R	R	R	R					R	R	R	R	R				
PHYLLODOCE										R	R	R		R	R	R			R					
ETEONE longa											R	R	R	R	R	R	R	R	R		R	R	R	
LITTORINA saxatilus												R												
CARCINUS maenas									R															
SPIONIDS	R		R		R		R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	

APPENDIX 8

Density - *Macoma* m^{-2}

	Aug	Nov	Jun	Sep	Dec	Mar	Mean
A_1	467	967	300	1233	667	800	739 ± 338
A_2	567	600	467	1133	400	367	589 ± 282
A_3	433	567	333	500	200	133	361 ± 171
A_4	333	333	400	300	367	33	294 ± 132
A_5	333	867	600	533	133	200	444 ± 276
B_1	0	0	67	100	133	300	100 ± 112
B_2	100	167	200	133	100	400	183 ± 113
B_3	167	433	500	300	33	33	244 ± 200
C_1	0	0	0	0	0	67	11 ± 27
C_2	367	533	500	567	367	500	472 ± 85
Mean	276.7 ±199	446.7 ±331	336.7 ±197	479.9 ±417	240 ±207	283.3 ±244	

APPENDIX 9

MACOMA Age composition data

Cohort		AUG 76	NOV 76	JUN 77	SEP 77	DEC 77	MAR 78
1972+	Mean shell height mm	8.93 ± 0.92 (n = 3)	8.32 ± 0.1 (n = 5)	9.76 ± 0.4 (n = 5)	10.13 ± 0.23 (n = 3)	10.3 (n = 1)	-
	Mean shell length mm	11.23	10.48	12.26	12.72	12.93	-
	Mean wt mg	12.06	9.44	19.77	17.32	16.88	-
1973	Mean shell height mm	7.08 ± 0.25 (n = 13)	7.59 ± 0.23 (n = 10)	8.17 ± 0.23 (n = 6)	8.71 ± 0.54 (n = 9)	9.3 ± 0.99 (n = 2)	9.2 (n = 1)
	Mean shell length mm	8.94	9.58	10.29	10.96	11.69	11.57
	Mean weight mg	6.20	7.35	11.78	11.23	12.78	12.41
1974	Mean shell height mm	5.64 ± 0.5 (n = 34)	6.32 ± 0.4 (n = 35)	6.75 ± 0.5 (n = 18)	7.07 ± 0.32 (n = 11)	8.15 ± 0.37 (n = 8)	8.06 ± 0.32 (n = 7)
	Mean shell length mm	7.16	8.00	8.54	8.93	10.27	10.16
	Mean weight mg	3.24	4.48	6.77	6.18	8.92	8.66
1975	Mean shell height mm	3.57 ± 0.79 (n = 32)	4.26 ± 0.95 (n = 72)	4.28 ± 0.78 (n = 57)	5.43 ± 0.77 (n = 23)	6.29 ± 0.59 (n = 14)	6.58 ± 0.58 (n = 5)
	Mean shell length mm	4.6	5.45	5.48	6.90	7.97	8.32
	Mean weight mg	0.89	1.55	1.82	2.91	4.42	4.99
1976	Mean shell height mm	2.0 (n = 1)	2.18 ± 0.3 (n = 12)	2.65 ± 0.3 (n = 14)	3.4 ± 0.4 (n = 27)	4.13 ± 0.72 (n = 19)	4.16 ± 0.7 (n = 25)
	Mean shell length mm	2.65	2.88	3.46	4.39	5.29	5.33
	Mean weight mg	0.18	0.26	0.47	0.78	1.43	1.45
1977	Mean shell height mm	-	-	0.8 (n = 1)	1.79 ± 0.43 (n = 71)	2.1 ± 0.5 (n = 28)	2.13 ± 0.52 (n = 47)
	Mean shell weight mm	-	-	1.17	2.39	2.78	2.82
	Mean weight mg	-	-	0.02	0.13	0.24	0.25

APPENDIX 10

1977 age classes MACOMA

	MIW $\bar{w}$ (mg	Popn density Nm^{-2}	Biomass $N\bar{w}$ (mg)	$\bar{N}$ over period	$\bar{w}$ over period	ΔN	$\Delta\bar{w}$	ΔP $\bar{N}\Delta\bar{w}$ mg	ΔM ($\bar{w}\Delta N$) mg
Aug 76	-	-	-	-	-	-	-	-	-
Nov 76	-	-	-	-	-	-	-	-	-
Jun 77	0.02	3.3	0.06	-	-	-	-	-	-
Sep 77	0.13	236.4	30.73	119.85	0.08	+233.1	+0.11	+13.18	+18.648
Dec 77	0.24	93.2	22.37	164.8	0.19	-143.2	+0.11	+18.128	-27.208
Mar 78	0.25	156.5	39.0	249.7	0.245	+ 63.3	+0.01	+ 2.497	+15.509

1976 age classes

Aug 76	0.18	3.3	0.594	-	-	-	-	-	-
Nov 76	0.26	40.0	10.4	21.65	0.22	+36.7	+0.08	+ 1.732	+ 8.07
Jun 77	0.47	46.6	21.902	43.3	0.37	+ 6.6	+0.21	+ 9.093	+ 2.44
Sep 77	0.78	90.0	70.2	68.3	0.63	+43.4	+0.31	+21.173	+27.34
Dec 77	1.43	63.3	90.519	76.65	1.11	-26.7	+0.65	+49.82	-29.637
Mar 78	1.45	83.3	120.79	73.3	1.44	+20.0	+0.02	+ 1.466	+28.8

APPENDIX 10 (cont'd)

1975 age class MACOMA

	MIW $\bar{w}$ (mg)	Popn density Nm^{-2}	Biomass $N\bar{w}$ (mg)	$\bar{N}$ over period	$\bar{w}$ over period	$-\Delta N$	$\Delta\bar{w}$	ΔP	Δm
Aug 76	0.89	106.7	94.874	-	-	-	-	-	-
Nov 76	1.55	240	372.0	173.3	1.22	+133.4	+0.66	+114.4	+162.748
Jun 77	1.82	190	345.8	215	1.69	- 50	+0.27	+ 58.05	- 84.5
Sep 77	2.91	76.7	222.9	133.3	2.37	-113.4	+1.09	+145.3	-268.76
Dec 77	4.42	46.7	206	61.6	3.67	- 30.0	+1.51	+ 93.02	-110.1
Mar 78	4.99	16.7	83.3	31.65	4.71	- 29.9	+0.57	+ 18.04	-140.829

1974 age class

Aug 76	5.64	113.2	638.4	-	-	-	-	-	-
Nov 76	6.32	116.6	736.9	114.9	5.98	+ 3.4	+0.68	+78.132	+ 20.332
Jun 77	6.75	59.9	404.3	88.25	6.54	-56.7	+0.43	+37.95	-370.818
Sep 77	7.07	36.6	258.8	48.25	6.91	-23.3	+0.32	+15.44	-161.003
Dec 77	8.15	26.6	216.8	31.6	7.61	-10	+1.08	+34.13	- 70.10
Mar 78	8.06	23.3	187.8	24.95	8.11	- 3.3	-0.09	- 2.24	- 26.76

APPENDIX 10 (cont'd)

1973+ age classes MACOMA

	MIW $\bar{w}$ (mg)	Popn density (Nm^{-2})	Biomass $N\bar{w}$ (mg)	$\bar{N}$ over period	$\bar{W}$ over period	$-\Delta N$	$\Delta\bar{w}$ mg	$\Delta P = \bar{N}\Delta\bar{w}$ mg m^{-2}	ΔM $\bar{w}\Delta N$ mg m^{-2}
Aug 76	6.20	43.3	268.5	-	-	-	-	-	-
Nov 76	7.35	33.3	244.8	38.3	6.78	+10.0	+1.15	+ 44.05	+ 67.8
Jun 77	11.78	20.0	235.6	26.7	9.57	-13.3	+4.43	+118.28	-127.281
Sep 77	11.23	30.0	336.9	25.0	11.51	+10.0	-0.55	- 13.75	+115.1
Dec 77	12.78	6.6	84.35	18.3	12.01	-23.4	+1.55	+ 28.37	-281.034
Mar 78	12.41	3.3	40.95	4.95	12.60	- 3.3	-0.37	- 1.83	- 41.58

1972+ age classes

Aug 76	12.06	10.0	120.6	-	-	-	-	-	-
Nov 76	9.44	16.7	157.6	13.35	10.75	+ 6.7	- 2.62	- 34.98	+ 72.025
Jun 77	19.77	16.7	330.2	16.7	14.61	+ 0	+10.33	+172.51	0
Sep 77	17.32	10.0	173.2	13.35	18.55	- 6.7	- 2.45	- 32.71	-124.285
Dec 77	16.88	3.3	55.70	6.65	17.1	- 6.7	- 0.44	- 2.93	-114.57
Mar 78	-	-	-	1.65	-	- 3.3	-	-	-

APPENDIX 11(a)

Analysis of Redshank pellets (18.11.77). Air temp 7°C

Pellet No.	HYDROBIA (whole + terminal whorls)	NEREIS (jaws)	MACOMA (hinge fragments)	CARCINUS (claws)	MYSIDS	COCKLE (fragments)	OLIGOCHAETES	"WORM" TUBES	SEEDS	NEMATODES (from intestine?)	UNIDENTIFIED (gelatinous objects)
1	4	20	76	1	-	-	-	-	-	-	-
2	-	4	39	-	2	-	2	10	1	2	-
3	4	5	19	1	-	-	2	9	-	-	-
4	63	4	34	3	-	-	-	-	-	-	-
5	26	12	112	-	-	1	-	-	-	-	-
6	-	7	26	carapace 3 claws + legs 24	-	-	-	1	-	-	2
7	-	4	32	2	-	-	-	2	-	-	-
8	168	58	21	1	-	-	-	1	1	-	-
9	14	11	23	6	-	-	-	1	-	-	-
10	13	4	27	14	-	-	-	1	-	-	1
11	105	8	3	-	-	-	-	-	-	-	-

APPENDIX 11(b)

Analysis of Redshank pellets (15.12.79). Air temp 4°C

Pellet No	Hydrobia (whole & terminal whorls)	Macoma (fragments)	Nereis jaws	Nematodes	Vegetable Matter
1	13	-	-	-	
2	14	2	6	p	p
3	18	-	1	-	-
4	13	-	4	-	-
5	10	2	1	-	-
6	16	-	2	-	-

APPENDIX 11(c)

Analysis of Redshank pellets (11.2.79). Air temp 2°C

Pellet No	Hydrobia (whole & terminal whorls)	Macoma (fragments)	Nereis jaws
1	27	-	-
2	32	-	-
3	18	-	-
4	34	small fragments	-
5	14	"	-
6	23	"	1

APPENDIX 12: Gut analysis of 4 Redshank collected from Kinneil Open Pan (18.12.75)

Gut No	Terminal whorls and whole shells of *Hydrobia*	Mean shell height ± ISD (mm)
1	101	$\bar{x} = 4.02 \pm 0.48$ $n = 32$
2	4	-
3	11	-
4	124	$\bar{x} = 4.09 \pm 0.72$ $n = 21$

APPENDIX 13

Depth distribution of Macoma (shell lengths mm)
on two occasions at four depth zones

November 77				January 78			
1 cm	1 - 4	4 - 7	7 - 10	1 cm	1 - 4	4 - 7	7 - 10
3.4	6.2	10.5		2.4	7.5	10.9	7.8
2.7	11.6	11.0		1.3	4.0	6.8	
2.4	11.8	10.0		2.4	2.4	9.3	
2.0	13.0	7.0		2.4	1.0	4.3	
3.0	5.6	9.2		1.2	10.0	2.5	
1.4	2.8	6.1		3.2	4.9		
1.9	5.9	10.4		4.3	6.7		
1.2	9.0	10.0		4.1	3.3		
2.2	5.5			2.9	3.1		
2.4	6.9			3.4	3.8		
	3.2			4.5	2.9		
	5.4			2.7			
	5.7			2.6			
	6.2			3.0			
	6.2			1.4			
	5.4			4.1			
	14.0			3.2			
	4.1			2.8			
	3.9						
	7.3						
	4.0						
	1.3						
	3.0						
	4.5						

APPENDIX 14

Analysis of Knot pellets from Skinflats

Pellet No	Terminal whorls and whole shells of _Hydrobia_	_Macoma_ hinge fragments p = present
1	136	p
2	1	p
3	0	p
4	64	-
5	0	p
6	2	p
7	76+	-
8	1	p
9	10	p
10	16	-

APPENDIX 15

Analysis of Dunlin pellets from Skinflats

Pellet No.	whole shells and terminal whorls of *Hydrobia*	*Nereis* jaws	*Macoma* hinge fragments	Oligochaetes	*Manayunkia*	Dipteran larvae	Vegetable matter p = present
1	2	14	9	2	1	-	-
2	33	2	-	-	-	-	-
3	2	17	-	1	-	1	-
4	-	1	-	-	-	-	-
5	17	6	-	-	-	-	-
6	4	8	-	-	-	-	-
7	26	-	-	-	1	-	-
8	42	10	-	-	-	-	-
9	1	1	2	-	1	-	-
10	27	1	-	-	-	-	-
11	7	1	-	-	-	-	p

APPENDIX 16

Analysis of Dunlin guts from Skinflats
(Gut 1 - 11) and Kinneil (Gut 12 - 15)

Gut No	Whole shells and terminal whorls of *Hydrobia*	*Nereis* jaws	*Macoma* hinge fragments p = present	Oligochaetes	Vegetable matter	Dipteran larvae
1	8	210	p		p	
2	161	28				
3	225	8				
4	71	3				
5	9	188	p			3
6	1	282			p	
7	-	12				
8	1	145				
9	61	-	p			
10	128	2				
11	6	26				
12	143	482				
13	2	-	p			
14	5	20		10		
15	104	14				

APPENDIX 17

Densities and Biomass of (a) *Nereis* (b) *Macoma* (c) *Hydrobia* (d) *Cardium* (e) Oligochaetes and *Manayunkia* (November 1976), together with densities and biomass of size classes of each taken by shorebird species

(a)

NEREIS	DENSITY (nm^{-2})			BIOMASS (gm^{-2})		
	Total	Redshank sizes	Dunlin sizes	Total	Redshank sizes	Dunlin sizes
A_1	900	167	400	0.52	0.31	0.37
A_2	100	67	33	0.89	0.60	0.14
A_3	400	33	67	0.12	0.14	0.12
A_4	133	0	0	0.04	0	0
A_5	600	67	100	0.54	0.08	0.09
B_1	0	0	0	0	0	0
B_2	133	67	133	0.10	0.60	0.38
B_3	300	100	133	0.60	0.72	0.58
C_1	267	33	67	0.13	0.04	0.05
C_2	33	0	0	0.03	0	0

(b)

A_1	967	700	675	2.81	2.97	2.46
A_2	600	467	469	1.64	1.68	1.50
A_3	567	233	411	1.10	1.02	1.00
A_4	333	233	235	1.07	1.03	0.70
A_5	867	300	381	1.54	2.12	1.30
B_1	0	0	0	0	0	0
B_2	167	100	88	0.26	0.33	0.29
B_3	433	167	323	0.72	0.51	0.65
C_1	0	0	0	0	0	0
C_2	533	300	352	1.10	1.16	0.9

APPENDIX 17 (cont'd)

(c)

HYDROBIA	DENSITY (nm^{-2})				BIOMASS (gm^{-2})			
	Total	Redshank sizes	Knot sizes	Dunlin sizes	Total	Redshank sizes	Knot sizes	Dunlin sizes
A_1	7600	5200	5200	6400	3.30	3.10	3.10	1.57
A_2	6800	5600	5600	6000	2.74	2.41	2.41	1.68
A_3	14400	12000	12000	14400	4.76	2.85	2.85	4.76
A_4	16000	15600	15600	14400	8.02	6.56	6.56	5.89
A_5	41200	36800	36800	38400	11.24	10.14	10.14	8.08
B_1	9200	4800	4800	7200	3.38	3.17	3.17	0.82
B_2	7600	5200	5200	7200	2.77	3.14	3.14	2.12
B_3	15600	5200	5200	15600	1.41	0.83	0.83	1.41
C_1	9200	6400	6400	4800	5.15	5.54	5.54	0.72
C_2	16800	6800	6800	16800	4.48	1.23	1.23	4.48

APPENDIX 17 (cont'd)

(d)

CARDIUM	DENSITY (nm^{-2})		BIOMASS (gm^{-2})	
	Total	Knot sizes	Total	Knot sizes
A_1	0	0	0	0
A_2	0	0	0	0
A_3	0	0	0	0
A_4	867	400	2.22	1.86
A_5	633	67	0.42	0.29
B_1	0	0	0	0
B_2	33	0	0.01	0
B_3	0	0	0	0
C_1	0	0	0	0
C_2	0	0	0	0

(e)

	OLIGOCHAETES		MANAYUNKIA	
	DENSITY (nm^{-2})	BIOMASS (gm^{-2})	DENSITY (nm^{-2})	BIOMASS (gm^{-2})
A_1	41600	8.29	14800	0.18
A_2	40000	7.96	400	0.004
A_3	28400	5.65	8400	0.10
A_4	18800	3.74	800	0.01
A_5	17200	3.42	0	0
B_1	4000	0.80	17200	0.21
B_2	41200	8.20	30800	0.40
B_3	9200	1.83	1200	0.01
C_1	18400	3.66	25200	0.30
C_2	19200	3.82	7600	0.09

APPENDIX 18

LT feeding densities of Redshank, Knot, Dunlin and Sheldfuck on Neap and Spring Tides at Skinflats 1976/77

	REDSHANK		KNOT		DUNLIN		SHELDUCK	
	Neap	Spring	Neap	Spring	Neap	Spring	Neap	Spring
A_1	0	1.85	0	0	3.6	6.9	0	0
A_2	0	1.38	15.0	10.0	3.8	20.5	0	0.15
A_3	0.25	1.0	15.0	0	5.0	9.0	0	1.2
A_4	0.17	2.25	30.0	7.5	4.35	21.5	0.08	7.5
A_5	3.375	2.6	216.5	9.6	25.1	21.5	1.38	8.28
B_1	0.17	0	0	8.8	0	1.4	0	0
B_2	2.58	2.3	0	13.1	11.5	9.0	0.6	4.0
B_3	5.92	2.3	0	0	24.3	22.9	2.5	7.06
C_1	0	10.25	0	0	5.2	6.5	0	3.8
C_2	8.67	4.55	0	0	1.2	7.0	0.92	6.49

APPENDIX 17 (cont'd)

(c)

HYDROBIA	DENSITY (nm^{-2})				BIOMASS (gm^{-2})			
	Total	Redshank sizes	Knot sizes	Dunlin sizes	Total	Redshank sizes	Knot sizes	Dunlin sizes
A_1	7600	5200	5200	6400	3.30	3.10	3.10	1.57
A_2	6800	5600	5600	6000	2.74	2.41	2.41	1.68
A_3	14400	12000	12000	14400	4.76	2.85	2.85	4.76
A_4	16000	15600	15600	14400	8.02	6.56	6.56	5.89
A_5	41200	36800	36800	38400	11.24	10.14	10.14	8.08
B_1	9200	4800	4800	7200	3.38	3.17	3.17	0.82
B_2	7600	5200	5200	7200	2.77	3.14	3.14	2.12
B_3	15600	5200	5200	15600	1.41	0.83	0.83	1.41
C_1	9200	6400	6400	4800	5.15	5.54	5.54	0.72
C_2	16800	6800	6800	16800	4.48	1.23	1.23	4.48

APPENDIX 17 (cont'd)

(d)

CARDIUM	DENSITY (nm^{-2})		BIOMASS (gm^{-2})	
	Total	Knot sizes	Total	Knot sizes
A_1	0	0	0	0
A_2	0	0	0	0
A_3	0	0	0	0
A_4	867	400	2.22	1.86
A_5	633	67	0.42	0.29
B_1	0	0	0	0
B_2	33	0	0.01	0
B_3	0	0	0	0
C_1	0	0	0	0
C_2	0	0	0	0

(e)

	OLIGOCHAETES		MANAYUNKIA	
	DENSITY (nm^{-2})	BIOMASS (gm^{-2})	DENSITY (nm^{-2})	BIOMASS (gm^{-2})
A_1	41600	8.29	14800	0.18
A_2	40000	7.96	400	0.004
A_3	28400	5.65	8400	0.10
A_4	18800	3.74	800	0.01
A_5	17200	3.42	0	0
B_1	4000	0.80	17200	0.21
B_2	41200	8.20	30800	0.40
B_3	9200	1.83	1200	0.01
C_1	18400	3.66	25200	0.30
C_2	19200	3.82	7600	0.09

APPENDIX 18

LT feeding densities of Redshank, Knot, Dunlin and Sheldluck on Neap and Spring Tides at Skinflats 1976/77

	REDSHANK		KNOT		DUNLIN		SHELDUCK	
	Neap	Spring	Neap	Spring	Neap	Spring	Neap	Spring
A_1	0	1.85	0	0	3.6	6.9	0	0
A_2	0	1.38	15.0	10.0	3.8	20.5	0	0.15
A_3	0.25	1.0	15.0	0	5.0	9.0	0	1.2
A_4	0.17	2.25	30.0	7.5	4.35	21.5	0.08	7.5
A_5	3.375	2.6	216.5	9.6	25.1	21.5	1.38	8.28
B_1	0.17	0	0	8.8	0	1.4	0	0
B_2	2.58	2.3	0	13.1	11.5	9.0	0.6	4.0
B_3	5.92	2.3	0	0	24.3	22.9	2.5	7.06
C_1	0	10.25	0	0	5.2	6.5	0	3.8
C_2	8.67	4.55	0	0	1.2	7.0	0.92	6.49

APPENDIX 19

Correlation analysis of the low-tide feeding densities of Redshank, Knot, Dunlin and Shelduck with various factors. Upper case - neap tides: Lower case - spring tides

VARIABLE	REDSHANK	KNOT	DUNLIN	SHELDUCK
Tidal height (m)	NS NS	-0.6932 NS	-0.8607*** -0.7160*	-0.7476** -0.8362***
Exposure time (h)	NS NS	NS NS	-0.7290** -0.7841**	-
% Silt and clay	-	-	-	-0.6399* NS
% Water content (Apr - May)	-	-	-	NS NS
<u>Hydrobia</u> density nm^{-2}	NS NS	+0.9308*** NS	NS NS	NS +0.6802*
<u>Hydrobia</u> 'preferred size-class' density nm^{-2}	NS NS	+0.9704*** NS	+0.6790* NS	-
<u>Hydrobia</u> biomass gm^{-2}	NS NS	+0.8421*** NS	NS NS	NS NS -
<u>Hydrobia</u> 'preferred size-class' biomass gm^{-2}	NS NS	+0.8249*** NS	-	-
<u>Nereis</u> density nm^{-2}	NS NS	-	-0.5842* -0.6399*	-
<u>Nereis</u> 'preferred size-class' density nm^{-2}	NS NS	-	NS NS	-
<u>Nereis</u> biomass gm^{-2}	NS NS	-	NS NS	-
<u>Nereis</u> 'preferred size-class' biomass gm^{-2}	NS NS	-	-	-
<u>Macoma</u> density nm^{-2}	NS NS	NS NS	-	-
<u>Macoma</u> 'preferred size-class' density nm^{-2}	NS NS	NS NS	-	-

APPENDIX 19 (cont'd)

VARIABLE	REDSHANK	KNOT	DUNLIN	SHELDUCK
Macoma biomass gm^{-2}	NS NS	NS NS	-	-
Macoma 'preferred size-class' biomass gm^{-2}	NS NS	NS NS	-	-
Oligochaete density nm^{-2}	-	-	NS NS	NS NS
Oligochaete biomass nm^{-2}	-	-	NS NS	NS NS
Cardium density nm^{-2}	-	+0.6251 NS	-	-
Cardium biomass gm^{-2}	-	NS NS	-	-
Cardium 'preferred size-class' density nm^{-2}	-	NS NS	-	-
Cardium 'preferred size-class' biomass gm^{-2}	-	NS NS	-	-
Total biomass (gm^{-2}) *Nereis* + *Macoma* + *Hydrobia*	NS NS	-	-	-
'Preferred size-class' total biomass gm^{-2} (*Nereis*, *Macoma* + *Hydrobia*)	NS NS	-	-	-
Biomass (gm^{-2}) of *Nereis* + *Macoma*	NS NS	-	-	-
'Preferred size-class' biomass (gm^{-2}) of *Nereis* + *Macoma*	NS NS	-	-	-
Biomass (gm^{-2}) of *Hydrobia* + *Cardium* + *Macoma*	-	+0.7841** NS	-	-
'Preferred size-class' biomass gm^{-2} of *Hydrobia* *Cardium* + *Macoma*	-	+0.8026** NS	-	-

APPENDIX 19 (cont'd)

VARIABLE	REDSHANK	KNOT	DUNLIN	SHELDUCK
'Preferred size-class' biomass gm^{-2} of *Hydrobia* + *Macoma*	-	+0.8506*** NS	-	-
'Preferred size-class' biomass gm^{-2} of *Cardium* + *Macoma*	-	NS NS	-	-
Biomass (gm^{-2}) of *Hydrobia* + *Nereis* + Oligochaetes	-	-	0.7049* 0.7154*	-
Biomass (gm^{-2}) of *Hydrobia* + Oligochaetes	-	-	-	NS NS
Biomass (gm^{-2}) of *Hydrobia* + Oligochaetes + *Manayunkia* + *Macoma* + *Nereis*	-	-	-	NS NS

APPENDIX 20

Compulation of daily energy intake by a Redshank in daylight and darkness during one year.
(a) Zone A (3.1 m; 100% sight feeding in daylight; 100% touch feeding at night)

	H. available for feeding in daylight day^{-1}	HYDROBIA			NEREIS			MACOMA			Total amount of energy ingested in daylight day^{-1} (kcal)	Energy assimilated in daylight day^{-1} (kcal)
		No. taken bird^{-1}	biomass (g) ingested bird^{-1}	energy equivalent kcal	No. taken bird^{-1}	biomass (g) ingested bird^{-1}	energy equivalent kcal	No. taken bird^{-1}	biomass (g) ingested bird^{-1}	energy equivalent kcal		
Jan	4.81	18276	877	4.21	784	4367	19.04	399.23	1278	6.09	29.34	23.47
Feb	5.71	2169.8	1042	5.00	931	5184	22.60	474	1517	7.23	34.83	27.86
Mar	6.90	2622	1259	6.04	1125	6265	27.32	573	1833	8.74	42.1	33.68
Apr	8.15	3097	1487	7.14	1328	7399	32.26	676	2165	10.33	49.73	39.78
May	9.03	3431	1647	7.91	1472	8198	35.74	749	2398	11.44	55.04	44.07
Jun	9.96	3785	1817	8.72	1623	9043	39.43	827	2645	12.62	66.77	48.62
Jul	9.77	3713	1782	8.55	1593	8870	38.67	811	2595	12.38	59.6	47.68
Aug	8.83	3355	1610	7.73	1439	8017	34.95	733	2345	11.19	53.87	43.1
Sep	7.55	2869	1377	6.61	1231	6855	29.89	627	2005	9.57	46.07	36.86
Oct	6.27	2383	1144	5.49	1022	5693	24.82	520	1665	7.94	38.25	30.6
Nov	5.12	1946	934	4.48	835	4648	20.27	425	1360	6.49	31.24	24.99
Dec	4.53	1721	826	3.97	738	4113	17.93	376	1203	5.74	27.64	22.11

H.available for feeding in darkness	No. Hydrobia taken bird^{-1}	biomass (g) ingested bird^{-1}	energy equivalent kcal
7.35 total night	10495	5038	24.18
6.54 total night	9339	4483	21.52
1.77 moon light	2528	1213	5.82
1.92 moon light	2742	1316	6.32
7.06 total night	10082	4839	23.23
7.63 total night	10896	5230	25.10

Total amount of energy ingested day^{-1} bird^{-1} daylight/darkness (kcal)	Total assimilated energy day^{-1} bird-1 (kcal)
53.52	42.82
56.36	45.09
47.92	38.34
49.73	39.28
55.09	44.07
66.77	48.62
59.6	47.68
53.87	43.10
46.07	36.86
44.57	35.66
54.47	43.58
52.74	42.19

APPENDIX 20 (cont'd)

(b) Zone B (3.1 - 4.4 m); 77% sight-feeding,
23% touch feeding in daylight;
100% touch feeding at night)

	H. available for feeding in daylight day^{-1}	H. available for feeding by sight day^{-1}	H. available for feeding by touch in daylight day^{-1}	HYDROBIA						Total amount of energy ingested day^{-1} (kcal)	NEREIS			MACOMA			Total amount of energy ingested day^{-1} in daylight	H. available for feeding in darkness	No. Hydrobia taken bird^{-1}	Biomass ingested bird^{-1}	energy equivalent kcal	Total amount of energy ingested day^{-1} bird^{-1} in daylight and darkness	Total assimilated energy day^{-1} bird^{-1} kcal
				sight-method			touch method				sight method			touch method									
				No. taken per bird	Biomass (g) ingested bird^{-1}	energy equiv-alent kcal	No. taken per bird	Biomass (g) ingested bird^{-1}	energy equiv-alent kcal		No. taken bird^{-1} day^{-1}	Biomass (g) ingested bird^{-1}	energy equiv-alent kcal	No. taken bird^{-1}	Biomass (g) ingested bird^{-1}	energy equiv-alent kcal							
Jan	2.52	1.94	0.58	737	354	1.70	828	398	1.91	3.61	316	1761	7.68	161	515	2.46	13.75	2.88 dark	4113	1974	9.48	23.23	18.58
Feb	2.75	2.12	0.63	806	387	1.86	900	432	2.07	3.93	346	1925	8.39	176	563	2.69	15.01	2.90 dark	4141	1988	9.54	24.55	19.64
Mar	3.24	2.49	0.75	946	454	2.18	1071	514	2.47	4.65	406	2261	9.86	206	661	3.16	17.67	1.20 moon	1714	823	3.95	21.62	17.30
Apr	3.94	3.03	0.91	1151	553	2.65	1299	624	2.99	5.64	494	2751	11.99	251	805	3.84	21.47					21.47	17.18
May	4.45	3.43	1.02	1303	626	3.00	1456	699	3.36	6.36	559	3114	13.58	285	911	4.35	24.29					24.29	19.43
Jun	4.51	3.47	1.04	1319	633	3.04	1485	713	3.42	6.46	566	3150	13.73	288	922	4.4	24.59					24.59	19.67
Jul	4.25	3.27	0.98	1243	596	2.86	1399	672	3.22	6.08	533	2969	12.94	271	869	4.14	23.16					23.16	18.53
Aug	3.88	2.99	0.89	1136	545	2.62	1271	610	2.93	5.55	487	2715	11.84	248	794	3.79	21.18					21.18	16.94
Sep	3.44	2.65	0.79	1007	483	2.32	1128	542	2.60	4.92	432	2406	10.49	220	704	3.36	18.77					18.77	15.02
Oct	2.90	2.23	0.67	847	406	1.95	957	459	2.20	4.15	363	2025	8.83	185	592	2.83	15.81	0.97 moon	1385	665	3.19	19.0	15.2
Nov	2.38	1.83	0.55	695	334	1.60	785	377	1.81	3.41	298	1661	7.24	152	486	2.32	12.99	3.25 dark	4641	2227	10.69	23.66	18.93
Dec	2.05	1.58	0.47	600	288	1.38	671	322	1.55	2.93	258	1434	6.25	131	420	2.00	11.18	3.28 dark	4684	2248	10.79	21.97	17.58

APPENDIX 20 (cont'd)

(c) Zone C (4.4 - 4.7 m); 55% touch feeding,
45% sight feeding in daylight;
100% touch feeding at night)

	H.available for feeding in daylight	H available for sight feeding (daylight)	H available for touch feeding (daylight)	HYDROBIA						Total amount of energy ingested day^{-1}	NEREIS			MACOMA			Total amount of energy ingested day in daylight	H.available for feeding in darkness	No. Hydrobia taken bird^{-1}	Biomass (g) ingested bird^{-1}	energy equivalent kcal	Total amount of energy ingested day^{-1} bird^{-1} in daylight and darkness	Total assimilated energy day^{-1} bird^{-1} (kcal)
				sight method			touch method				sight method			sight method									
				No. taken bird^{-1}	Biomass (g) ingested bird^{-1}	energy equivalent (kcal)	No. taken bird^{-1}	Biomass (g) ingested bird^{-1}	energy equivalent (kcal)		No. taken bird^{-1}	Biomass (g) ingested bird^{-1}	energy equivalent (kcal)	No. taken bird^{-1}	Biomass (g) ingested bird^{-1}	energy equivalent (kcal)							
Jan	0.66	0.3	0.36	114	55	0.26	514	247	1.18	1.44	48.9	272	1.19	24.9	79.7	0.38	3.01	1.67 total	2385	1145	5.49	8.5	6.8
Feb	0.85	0.38	0.47	144	69	0.33	671	322	1.55	1.88	61.9	345	1.50	31.5	100.9	0.48	3.86	0.87 total	1242	596	2.86	6.72	5.38
Mar	1.02	0.46	0.56	174.8	84	0.40	800	384	1.84	2.24	75.0	418	1.82	38.2	122	0.58	4.64	0.23 moon	328	158	0.76	5.4	4.32
Apr	1.10	0.5	0.6	190	91.2	0.44	857	411	1.97	2.41	81.5	454	1.98	41.5	133	0.63	5.02					5.02	4.02
May	1.19	0.53	0.66	201.4	96.7	0.46	942	452	2.17	2.63	86.4	481	2.1	44	141	0.67	5.4					5.4	4.32
Jun	1.68	0.76	0.92	289	139	0.67	1314	631	3.03	3.70	124	690	3.0	63	202	0.96	7.66					7.66	6.13
Jul	1.88	0.85	1.03	323	155	0.74	1471	706	3.39	4.13	139	772	3.37	70.6	226	1.08	8.58					8.58	6.86
Aug	1.47	0.66	0.81	251	120	0.58	1157	555	2.66	3.24	108	599	2.61	54.8	175	0.84	6.69					6.69	5.35
Sep	1.11	0.50	0.61	190	91	0.44	871	418	2.01	2.45	81.5	454	1.8	41.5	133	0.64	4.88					4.88	3.90
Oct	0.84	0.38	0.46	144	69	0.33	657	315	1.51	1.84	61.9	345	1.50	31.5	101	0.48	3.82	0.38 moon	542	260	1.25	5.07	4.06
Nov	0.65	0.29	0.36	110	53	0.25	514	247	1.18	1.43	47.3	263	1.15	24.1	77	0.37	2.95	0.98 total	1399	672	3.22	6.17	4.94
Dec	0.57	0.26	0.31	99	47	0.23	443	212	1.02	1.25	42.4	236	1.03	21.6	69	0.33	2.61	1.33 total	1899	912	4.38	6.99	5.59

APPENDIX 20 (cont'd)

(d) Zone D (4.7 - 5 m; 100% touch feeding)

	H.exposed day^{-1} in daylight	HYDROBIA			H.exposed day^{-1} in darkness for feeding	HYDROBIA			Total energy intake (kcal) bird^{-1} day^{-1}	Total energy assimilated (kcal) - 80% efficiency
		No. taken bird^{-1}	Biomass (g) ingested bird^{-1}	energy equivalent (kcal)		No. taken bird^{-1}	Biomass (g) ingested bird^{-1}	energy equivalent (kcal)		
Jan	0.75	1078	517	2.48	1.15	1644	789	3.79	6.27	5.02
Feb	0.74	1054	506	2.43	0.74	1060	509	2.44	4.87	3.90
Mar	0.99	1411	677	3.25	0.25	352	169	0.81	4.06	3.25
Apr	1.10	1575	756	3.63					3.63	2.90
May	1.36	1944	933	4.48					4.48	3.58
Jun	1.53	2185	1049	5.03					5.03	4.02
Jul	1.66	2367	1136	5.45					5.45	4.36
Aug	1.29	1848	887	4.26					4.26	3.41
Sep	1.07	1523	731	3.51					3.51	2.81
Oct	0.95	1352	649	3.11	0.38	539	259	1.24	4.35	3.48
Nov	0.75	1074	516	2.48	1.00	1434	688	3.30	5.78	4.62
Dec	0.79	1129	5417	2.60	1.23	1762	846	4.06	6.66	5.33