ASPECTS OF THE ECOLOGY OF MIGRANT SHOREBIRDS (AVES: CHARADRII) AT THE BERG RIVER ESTUARY, SOUTH AFRICA

by

Bozena Kalejta

Thesis submitted for the degree
of Doctor of Philosophy

Department of Zoology
Faculty of Science
University of Cape Town
August 1991

Dedicated to...

my parents and Arek,

for their love and belief in me

TABLE OF CONTENTS

ABSTRACT

Kalejta, Bozena. 1991. Aspects of the ecology of migrant shorebirds (Aves: Charadrii) at the Berg River estuary, South Africa. PhD Thesis, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa (vii) + 296 pp.

The waterbird populations of the Berg River estuary, South Africa, were studied from September 1987 to April 1989. The main objectives of the study were to assess the importance of the estuary for Palearctic-breeding migratory waders and to identify the factors affecting their distribution, abundance and behavioural patterns. The findings were related to the dispersion patterns of waders on the east Atlantic seaboard, and their significance was evaluated in the light of predictions of current models for the migratory behaviour of shorebirds. Controversy over the winter competition model is discussed.

The intertidal mudflats (144 ha) at the Berg River estuary support an exceptionally high density of migratory shorebirds during the austral summer. The high density of birds results in a high predation pressure. Although the rate of prey removal by birds is one of the highest recorded in the east Atlantic, it represents only 17% of the annual production of invertebrates. A bird-exclusion experiment confirmed that birds have little impact on their prey populations. Although the energy balance for the majority of species was apparently negative for much of the austral summer, the energy deficits measured in the field were less than those recorded in north temperate estuaries. The highest predation pressure by birds coincided with the period of highest production of the most important invertebrate prey.

Because of low prey diversity in the estuary, there was considerable overlap in the prey species taken by different bird species. The preferred prey of most species were nereid worms. Within this prey class there were clear differences in the size classes of worms eaten by different birds. The distribution of birds on the estuary was related to both biotic and abiotic factors. The observed patterns of partitioning of both food and space resources was attributed to the superabundance of prey and to interspecific differences in foraging techniques unrelated to competition. The spatial redistribution of birds within the estuary during the first four months after their arrival from the breeding grounds was related to changes in feeding conditions on their preferred foraging sites, rather than density-dependent factors mediated by competition.

I propose that a combination of high prey abundance and production, coupled with an apparently low level of competition, makes the Berg River an attractive nonbreeding site for migrant waders. Their relatively sound energy budgets and the benign climate may enhance nonbreeding survivorship sufficiently to offset any additional risks incurred in long-distance migration.

ACKNOWLEDGEMENTS

My sincere thanks go to Dr Philip A. R. Hockey for the supervision of this project. In moments of despair or panic his enthusiasm and readiness to discuss aspects of the thesis were always a great source of encouragement. I also thank him for the valuable comments and constructive criticism on all the chapters of this dissertation. I thank Prof. Roy Siegfried, director of the P.F.I.A.O., for his support of this study.

I would like to thank Prof. George Branch and Dr Bruce Bennett for valuable comments on the drafts of Chapters 1 and 2, Dr Nigel Adams for comments on Chapter 5 and Rene Navarro for comments on Chapter 6. I am indebted to Rene Navarro for his continuous advice on statistical matters and mysteries of the computer world. Colleagues of mine; Nigel Adams, Yolanda van Heezik, Philip Seddon, Jane Turpie, David Allan and Alison Sakko were always willing to discuss aspects of the thesis, and provide advice and support. I thank them all for this. My special thanks go to Claudio Velasquez who accompanied me during many hours of field work and was always willing to help and offer advice. Chapter 1 of this dissertation is a result of our joint research.

The hospitality, friendship and help of several people during the field work study period at Velddrif was much appreciated. I especially thank the families Kinross, Tredoux, Smit and Bester. Donald Kinross kindly lent me his hide for the bird-exclusion experiment. Robert Smit trustfully lent me his antique shot-gun, never doubting the "good" purpose it served. Anton van Eck's continuous supplies of chocolates and his unforgettable lessons on South African wines helped me through rough times. I also thank Mr J. Basson for helping to collect the fish samples.

I am indebted to Mr M. Meyer, manager of the Cerebos Foods factory in Velddrif, who was always ready to provide logistical support. In particular, I thank him for lending me the service of his "A" team to go wading in mud with me instead of increasing the salt production.

This research was supported financially by Cerebos Foods (Pty) Ltd., the Southern African Nature Foundation, the Research Committee of the University of Cape Town and the Foundation for Research Development. I gratefully acknowledge support from the above sources.

GENERAL INTRODUCTION

The majority of shorebirds (Charadrii) breed at high Arctic and sub-Arctic latitudes and migrate southwards before the boreal winter. Seasonal, synchronized movements of shorebirds have attracted ecological interest for decades, and several hypotheses have been put forward to explain this phenomenon. Particular attention has been paid to the rôle of competition in the evolution of dispersion patterns and migration systems of shorebirds (Cox, 1968). There is, however, no single, simple index with which to quantify competition, and several aspects of shorebird ecology have been examined in order to try to demonstrate its existence.

Shorebird diets have well been studied, and dietary specialization and niche differentiation have been interpreted as consequences of competition for limited food resources (Baker & Baker, 1973). Redistribution of birds at high densities has been linked to competition for both food and space (Goss-Custard, 1977a & b; Zwarts, 1981). Increased aggression levels at high bird density have been reported for several species and are considered as a direct indication of competition for limited resources (Recher & Recher, 1969; Burger *et al.*, 1979).

Early departure of migratory shorebirds from their breeding grounds has been explained in terms of a reduced risk of long distance migration and avoidance of a subsequent collapse of food supplies along the migration route (Myers, 1981). However, evidence for depletion of food supplies has only been reported from north temperate latitudes (O'Connor & Brown, 1977; Boates & Smith, 1979; Schneider & Harrington, 1981; Quammen, 1984). Recent studies in tropical (Duffy *et al.*, 1981; Schneider, 1985) and south temperate localities (Kent & Day, 1983) failed to demonstrate this phenomenon.

More recently, it has been proposed that asymmetric competition for resources during the nonbreeding season is responsible for latitudinal segregation of populations and species (Pienkowski and Evans, 1984; 1985). This model proposes that is advantageous for all birds to spend the nonbreeding season as close to the breeding grounds as possible, but that some are prevented from doing so by competition. One prediction arising from this model is that competition for food resources during the nonbreeding season should be greater at north temperate localities than in tropical or south temperate areas.

Competition between waders for food and space have well been documented at sites in Europe and North America, but there is a lack of information from tropical and south temperate localities. The majority of models which try to explain the mechanisms shaping migratory patterns of shorebirds have therefore based their predictions and conclusions almost entirely on data from north temperate and Arctic latitudes. However, the most extreme migrations of all, in terms of distance, are undertaken by birds which migrate between Arctic and south temperate latitudes. Although it is these birds which may provide many of the clues to unravelling the evolution of migration patterns, to date they have been little studied from this perspective anywhere in the southern hemisphere.

A primary aim of this study was to examine the rôle played by competition between shorebirds in shaping their distribution and behaviour patterns in a south temperate estuary, and to relate the findings to the dispersion of waders along the east Atlantic seaboard. Four principal aspects of shorebird ecology were examined:

1. Dietary specialization and the partitioning of food resources;
2. Predatory impact on the prey populations;
3. Habitat selection; and,
4. Aggression

STUDY AREA

The Berg River estuary (32°47'S, 18°10'E), South Africa, is situated close to the southern extreme of the Palearctic-Afrotropical migration route and therefore represents a counterpart to northwestern European estuaries which form the northern limit to the nonbreeding distribution of migratory shorebirds. The Berg River estuary supports the second largest population of waders in the southwestern Cape Province (Summers *et al.*, 1976; Ryan *et al.*, 1988). Summers *et al.* (op. cit.) considered the Berg River estuary as a wetland of international importance and proposed its registration with the RAMSAR convention.

The study area extends from the Berg River mouth upstream to a bridge on the Sishen-Saldanha railway line, and incorporates 144 ha of intertidal mudflats, 242 ha of saltmarshes, 222 ha of commercial saltpans and 232 ha of subtidal area (Fig I). Despite its national and international importance as a waterbird refuge, little is known of the ecology of any of the component habitats, particularly the intertidal mudflats, which are the most important foraging habitat for shorebirds within the estuary.

The saltmarsh vegetation is dominated by *Sarcocornia perenne*, *S. pillansii* and *Chenolea diffusa*, and the invertebrate macrofauna comprises mainly gastropods, isopods and amphipods (van Wyk, 1983).

The saltpan network consists of concentration pans (salinities of 20-180 ppt) and crystallization pans (salinity $\geqslant$180 ppt). Very few invertebrates occur in crystallization pans. In the high salinity concentration pans ($\geqslant$100 ppt) brine shrimps *Artemia* sp. are abundant, but there are no benthic invertebrates. At salinities of 30-60 ppt, benthic invertebrates are abundant, particularly chironomid fly larvae, polychaetes and amphipods (Velasquez, unpubl. data).

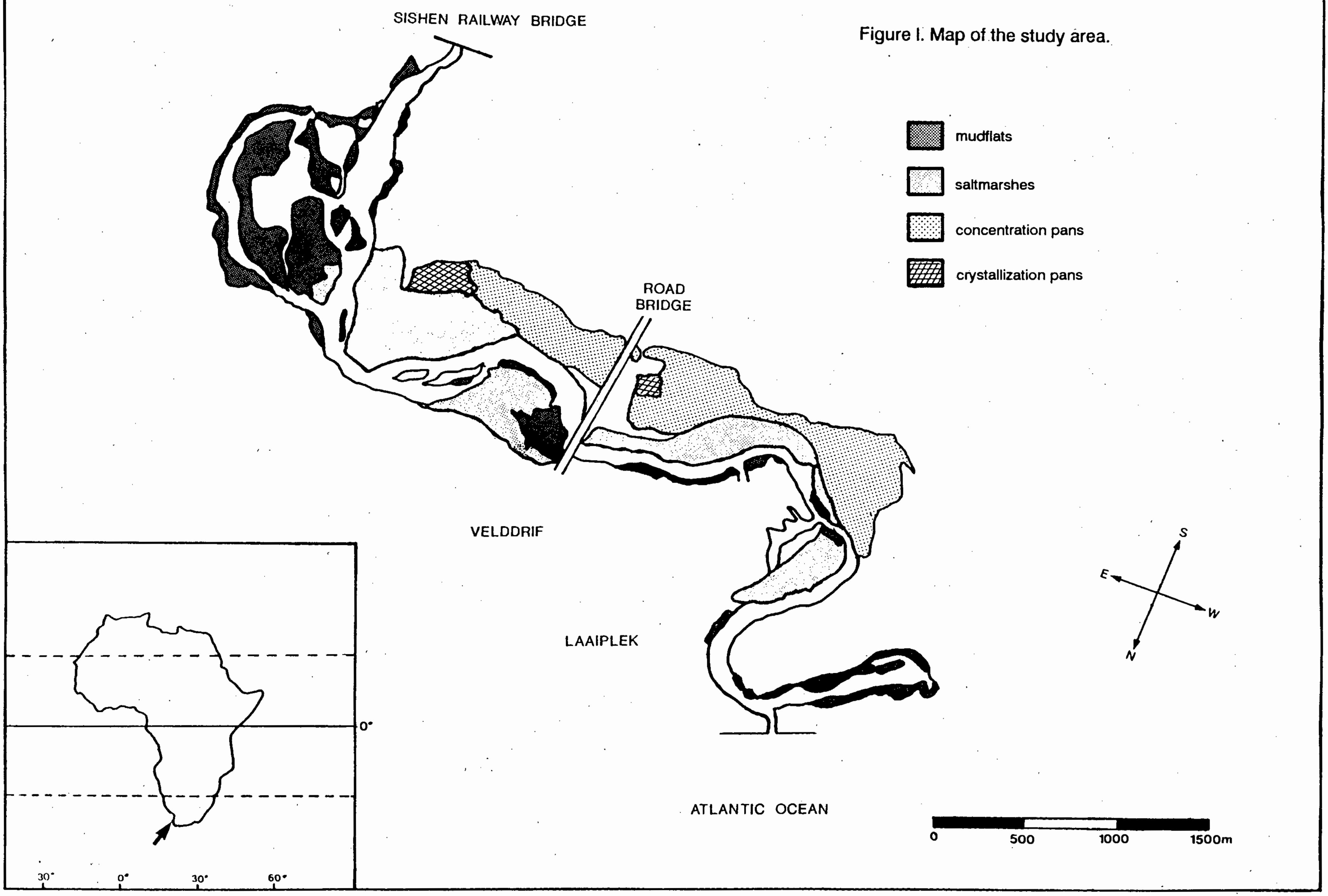


Figure I. Map of the study area.

In the subtidal area, Southern Mullet *Liza richardsonii* and Elf *Pomatomus saltatrix* occur commonly (pers. obs.).

STRUCTURE OF THE THESIS

Chapter 1 details the seasonal abundance and distribution of waterbirds at the Berg River estuary. The national importance of the estuary for resident and migratory species is assessed.

Chapters 2 and 3 detail the distribution, abundance, biomass and productivity of benthic invertebrates in the estuarine mudflats and examine biotic and abiotic factors influencing the profitability of the mudflats for foraging birds. The population dynamics of the most important prey for the majority of waders are described in detail. The relationship between estuarine productivity and latitude is investigated.

Diets of selected migrant and resident waders are described in Chapter 4. Diet is assessed using several techniques, including direct observation, and analysis of stomach contents, pellets and droppings. The potential for, and avoidance of, interspecific competition for food is discussed.

Chapters 5 and 6 investigate the predatory impact of waders on their prey population by means of theoretical calculations, direct observations and a bird exclosure experiment. Energy budgets of migrant and resident waders are estimated, and the seasonal contribution of nocturnal foraging is discussed and compared with data from north temperate estuaries.

Dispersion patterns and habitat segregation of waders are described in Chapter 7. Site preferences of birds using different foraging techniques are discussed and related to the distribution of their preferred prey and to environmental factors.

In Chapter 8, aggressive interactions of migrant and resident waders are analyzed. The influence of aggression on the foraging efficiences of birds with different foraging techniques is described, and the significance of aggression in shaping the dispersion patterns of birds within the estuary is assessed.

Chapter 9 synthesizes the findings of the site-specific study and places these in a broader theoretical framework in relation to the nonbreeding dispersion of migrant waders along the east Atlantic seaboard. In the light of information from the Berg River estuary, predictions of current models of migratory behaviour are re-examined and the significance of the Berg River study is evaluated with regard to the ways in which it might influence current thinking about the evolution of migration patterns.

Each chapter of this dissertation is writen as a discrete paper. As a consequence, some repetition, particularly methodological, is inevitable.

REFERENCES

Baker, M. C. & Baker, E. M. 1973 Niche relationships among six species of shorebirds on their wintering and breeding ranges. *Ecological Monographs* **43**, 193-212.

Burger, J., Hawn, D. C. & Chase, J. 1979 Aggressive interactions in mixed-species flocks of migrating shorebirds. *Animal Behaviour* **27**, 459-469.

Boates, J. S. & Smith, P. C. 1979 Length-weight relationship, energy content and the effects of predation on *Corophium volutator* (Pallas) (Crustacea: Amphipoda). *Proceedings of the Nova Scotia Institute of Science* **29**, 489-499.

Cox, G. W. 1968 The role of competition in the evolution of migration. *Evolution* **22**, 180-192.

Duffy, D. C., Atkins, N. & Schneider, D. 1981 Do shorebirds compete in the tropics? *Auk* **98**, 215-229.

Goss-Gustard, J. D. 1977a Predator responses and prey mortality in the Redshank *Tringa totanus* (L.), and a preferred prey, *Corophium volutator* (Pallas). *Journal of Animal Ecology* **46**, 21-35.

Goss-Gustard, J. D. 1977b The ecology of the Wash III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology* **14**, 721-739.

Kent, A. C. & Day, R. W. 1983 Population dynamics of an intertidal polychaete: the effect of predators and an adult-recruit interaction. *Journal of Experimental Marine Biology and Ecology* **73**, 185-203.

Myers, J. P. 1981 On cross-seasonal interactions in the evolution of sandpiper social systems. *Behavioural Ecology and Sociobiology* **8**, 195-202.

O'Connor, R. J. & Brown, R. A. 1977 Prey depletion and foraging strategy in the Oystercatcher *Haematopus ostralegus*. *Oecologia* **27**, 75-92.

Pienkowski, M. W. & Evans, P. R. 1984 Migratory behaviour of shorebirds in the western Palearctic In: *Behaviour of Marine Animals, Vol* **6**,. *Shorebirds:*

Migration and Foraging Behaviour (Burger, J. & Olla, B. L., eds). Plenum Press, New York & London, pp 73-123.

Pienkowski, M. W & Evans, P. R. 1985 The role of migration in the population dynamics of birds. In: *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (Sibly, R. M. & Smith, R. H., eds). Blackwell, Oxford, pp 321-352.

Quammen, M. L. 1984 Predation by shorebirds, fish and crabs on invertebrates in intertidal mudflats: an experimental test. *Ecology* **62**, 529-537.

Recher, H. F. & Recher, J. A. 1969 Some aspects of the ecology of migrant shorebirds. II. Aggression. *The Wilson Bulletin* **81**, 140-154.

Ryan, P. G., Underhill, L. G., Cooper, J. & Waltner, M. 1988 Waders (Charadrii) and other waterbirds on the coast, adjacent wetlands and offshore islands of the southwestern Cape Province. *Bontebok* **6**, 1-19.

Schneider, D. 1985 Migratory shorebirds: resource depletion in the tropics? *Neotropical Ornithological Monographs* **36**, 546-562.

Schneider, D. & Harrington, B. A. 1981 Timing of shorebird migration in relation to prey depletion. *Auk* **98**, 801-811.

Summers, R. W., Pringle, J. S. & Cooper, J. 1976 *The Status of Coastal Waders in the Southwestern Cape, South Africa*. Cape Town: Western Cape Wader Study Group.

van Wyk, A. C. 1983 Effects of dredging on the Berg River estuary. Unpubl. M.Sc. Thesis, University of Cape Town, Cape Town, South Africa.

Zwarts, L. 1981 Habitat selection and competition in wading birds. In: *Birds of the Wadden Sea* (Smit, C. J. & Wolff, W. J., eds). A. A. Balkema, Rotterdam, pp 271-278.

CHAPTER 1

SEASONAL ABUNDANCE, HABITAT SELECTION AND ENERGY CONSUMPTION OF WATERBIRDS AT THE BERG RIVER ESTUARY, SOUTH AFRICA

with C. R. Velasquez & P. A. R. Hockey,

Ostrich (1991)

SUMMARY

The distribution and abundance of waterbirds at the Berg River estuary were studied between September 1987 and April 1989. The estuary supports an unusually high density of waterbirds, especially of Palearctic migrant waders, and is a site of subregional importance for at least nine species. Intertidal mudflats are the favoured feeding habitat of the majority of species on the estuary during the low tide period. Low tide feeding densities on saltmarshes are much less than on mudflats, but saltmarshes are important as roost sites, high tide feeding sites, and in counteracting the negative hydrological consequences of development. The current conservation status of the estuary is not commensurate with its importance as a waterbird habitat and, given the current threats facing the estuary, enhanced protection at the national level is considered a greater priority than registration with, for example, the RAMSAR Convention.

INTRODUCTION

Many of the world's waders and terns (Aves: Charadriiformes) breed at high Arctic and sub-Arctic latitudes and migrate southwards during the boreal winter. The migrations of some species take them to the southerly limits of the continental land masses.

Because of its geographical position, South Africa is the southerly end-point for migratory waders using the East Atlantic, Mediterranean and Middle East Flyways (*sensu* Smit & Piersma, 1989). A large proportion of the Palearctic waders which reach South Africa are concentrated at tidal wetlands on the west coast (Summers *et al.*, 1977; Cooper & Hockey, 1981). Because South Africa is predominantly arid, there are few perennial estuaries, especially in the western part of the country (Siegfried, 1970; Le Roux, 1972; Cooper *et al.*, 1976). These few wetlands are under pressure from residential, industrial, agricultural and recreational development.

On the west coast, Cooper *et al.*, (1976) and Ryan *et al.*, (1988) identified Langebaan Lagoon and the Berg River estuary as wetlands of international importance, and suggested that both should be registered with the RAMSAR Convention on "Wetlands of International Importance, Especially as Waterfowl Habitat" (Carp, 1972). Langebaan Lagoon has subsequently been registered with the Convention, but the Berg River estuary has not been accorded international recognition.

The waterbird populations at Langebaan Lagoon have been well studied with respect to seasonal and inter-annual fluctuations in numbers of birds and their energy consumption (Pringle & Cooper, 1975; Summers, 1977; Puttick, 1980; Robertson, 1981; Baird *et al.*, 1985; Underhill, 1987). By contrast, the international importance of the Berg River was identified by Cooper *et al.*, (1976) and Ryan *et al.*, (1988) on the basis of two summer surveys, one incomplete, and without any information on interannual or seasonal variations in bird numbers and species composition.

This chapter describes the seasonal abundance, habitat preferences and energy consumption of waterbirds at the Berg River estuary over a twenty-month period spanning two austral summers and one winter. These data are used to assess the national significance of the Berg River estuary for resident and migratory waterbirds. Because waders arrive in South Africa along three different migratory flyways (SAFRING, unpubl. data), estimating 1% international flyway populations, as attempted by Smit & Piersma (1989) for sites on the East Atlantic Flyway, is not yet possible.

STUDY AREA AND METHODS

Study area and methods

The Berg River estuary (32°47'S, 18°10'E) is situated 140 km north of Cape Town, in the southwestern Cape Province, South Africa. The study area extends from the river mouth upstream to the bridge on the Sishen-Saldanha railway line and incorporates 144 ha of intertidal mudflats, 242 ha of saltmarshes, 222 ha of commercial saltpans and 232 ha of subtidal area (Fig 1.1).

Counts of all waterbirds on the entire estuary at low tide were made twice a month at spring tides between September 1987 and April 1989. Given the short period of tidal exposure, it was impossible to survey the entire area in one day: surveys took place over three consecutive days and were conducted on foot, by car and by boat. Twenty one intertidal mudflats were grouped into five sections. There were four major sections: A, B, C and D. The fifth section comprised small and scattered mudflats between sections A and B (mudflats 6-11) (Fig 1.1). Saltmarshes and saltpans also were counted individually.

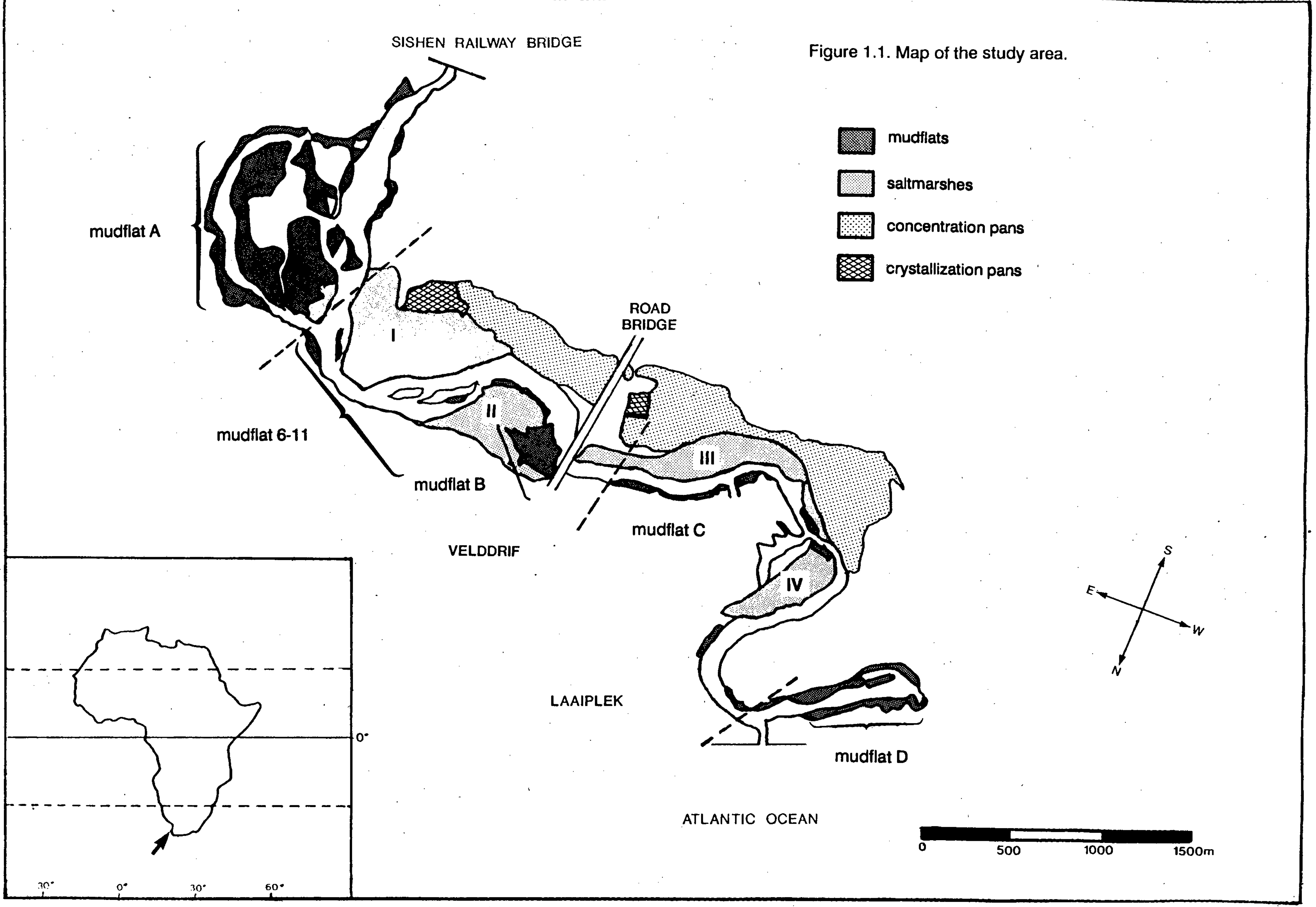


Figure 1.1. Map of the study area.

Maximum counts were used to identify species for which the Berg River estuary is of particular importance and which would qualify the estuary for registration with the RAMSAR Convention. Because insufficient data exist to determine 1% population levels within southern Africa (Africa south of the Kunene and Zambesi Rivers), a cut off point of 5% of the South African national coastal population was used to indicate a population of national importance. The populations at the Berg River were evaluated in terms of this 5% level, taking cognizance of whether or not the species occurs away from the coast. National coastal bird populations were obtained for the Cape Province and Transkei from Cooper & Hockey (1981) and for Natal from Ryan *et al.* (1986). The sum of maximum counts was used to determine the minimum numbers of birds which utilized the Berg River during the study period.

Habitat selectivity (E_i) of individual species was calculated on a seasonal basis using Jacobs' (1974) modification of Ivlev's Index.

$$E_i = (p_i - q_i)/(p_i + q_i - 2p_iq_i).$$

where $p_i = N_i/N_t$ and $q_i = A_i/A_t$.

Mean monthly abundance (N_i) was totalled within a season for mudflats, saltmarshes and salt pans separately. N_t is the total abundance in all three habitats combined. A_i is the area of habitat *i*, and A_t is the total area (608 ha.). E_i ranges from -1 to +1, with positive values indicating preference and negative values indicating avoidance of a particular habitat.

FMR (Field Metabolic Rate) of birds was calculated for each species using the formula FMR = $10.9M^{0.640}$, where M is the wet mass of the species in g (Nagy, 1987). Bird weights were taken from Maclean (1985). To obtain an estimate of DEI (Daily Energy Intake, including metabolized and non-metabolized energy), FMR was corrected for Assimilation Efficiency (AE). Values of AE used were 58% for herbivores (Fairall, 1981; Halse, 1984; Stewart & Bally, 1985), 75% for invertebrate eaters and piscivores (Cooper, 1978; Hockey, 1984), and 67% for omnivores (the average AE of herbivores and invertebrate eaters). DEI was calculated for all bird species and four major guilds: herbivores, invertebrate feeders, piscivores and omnivores. Feeding guilds were determined from details of diet in Maclean (1985). For cross-seasonal comparisons, winter was considered to extend from from May to August (123 days) and summer from September to April (242 days).

Division of the seasons in this way was determined not by the total number of birds on the estuary (which is relatively low in September), but by species composition, in particular the arrival and departure times of Palearctic migrants (Fig 1.2). During September, an influx of Palearctic migrants is counterbalanced by the departure of winter visitors such as Redknobbed Coots.

The percentage of overwintering Palearctic migrants was calculated by dividing the average 1988 midwinter (June and July) count by the average 1987/88 midsummer (November to March) count.

Scientific names of species mentioned in the text and tables are listed in Appendix 1.1, along with their feeding guilds and the habitats in which they forage at the Berg River.

RESULTS

Waterbird abundance

Eighty-four species of waterbird were recorded at the Berg River estuary between September 1987 and April 1989. Twenty-eight of these species (35%) were recorded on 25% or less of all surveys (Tables 1.1 & 1.2). Based on the maximum counts of individual species, a minimum of 37 141 birds visited the Berg River during the study period.

Table 1.1. Numbers of birds (minimum and maximum) per month at the Berg River estuary between September 1987 and April 1989. Maximum counts of rare and infrequently recorded species are detailed in Table 1.2.

SPECIES	September		October	
	1987	1988	1987	1988
Great Crested Grebe	0	1 - 9	1	0 - 2
Blacknecked Grebe	0 - 21	0 - 1	11	1 - 1
Dabchick	0	0	0	0
White Pelican	7 - 8	44 - 48	127	84 - 125
Whitebreasted Cormorant	0 - 23	22 - 85	4	42 - 43
Cape Cormorant	0 - 70	32 - 94	17	6 - 360
Reed Cormorant	0	44 - 113	1	17 - 49
Darter	0 - 3	11 - 34	6	2 - 40
Grey Heron	2 - 2	22 - 25	9	21 - 24
Blackheaded Heron	0 - 1	0 - 1	2	0
Purple Heron	0 - 1	1 - 2	1	0 - 2
Little Egret	5 - 5	15 - 33	22	18 - 29
Blackcrowned Night Heron	0	1 - 11	0	4 - 6
Sacred Ibis	0 - 8	59 - 78	20	22 - 28
Glossy Ibis	0	1 - 10	0	4 - 22
African Spoonbill	10 - 12	29 - 69	29	34 - 48
Greater Flamingo	780 - 1227	7 - 11	1774	103 - 213
Lesser Flamingo	886 - 693	20 - 30	939	5 - 556
Egyptian Goose	3 - 20	25 - 98	24	19 - 99
S.A. Shelduck	8 - 32	15 - 34	264	230 - 358
Yellowbilled Duck	0 - 5	13 - 23	6	8 - 14
Cape Teal	11 - 19	58 - 97	24	49 - 70
Cape Shoveller	0 - 53	6 - 23	42	1 - 2
Redknobbed Coot	1144 - 1219	384 - 788	560	498 - 1184
A. Black Oystercatcher	1 - 3	2 - 4	2	0 - 22
Ringed Plover	0 - 5	0 - 19	41	20 - 24
Whitefronted Plover	18 - 33	120 - 141	40	77 - 78
Chestnutbanded Plover	8 - 10	2 - 4	12	6 - 10
Kittlitz's Plover	51 - 61	69 - 228	75	84 - 88
Threebanded Plover	0	2 - 2	0	2 - 5
Grey Plover	92 - 216	96 - 239	313	199 - 267
Blacksmith Plover	17 - 31	27 - 46	19	48 - 50
Turnstone	1 - 10	0 - 4	1	11 - 12
Common Sandpiper	0	1 - 2	1	2 - 6
Marsh Sandpiper	9 - 11	15 - 47	6	20 - 28
Greenshank	166 - 191	451 - 594	225	320 - 434
Knot	0	1 - 5	0	0 - 3
Curlew Sandpiper	1476 - 2050	2429 - 3329	3572	5201 - 7001
Little Stint	7 - 118	84 - 280	260	213 - 251
Sanderling	0 - 3	0 - 1	10	0
Ruff	28 - 181	26 - 73	349	52 - 162
Bartailed Godwit	9 - 18	6 - 11	15	16 - 50
Curlew	0 - 3	0 - 4	0	2 - 4
Whimbrel	8 - 11	25 - 31	18	22 - 60
Avocet	104 - 182	53 - 83	226	47 - 66
Blackwinged Stilt	24 - 54	71 - 97	37	36 - 68
Kelp Gull	5 - 24	924 - 1134	216	254 - 381
Greyheaded Gull	0 - 4	0	3	0 - 2
Hartlaub's Gull	167 - 744	850 - 930	394	711 - 820
Caspian Tern	5 - 20	6 - 23	9	15 - 63
Swift Tern	0 - 1	7 - 28	3	23 - 77
Sandwich Tern	0	1 - 45	0	79 - 154
Common Tern	0 - 807	93 - 212	523	539 - 540
Little Tern	0	0	0	0
Whitewinged Tern	20 - 117	137 - 263	157	2147 - 2623
Pied Kingfisher	0 - 15	22 - 23	0	23 - 49

Table 1.1 (cont.)

November		December		January	
1987	1988	1987	1988	1988	1989
0	0 - 1	1	0 - 1	0 - 1	0 - 1
4 - 17	0 - 1	0	0 - 1	2 - 5	1 - 2
0	0	0	0 - 4	0	0 - 2
23 - 42	9 - 17	2	7 - 18	13 - 46	74 - 82
13 - 16	31 - 45	9	74 - 89	54 - 67	64 - 124
66 - 149	253 - 477	18	135 - 258	14 - 165	149 - 333
0	14 - 28	0	14 - 40	0	33 - 39
1 - 3	0 - 5	0	0	0 - 4	0
6 - 6	18 - 96	10	21 - 24	5 - 29	34 - 43
0 - 1	0	0	0	1 - 2	0 - 1
1 - 3	1 - 1	3	2 - 11	1	7 - 7
45 - 76	26 - 36	32	32 - 66	51 - 128	38 - 62
0 - 1	2 - 3	0	0	0	0 - 6
9 - 10	20 - 1	31	32 - 48	46 - 55	76 - 90
0	0 - 1	0	0	0	0
17 - 42	31 - 32	16	6 - 17	42 - 69	40 - 67
1333 - 1393	119 - 191	1309	108 - 261	2232 - 2313	550 - 604
292 - 524	612 - 1248	39	29 - 138	151 - 376	14 - 116
0 - 10	0 - 152	0	0	0	0 - 6
15 - 253	13 - 247	19	17 - 25	15 - 114	88 - 189
2 - 3	2 - 13	0	0	0	0 - 199
20 - 42	16 - 17	83	56 - 128	100 - 190	81 - 180
0 - 4	0 - 11	0	13 - 31	0 - 11	0 - 28
647 - 750	578 - 668	424	363 - 751	489 - 806	43 - 132
0	0 - 2	0	0 - 3	0	0
40 - 72	87 - 91	67	91 - 119	10 - 69	48 - 62
55 - 65	87 - 104	40	63 - 95	9 - 61	41 - 83
8 - 44	5 - 16	1	20 - 33	18 - 34	18 - 54
53 - 114	98 - 128	83	78 - 176	112 - 258	154 - 261
1	0 - 3	0	1 - 5	1 - 2	5 - 12
227 - 274	245 - 251	223	174 - 196	143 - 274	165 - 169
20 - 32	30 - 31	20	24 - 63	31 - 106	42 - 69
0	11 - 25	0	3 - 9	0	2 - 9
2 - 6	3 - 7	6	2 - 7	0 - 2	1 - 2
44 - 46	7 - 19	7	19 - 48	2 - 43	2 - 7
277 - 331	342 - 422	229	269 - 354	81 - 235	82 - 175
4 - 21	4 - 7	0	8 - 11	3 - 7	0 - 5
5207 - 7484	6261 - 7478	4685	5445 - 5956	3879 - 7375	6624 - 7132
482 - 527	127 - 338	190	279 - 545	118 - 340	424 - 574
0	0 - 13	1	0 - 3	0 - 3	0 - 6
85 - 88	69 - 178	89	0 - 57	55 - 151	71 - 77
17 - 17	41 - 49	14	61 - 63	2 - 4	34 - 50
1 - 7	0 - 12	19	2 - 24	2 - 20	1 - 19
21 - 23	27 - 36	36	25 - 41	15 - 20	31 - 37
49 - 280	157 - 175	45	111 - 157	99 - 186	158 - 187
54 - 82	65 - 71	74	107 - 118	111 - 135	79 - 153
146 - 180	175 - 209	30	249 - 580	198 - 269	226 - 277
0 - 4	0	0	0 - 2	0	0
480 - 649	604 - 764	487	424 - 750	629 - 847	1086 - 1128
5 - 31	56 - 61	0	70 - 85	17 - 89	48 - 90
1 - 7	10 - 37	38	35 - 109	12 - 34	49 - 646
4 - 198	347 - 452	105	507 - 1455	213 - 600	615 - 1125
375 - 1217	76 - 128	294	504 - 1026	407 - 1225	283 - 409
0	0 - 9	0	0	0 - 2	1 - 3
46 - 302	654 - 788	3	252 - 257	203 - 261	53 - 131
11 - 28	39 - 40	26	24 - 59	16 - 128	30 - 43

Table 1.1 (cont.)

February		March		April	
1988	1989	1988	1989	1988	1989
1 - 2	4 - 5	1 - 4	7 - 13	3 - 3	10 - 29
0	1	1 - 2	0	1	1 - 5
0	1 - 2	0	6 - 13	3 - 10	6 - 11
28 - 33	190 - 347	35 - 188	367 - 481	59 - 93	102 - 153
0	79 - 98	0	91 - 127	0	108 - 131
0	272 - 401	0	250 - 462	0	242 - 441
0	54 - 77	0	79 - 238	0	131 - 167
0	0 - 5	0 - 2	1 - 3	0 - 6	0 - 27
24 - 37	37 - 39	48 - 48	41 - 47	33 - 54	31 - 45
1 - 4	1 - 5	0 - 2	0 - 2	0 - 1	1 - 2
3 - 9	9 - 9	7 - 7	4 - 8	9 - 11	3 - 9
74 - 78	73 - 114	50 - 86	36 - 68	44 - 92	48 - 48
0	0	0	0	0 - 49	0
66 - 71	105 - 123	109 - 144	113 - 203	150 - 183	120 - 197
0	0 - 3	0	0 - 1	0	0
27 - 80	60 - 101	53 - 119	105 - 177	27 - 120	134 - 150
674 - 1289	278 - 485	358 - 450	129 - 280	444 - 646	121 - 144
97 - 109	25 - 79	110 - 225	22 - 23	93 - 142	22 - 52
0	0	0	0 - 9	0	1 - 18
49 - 87	42 - 58	6 - 38	62 - 166	24 - 60	9 - 86
0	110 - 231	25 - 66	63 - 309	30 - 132	0 - 9
189 - 228	179 - 241	139 - 143	114 - 169	63 - 135	52 - 78
0 - 6	0 - 10	0	5 - 5	0 - 1	4 - 61
72 - 350	1 - 20	29 - 43	3 - 3	1 - 23	122 - 233
0	0	0 - 1	0	0	0
18 - 125	98 - 142	56 - 80	39 - 60	95 - 118	50 - 141
22 - 37	33 - 47	13 - 35	22 - 40	3 - 11	9 - 53
2 - 12	7 - 35	30 - 43	28 - 30	22 - 29	6 - 16
390 - 1087	149 - 192	163 - 517	142 - 164	117 - 276	82 - 133
0 - 3	2 - 2	2 - 4	0	1 - 3	0 - 7
291 - 310	183 - 202	254 - 263	224 - 268	217 - 363	243 - 311
36 - 72	67 - 88	58 - 84	52 - 81	72 - 120	51 - 53
0 - 1	0 - 4	0 - 2	0 - 2	0 - 3	3 - 17
2 - 6	3 - 6	3 - 3	0 - 6	0	0 - 1
24 - 67	3 - 12	13 - 20	1 - 38	1	0 - 1
353 - 446	361 - 366	379 - 459	335 - 419	95 - 350	86 - 215
0	0 - 3	0 - 28	0 - 15	0	0 - 5
5299 - 7075	9146 - 9879	5397 - 6404	8055 - 8125	778 - 3846	2860 - 702
438 - 695	494 - 817	619 - 990	614 - 695	952 - 967	264 - 903
0	0 - 2	0 - 18	0 - 14	0	0
59 - 95	121 - 157	85 - 145	75 - 168	78 - 130	47 - 67
22 - 24	25 - 43	15 - 32	38 - 51	3 - 11	38 - 47
7 - 19	5 - 20	11 - 16	13 - 23	12 - 12	2 - 8
26 - 28	38 - 49	18 - 20	25 - 56	14 - 20	17 - 40
81 - 160	154 - 215	39 - 44	112 - 133	4 - 9	67 - 79
102 - 110	107 - 117	122 - 141	121 - 171	152 - 173	162 - 172
306 - 487	351 - 394	528 - 603	607 - 680	543 - 593	753 - 101
1 - 5	0	2 - 12	0	1 - 8	1 - 1
1433 - 2420	1357 - 1850	1852 - 2030	1118 - 1690	805 - 958	231 - 446
15 - 31	40 - 199	30 - 79	39 - 50	50 - 63	15 - 36
2 - 11	32 - 65	14 - 90	173 - 275	48 - 69	25 - 35
427 - 445	254 - 325	38 - 396	205 - 443	64 - 155	120 - 313
643 - 1923	222 - 356	347 - 2500	88 - 95	118 - 507	10 - 65
0 - 1	0 - 1	3 - 3	0 - 3	0	1 - 3
50 - 81	48 - 86	93 - 93	293 - 459	0 - 6	9 - 259
33 - 39	35 - 48	32 - 33	36 - 49	32 - 42	49 - 57

Table 1.1 (cont.)

May 1988	June 1988	July 1988	August 1988
1 - 3	0	0 - 0	0 - 3
3 - 4	0 - 4	0 - 2	1 - 1
19 - 35	21 - 29	15 - 19	2 - 10
76 - 130	76 - 161	34 - 144	52 - 289
0 - 132	53 - 54	62 - 72	38 - 64
256 - 449	106 - 126	64 - 99	79 - 90
148 - 191	2 - 56	48 - 98	101 - 154
16 - 64	23 - 43	28 - 52	11 - 21
30 - 44	17 - 26	22 - 25	9 - 25
1 - 2	0 - 3	0 - 1	0 - 1
2 - 5	0 - 1	0 - 1	0 - 1
37 - 62	27 - 27	31 - 68	37 - 43
0 - 54	12 - 28	0 - 1	0 - 22
283 - 385	160 - 207	134 - 174	47 - 63
0 - 2	0 - 1	0 - 19	0
97 - 236	89 - 129	77 - 94	41 - 42
180 - 276	226 - 292	81 - 178	46 - 49
128 - 262	8 - 37	28 - 41	5 - 6
55 - 426	18 - 132	17 - 60	60 - 415
124 - 242	2 - 91	63 - 93	32 - 163
138 - 158	53 - 130	32 - 39	24 - 24
84 - 133	51 - 80	66 - 71	39 - 55
0 - 11	32 - 33	8 - 11	5 - 24
47 - 814	1237 - 1285	967 - 1363	1281 - 3330
0	0	0 - 2	0 - 2
0 - 15	0	0	0
18 - 98	55 - 83	110 - 128	113 - 148
12 - 24	16 - 47	41 - 92	22 - 29
218 - 522	79 - 288	116 - 550	152 - 441
4 - 13	2 - 11	2 - 9	2 - 12
23 - 172	21 - 25	22 - 43	38 - 67
83 - 231	24 - 215	42 - 64	28 - 53
0 - 8	1 - 35	0 - 1	0 - 3
0	0	0	0 - 3
1 - 5	0	0	2 - 21
59 - 152	101 - 112	147 - 191	217 - 417
0 - 2	0	0	0
216 - 420	239 - 340	370 - 372	597 - 680
7 - 47	0 - 4	0	0 - 43
0	0	0	0
0 - 32	0	0	14 - 26
1 - 13	0 - 11	0 - 10	8 - 8
1 - 32	0 - 1	0 - 1	0 - 1
12 - 15	2 - 7	4 - 4	9 - 18
0	0	17 - 52	45 - 48
157 - 196	127 - 174	109 - 148	91 - 135
568 - 941	557 - 1127	1601 - 1640	752 - 1172
0 - 1	0	0	2 - 3
846 - 1035	425 - 692	756 - 767	714 - 954
8 - 39	0 - 3	9 - 11	12 - 21
5 - 16	5 - 62	9 - 25	13 - 18
3 - 41	4 - 9	1 - 69	3 - 30
29 - 302	9 - 13	0 - 2	3 - 5
0	0	0	0
0 - 4	1 - 1	1 - 26	49 - 73
42 - 71	24 - 65	52 - 69	40 - 68

Table 1.2. Species recorded during less than 25% of surveys at the Berg River estuary between September 1987 and April 1989.

Species	Number of counts when birds were recorded	Maximum number recorded
Great White Egret	6	1
Yellowbilled Egret	1	1
Little Bittern	1	2
Glossy Ibis	8	22
Redbilled Teal	5	5
Spurwinged Goose	3	18
African Fish Eagle	1	1
African Marsh Harrier	10	1
Osprey	3	1
Black Crake	1	1
Purple Gallinule	8	3
Moorhen	1	1
African Rail	1	1
Mongolian Plover	2	1
Sand Plover	2	2
Crowned Plover	5	53
Terek Sandpiper	2	1
Wood Sandpiper	1	2
Redshank	*	3
Broadbilled Sandpiper	*	1
Blacktailed Godwit	1	1
Pectoral Sandpiper	*	1
Rednecked Phalarope	2	1
Spotted Dikkop	8	13
Water Dikkop	3	2
Franklin's Gull	*	1
Giant Kingfisher	2	1
Malachite Kingfisher	5	1

* not recorded during routine surveys

On average, more than 12 000 birds were counted at the estuary during summer surveys and more than 6 000 during winter surveys. Palearctic migrants dominated the avifauna numerically during the summer, accounting for 66% of all birds present. Eighty-five percent of all Palearctic migrants were waders, the remainder being terns. The most abundant bird on the estuary during summer was the Curlew Sandpiper, which accounted for between 42% (1987/88) and 51% (1988/89) of all birds. Other abundant species were Greater Flamingo (2-10%), Hartlaub's Gull (7-8%), Common Tern (2-7%) and Whitewinged Tern (1-4%).

Redknobbed Coots and Kelp Gulls were the most abundant species during the winter, accounting respectively for 17.5% and 16% of all birds present at this time. Although the majority of Curlew Sandpipers left the estuary during the winter, this species was still the most abundant wader present in winter, accounting for 13.9% of all birds.

Peak numbers of nine species exceeded 1 000 birds. In terms of their contribution to the national coastal wetland population, 38 species exceeded 5% of the total and two species exceeded 50% of the total. Taking into consideration both coastal wetlands and the open coastline, maximum counts of 34 species at the Berg River exceeded 5% of the national coastal total and five species (Sacred Ibis, African Spoonbill, Kittlitz's and Crowned Plovers and Caspian Tern) exceeded 25% of the total (Table 1.3).

Seasonal patterns of abundance and biomass

There were marked seasonal changes in the abundance of many species. The main migratory influx of Palearctic migrants occurred during September and October. In both summers, numbers of Palearctic migrants decreased in December, and this was followed by a second peak in abundance prior to northward migration in February

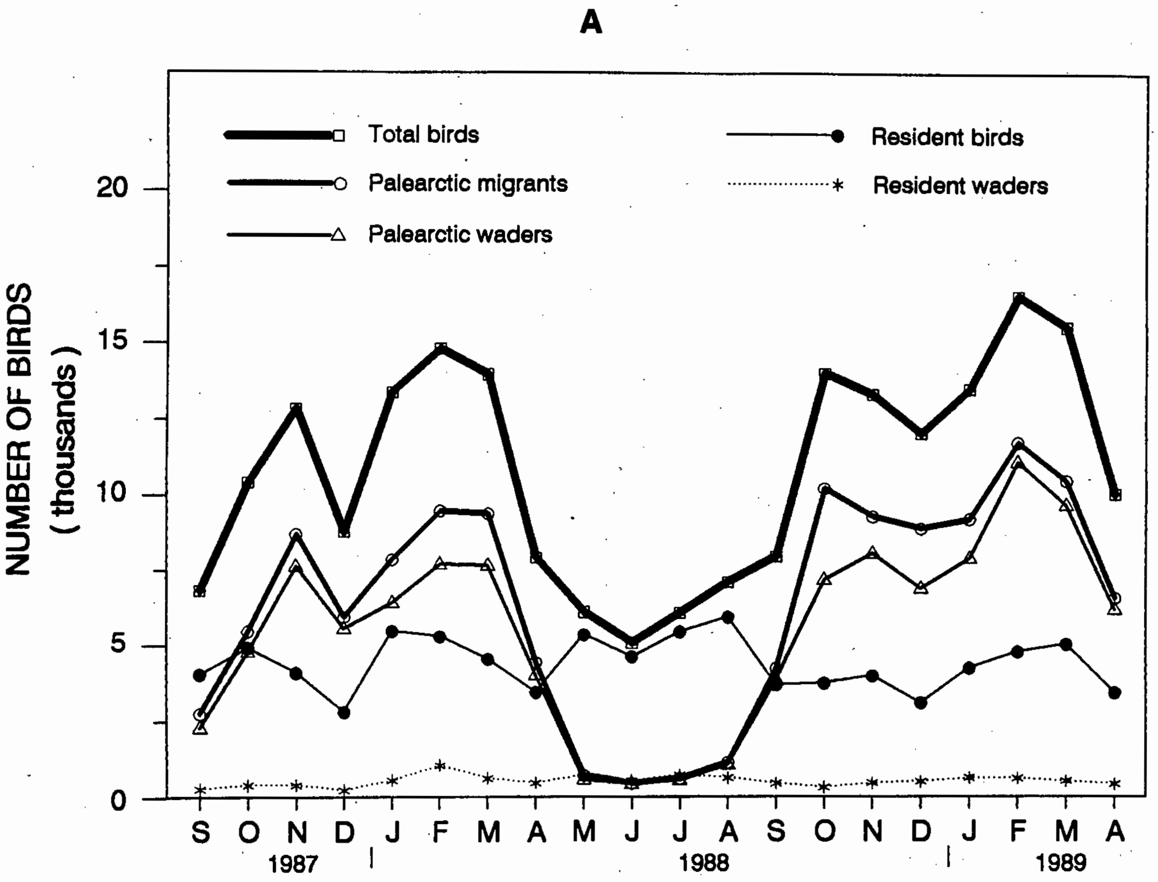
Table 1.3. Maximum counts of waterbirds at the Berg River Estuary and their percentage contribution to the estimated total numbers occuring at South African coastal wetlands (including Walvis Bay) and on the entire South African Coastline. the Month in which maximum numbers were recorded is given in parentheses.

		% of national coastal population	
	Maximum numbers	Wetlands	Total
Great Crested Grebe	29 (4)	8.2	7.8
White Pelican	481 (3)	22.6	20.3
Whitebreasted Cormorant	132 (5)	5.1	1.5
Reed Cormorant	238 (3)	8.3	8.2
Darter	64 (5)	5.2	5.2
Grey Heron	96 (11)	11.6	10.4
Purple Heron	11 (4.12)	9.2	9.2
Little Egret	28 (1)	11.1	9.0
Blackcrowned Night Heron	54 (5)	29.0	22.9
Sacred Ibis	385 (5)	68.3	39.2
Glossy Ibis	22 (10)	13.6	13.6
African Spoonbill	236 (5)	25.7	25.7
Greater Flamingo	2313 (1)	7.5	7.5
Lesser Flamingo	1248 (11)	5.7	5.7
Egyptian Goose	426 (5)	11.3	11.2
South African Shelduck	358 (10)	15.6	15.4
Cape Teal	241 (2)	5.5	5.5
Spurwinged Goose	18 (5)	5.8	5.6
Redknobbed Coot	3330 (8)	6.0	6.0
African Black Oystercatcher	22 (10)	6.3	0.5
Whitefronted Plover	148 (8)	4.9	1.0
Kittlitz's Plover	1087 (2)	42.7	37.7
Crowned Plover	53 (2)	88.3	40.5
Blacksmith Plover	231 (5)	11.6	11.1
Marsh Sandpiper	67 (2)	6.8	6.8
Greenshank	594 (9)	17.2	15.3
Curlew Sandpiper	9879 (2)	12.0	9.5
Little Stint	990 (3)	5.0	4.9
Bartailed Godwit	63 (12)	6.8	5.7
Curlew	32 (5)	7.2	7.0
Avocet	280 (11)	4.5	4.4
Blackwinged Stilt	196 (5)	7.2	7.2
Spotted Dikkop	13 (9)	18.8	6.6
Kelp Gull	1640 (7)	20.0	3.7
Hartlaub's Gull	2420 (2)	21.7	7.2
Caspian Tern	199 (2)	38.0	35.0
Swift Tern	646 (1)	27.9	6.5
Sandwich Tern	1455 (12)	39.9	16.4
Whitewinged Tern	2623 (10)	24.1	24.1
Pied Kingfisher	128 (1)	20.2	18.5

(Fig 1.2A). Although most migratory species arrived in September, the first Curlew Sandpipers, Little Stints, Greenshanks and Whimbrels arrived during August. There were differences in the timing of northward migration between species. Marsh Sandpipers and Whitewinged Terns left the estuary in March. The majority of Curlew Sandpipers, Ringed Plovers and Greenshanks departed in early April, whereas Grey Plovers, Little Stints, Ruffs and Sandwich Terns remained until late April. Curlews, Whimbrels and Common Terns did not leave the estuary until mid-May (Table 1.1).

The percentage of overwintering Palearctic migrants varied from 0% for Ruffs, Marsh Sandpipers and Ringed Plovers, to 0.2-0.7% for Little Stints and Common Terns, 6-8% for Curlews, Curlew Sandpipers and Sandwich Terns, 11-18% for Grey Plovers and Whimbrels, and 34% and 46% for Bartailed Godwits and Greenshanks, respectively.

Resident species fluctuated considerably in numbers throughout the year. Numbers during winter were 23% higher than average numbers during the two summers. With the exception of Avocets, resident waders peaked in numbers during mid-winter. Kittlitz's Plover was the most abundant resident wader during winter. However, there was an influx of this species to the estuary in February 1988. Blackwinged Stilts were most abundant during autumn and winter, but decreased in numbers before the main influx of Palearctic waders occurred in spring. The majority of waterfowl attained peak numbers in mid-summer, with the exception of Redknobbed Coots and Egyptian Geese which were most abundant during winter. Apart from Kelp Gulls, some of which leave to breed elsewhere during summer, resident gulls and terns were most abundant during summer. Numbers of pelicans, egrets and herons fluctuated greatly throughout the year, although there was a tendency for numbers to be greatest during summer (Table 1.1).



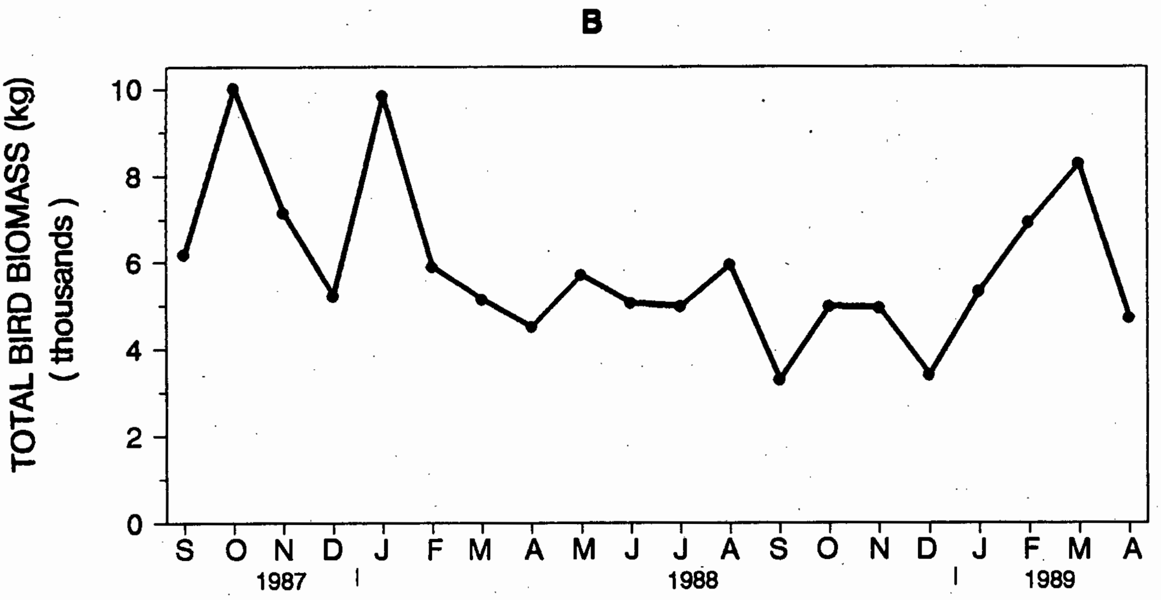


Figure 1.2. Average monthly numbers (A) and biomass (B) of birds recorded at the Berg River estuary, September 1987-April 1989.

There were marked interannual differences in species abundance, with total bird numbers in the summer of 1988/89 being 13.5% higher than in 1987/88 (Fig 1.2A). To a large extent this difference was due to higher numbers of Curlew Sandpipers, Bartailed Godwits, Whimbrels, Greenshanks and Sandwich Terns in the summer of 1988/89 as compared with the previous summer. In addition, numbers of White Pelicans and the three cormorant species were respectively 60% and 70-100% higher during summer 1988/89 than in 1987/88. The reverse was true for Greater and Lesser Flamingos which decreased by 79% and 28% respectively.

The total biomass of birds at the Berg River ranged between 3 289 kg and 10 013 during the study period, but fluctuated on a seasonal basis less than did bird numbers (Figs 1.2A & B). The mean summer biomass was 5989.5 kg and the mean winter biomass was 5419.0 kg (Fig 1.2B). Although the average summer biomass was close to the 1988 winter biomass, there was a marked difference in biomass between the two summers. In summer 1987/88, avian biomass was 22.4% higher than in 1988/89. This difference is attributable to flamingos, which contributed 63% to the total biomass in summer 1987/88 and only 19% in the following summer.

Habitat selection by birds

Of the intertidal foraging habitats, mudflats were the most important feeding habitat during low tide, supporting, on average, 75% of all birds. In comparison, the saltpans supported 19% of birds and only 6% utilized saltmarshes. The relative proportion of birds occupying each habitat was stable throughout the year.

Intertidal mudflats supported the highest densities of birds throughout the year with a peak of 94 birds ha^{-1} in February 1989 (Fig 1.3). During the summers of 1987/88 and 1988/89 the average densities of Palearctic waders on mudflats were 34.5 and 47.2 birds ha^{-1}, respectively. In February 1989, density peaked at 70.8 migrant

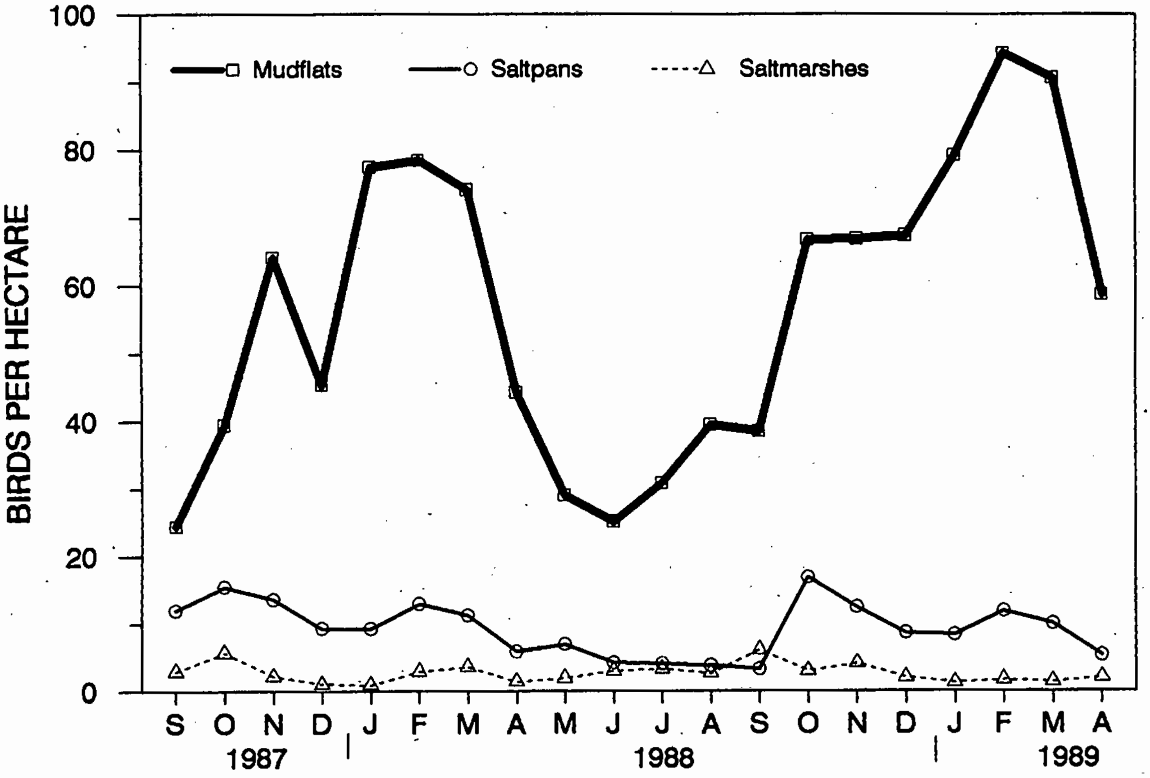


Figure 1.3. Average monthly densities of birds on mudflats, saltmarshes and saltpans at the Berg River estuary, September 1987-April 1989.

waders ha^{-1}. Mudflat A, the largest and farthest from the river mouth, supported the highest numbers, but not the highest density, of birds throughout the year (Fig 1.4, Table 1.4). The least preferred mudflat was mudflat D, at the mouth of the river, where the sediment is coarsest. Mudflat C comprised small intertidal mudflats and supported the highest densities of birds, especially during the summer of 1988/89 (Table 1.5), due mainly to large numbers of terns and gulls roosting at low tide. Densities on the saltpans ranged between 3.2 and 6.9 birds.ha^{-1} during winter and reached maxima of 15.4 and 16.7 birds.ha^{-1} in October of 1987 and 1988, respectively (Fig 1.3). The peak usage of saltpans at this time in 1987 was due to the arrival of flamingos, and the peak in 1988 was due to an influx of Whitewinged Terns. High densities of birds at the saltpans during February and March 1989 was due largely to Hartlaub's Gulls, which bred on the retaining walls of the pans. The number of birds utilizing concentration pans was highest during the summer months, whereas crystallization pans were used most during the winter when salinity levels were lowest (Fig 1.4). Densities in crystallization pans peaked at 70 birds ha^{-1} in March 1988. The density of birds on the saltmarshes ranged between 1.2 and 3.2 birds ha^{-1} throughout the year (Fig 1.3), except in late spring when the arrival of Ruffs and South African Shelducks elevated densities to 6.0 birds ha^{-1} in both years. Overall, the numbers of birds using the saltmarshes fluctuated more erratically than in other habitats (Fig 1.4).

In terms of individual species' feeding habitat preferences, the large majority of species strongly favoured mudflats in both summer and winter (Table 1.5). At all times of the year, however, saltmarshes were favoured by Blackheaded Herons, Redbilled Teals and Ruffs. During summer, both flamingo species, Chestnutbanded and Crowned Plovers, Ruffs, Cape Teals, Avocets, Blackwinged Stilts and Whitewinged Terns showed positive selection for saltpans. During winter this preference was retained only by the latter four species. A substantial increase in the

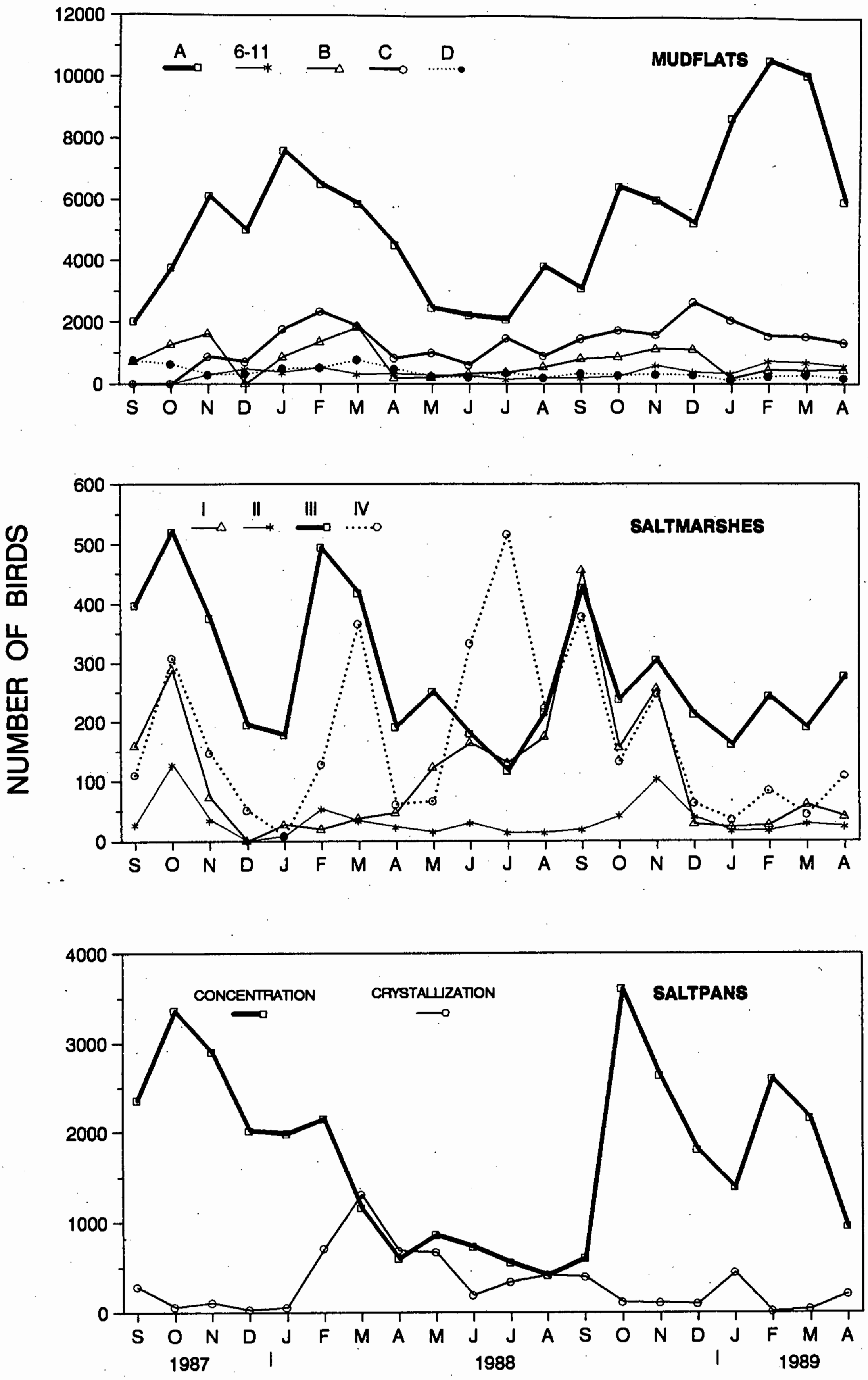


Figure 1.4. Average monthly numbers of birds using different habitats and sites within the Berg River estuary, September 1987-April 1989.

Table 1.4. Average seasonal densities of birds utilizing different habitats within the Berg River estuary. September 1987-April 1989. See Fig 1.1 for site details.

		DENSITY (birds ha^{-1})			
Habitat	Area ha^{-1}	Summer 1987/88	Summer 1988/89	Winter 1988	Average
MUDFLATS					
A	90.6	57.2	77.6	29.2	59.7
6-11	5.5	51.1	81.5	38.8	60.8
B	17.6	55.9	38.2	20.8	41.8
C	12.3	85.1	140.7	80.8	106.5
D	17.7	30.3	14.2	14.3	20.7
Total	143.7	55.9	70.2	31.1	56.7
SALTMARSHES					
I	108.7	0.7	1.2	1.4	1.0
II	48.3	0.8	0.7	0.4	0.7
III	55.6	6.2	4.6	3.4	5.0
IV	29.8	4.9	4.6	9.5	5.7
Total	242.4	2.5	2.6	2.7	2.6
SALTPANS					
Concentration	204.1	10.1	9.6	3.1	8.5
Crystallization	17.9	22.7	9.8	22.5	17.5
Total	222.0	11.1	9.5	4.7	9.2
ALL HABITATS	608.1	18.3	21.2	10.1	17.8

Table 1.5. Summer and winter habitat selectivity indices (Jacobs, 1974) of waterbirds at the Berg River estuary. Diving and aerially-foraging piscivores are excluded.

	SUMMER			WINTER		
Species	mud flats	salt marshes	salt pans	mud flats	salt marshes	salt pans
White Pelican	0.91	-0.85	-0.74	0.75	-0.51	-0.57
Darter	0.99	-0.95	-1.00	0.98	-0.92	-0.99
Grey Heron	0.89	-0.69	-0.81	0.77	-0.52	-0.62
Blackheaded Heron	-0.17	0.40	-0.36	-1.00	0.35	0.12
Purple Heron	0.72	-0.11	-1.00	0.76	-0.19	-1.00
Great White Egret	1.00	-1.00	-1.00	0.69	-1.00	0.02
Little Egret	0.84	-0.65	-0.69	0.59	-0.31	-0.40
Blackcrowned Night Heron	0.89	-0.83	-0.68	0.99	-1.00	-0.97
Sacred Ibis	0.67	-0.09	-0.88	0.62	-0.00	-0.89
Glossy Ibis	0.89	-0.55	-1.00	-0.03	-0.12	0.14
African Spoonbil	0.92	-0.68	-0.97	0.85	-0.66	-0.70
Greater Flamingo	0.54	-1.00	0.26	0.80	-1.00	-0.23
Lesser Flamingo	-0.49	-1.00	0.89	0.86	-1.00	-0.40
Egyptian Goose	0.95	-0.85	-0.92	0.90	-0.66	-0.93
S.A. Shelduck	0.96	-0.94	-0.88	0.96	-0.86	-0.92
Yellowbilled Duck	0.99	-0.95	-1.00	0.75	0.54	-0.92
Cape Teal	-0.25	-0.86	0.74	-0.26	-0.29	0.39
Redbilled Teal	-1.00	0.50	-0.07	-0.21	0.77	1.00
Cape Shoveller	0.80	-0.35	-0.94	0.59	-0.03	-0.78
Spurwinged Goose	1.00	-1.00	-1.00	1.00	-1.00	-1.00
Purple Gallinule	1.00	-1.00	-1.00	1.00	-1.00	-1.00
Redknobbed Coot	0.99	-0.98	-0.98	1.00	-1.00	-1.00
African Black Oystercacher	1.00	-1.00	-1.00	1.00	-1.00	-1.00
Ringed Plover	0.93	-0.92	-0.72	0.96	-1.00	-0.81
Whitefronted Plover	0.87	-0.89	-0.54	0.92	-0.83	-0.79
Chestnutbanded Plover	-0.42	-0.90	0.82	-0.19	0.15	-0.02
Kittlitz's Plover	0.15	0.02	-0.13	0.69	-0.37	-0.58
Threebanded Plover	0.69	-0.68	-0.59	0.65	-0.57	-0.27
Grey Plover	0.96	-0.93	-0.85	0.98	-0.98	-0.97
Crowned Plover	-0.21	-0.97	0.78	-1.00	-1.00	1.00
Blacksmith Plover	0.78	-0.58	-0.59	0.83	-0.57	-0.74
Turnstone	0.82	-0.92	-0.35	1.00	-1.00	-1.00
Common Sandpiper	0.69	-0.89	-0.07	0.24	-1.00	0.55
Marsh Sandpiper	0.80	-0.57	-0.66	0.99	-0.97	-1.00
Greenshank	0.89	-0.64	-0.92	0.86	-0.49	-0.96
Knot	0.97	-1.00	-0.84	1.00	-1.00	-1.00
Curlew Sandpiper	0.95	-0.92	-0.84	0.83	-0.57	-0.74
Little Stint	0.77	-0.59	-0.54	0.51	0.05	-0.70
Sanderling	0.85	-0.96	-0.40	1.00	-1.00	-1.00
Ruff	-0.87	0.23	0.17	-0.92	0.78	-0.86
Bartailed Godwit	0.99	-1.00	-0.95	1.00	-1.00	-1.00
Curlew	0.99	-0.97	-1.00	1.00	-1.00	-1.00
Whimbrel	0.93	-0.83	-0.83	0.76	-0.50	-0.61
Avocet	-0.65	-0.70	0.79	-0.08	-0.12	0.17
Blackwinged Stilt	0.17	-0.56	0.34	0.31	-0.30	0.00
Whitewinged Tern	-0.35	-0.83	0.77	0.00	-0.80	0.67

use of saltpans during winter, when salinities are at their lowest, was recorded for Blackheaded Herons and Glossy Ibises (Table 1.5).

Energy consumption by birds

Using values of DEI obtained by correcting FMR for variable AE between guilds, the average summer DEI of the entire bird assemblage was $7.31*10^6$ kJ day^{-1}. The two most important consumers on the estuary during summer, Greater Flamingos and Curlew Sandpipers, respectively accounted on average for 23% and 15% of the total consumption. Total DEI in winter was $6.46*10^6$ kJ day^{-1}. Of this, Redknobbed Coots accounted for 25% and Kelp Gulls for 19% (Table 1.6).

The total estimated annual energy intake of all birds at the Berg River estuary was $2\,564*10^6$ kJ. Waders accounted for $434*10^6$ kJ (17%), and all invertebrate feeders combined for $1\,230*10^6$ kJ (48%). Assuming an average prey energy content of 20 kJ g^{-1} dry mass, the total food consumption by birds within the estuary amounts to ca 128 t y^{-1}.

Seasonal patterns of DEI

Avian DEI at the Berg River estuary varied little during the year, but on average was higher during summer than winter (Fig 1.5a). Invertebrate feeders and herbivores showed pronounced seasonal fluctuations in DEI (Figs 1.5b & 1.5d). The former accounted for the majority of the energy transfer to birds during summer, whereas the importance of herbivores was maximal during winter. Piscivores showed no clear seasonal pattern of DEI (Fig 1.5c).

Seasonal fluctuations in the DEI of invertebrate feeders were determined largely by the energy demands of Greater Flamingos and migrant waders (Fig 1.5b). Although

Table 1.6. Daily energy intake (DEI, in KJ) of birds at the Berg River estuary. Species which contributed less than 0.1% to the total energy intake are grouped as "total others". The habitats in which each species foraged are detailed in Appendix 1.1.

POPULATION DAILY ENERGY INTAKE

SPECIES	Individual DEI	Summer 1987/88 kJ day^{-1}*10^{3}	Summer 1988/89 kJ day^{-1}*10^{3}	Winter 1988 kJ day^{-1}*10^{3}
White Pelican	5107	265.88	685.61	603.48
Whitebreasted Cormorant	1632	20.30	127.81	102.07
Cape Cormorant	1380	46.06	359.23	218.85
Reed Cormorant	816	0.10	57.99	80.27
Darter	1572	3.05	12.58	49.39
Grey Heron	1499	31.10	53.21	36.35
Little Egret	721	37.94	33.44	30.31
Sacred Ibis	1396	83.15	116.92	249.59
African Spoonbill	1755	77.66	120.66	169.07
Greater Flamingo	2441	2945.22	549.84	401.14
Lesser Flamingo	2212	819.11	413.57	142.23
Egyptian Goose	2520	12.76	67.25	334.54
South African Shelduck	1384	109.60	141.77	139.78
Yellowbilled Duck	1260	21.65	78.26	94.69
Cape Teal	752	70.21	74.54	54.99
Cape Shoveler	1020	10.14	12.75	15.34
Spurwinged Goose	5023	3.77	0.00	12.56
Redknobbed Coot	1279	602.70	461.24	1633.90
Ringed Plover	205	11.58	13.98	0.27
Whitefronted Plover	176	5.74	12.02	16.86
Kittlitz's Plover	161	35.37	22.40	46.26
Blacksmith Plover	369	17.46	18.96	32.53
Grey Plover	499	124.63	107.04	22.95
Marsh Sandpiper	231	4.43	3.85	0.86
Greenshank	465	124.13	151.85	81.90
Curlew Sandpiper	191	868.86	1216.96	77.43
Little Stint	111	49.62	47.88	1.26
Ruff	347	44.59	30.36	2.66
Bartailed Godwit	612	8.87	23.83	3.70
Whimbrel	737	15.29	25.80	6.63
Avocet	581	64.60	70.95	11.77
Blackwinged Stilt	399	36.96	42.77	56.82
Kelp Gull	1149	314.11	589.58	1214.83
Hartlaub's Gull	531	490.38	489.81	414.09
Caspian Tern	931	26.36	52.14	11.87
Swift Tern	624	14.47	63.41	11.80
Sandwich Tern	500	85.94	201.25	9.42
Common Tern	347	253.81	100.76	13.62
Whitewinged Tern	193	19.20	102.04	3.71
Pied Kingfisher	232	6.68	9.08	12.66
TOTAL OTHERS		28.88	35.27	32.62
TOTAL		7814.88	6801.20	6460.04

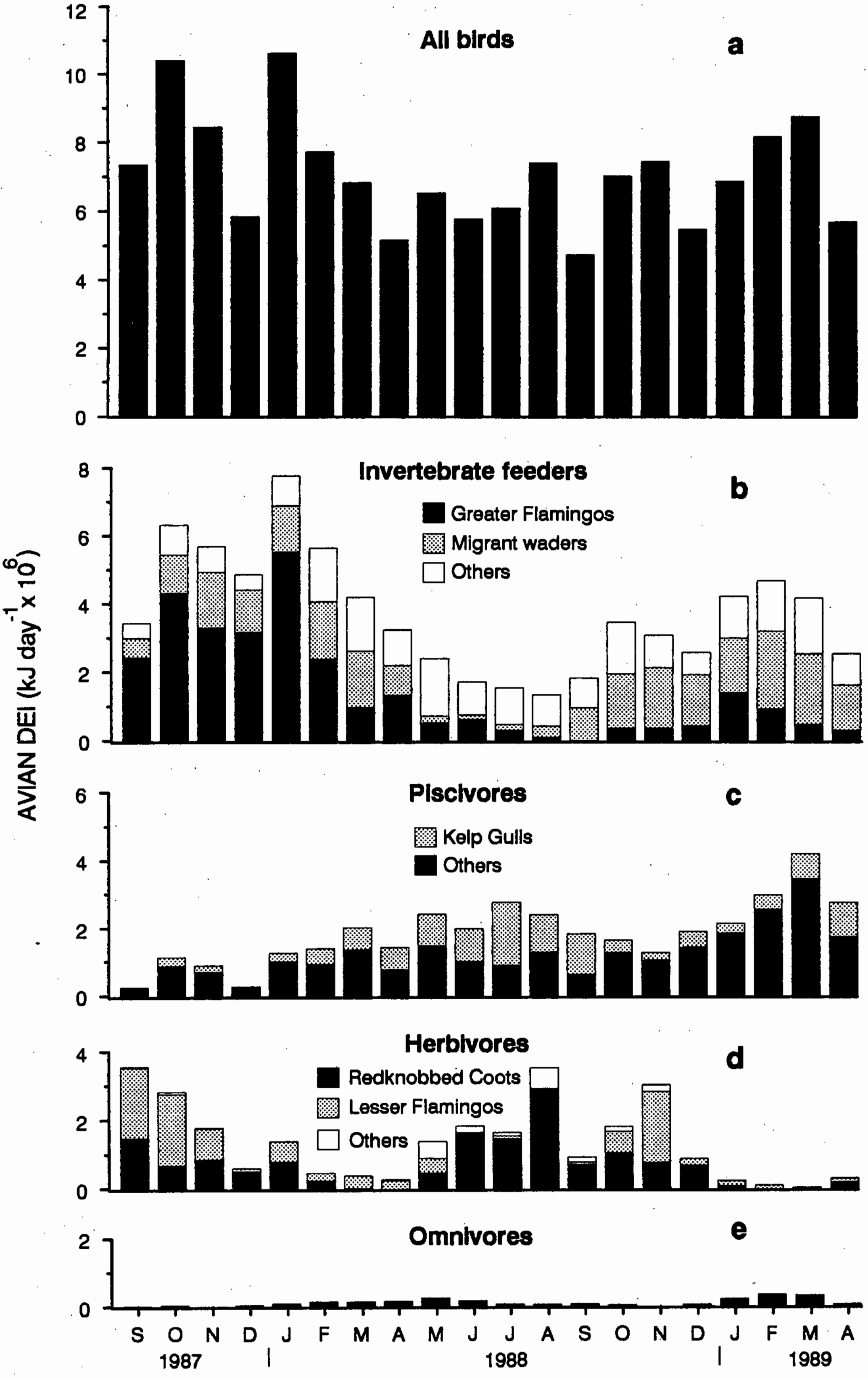


Figure 1.5. Seasonal patterns of DEI of avian feeding guilds at the Berg River estuary. Although Kelp Gulls are predominantly scavengers (Appendix 1.1), they scavenge mainly on fish and are included with piscivores in this figure.

there were fewer birds on the estuary in summer 1987/88 than 1988/89, the DEI of invertebrate feeders was higher in the 1987/88 summer due to the large numbers of Greater Flamingos present at this time (Table 1.1, Fig 1.5b). The DEI of migrant waders in summer 1988/89 was higher than in the previous summer (Fig 1.5b). The winter peak in herbivore energy demand was accounted for largely by Redknobbed Coots and Lesser Flamingos (Fig 1.5d). Omnivores contributed little to the total DEI throughout the year (Fig 1.5e).

DISCUSSION

Numbers and seasonal fluctuations

Prior to these surveys, there was only one complete count of waterbirds at the Berg River estuary, made in the Austral summer of 1980/81 (Ryan *et al.*, 1988). Maximum counts of most species made during the present surveys exceeded, or were equivalent to the 1980/81 counts. Whilst it is difficult to infer population increases with only one count for comparison, there are six species which may have undergone population decreases (1980/81 count *vs* maximum count in 1987-1989 in parentheses). These are Little Egret (77 *vs* 28), Lesser Flamingo (1 597 *vs* 1 248), Cape Shoveller (106 *vs* 61), Ringed Plover (180 *vs* 142), Knot (131 *vs* 28) and Ruff (1 422 *vs* 349). In view of the diverse habitat preferences and feeding techniques of this group of species, no single reason can be invoked for the apparent decreases. In absolute terms, the greatest decrease has been of Ruff; this may be due to saltmarsh degradation (see below).

The density of waterbirds at the Berg River estuary is higher than that reported from any other coastal wetland in southern Africa where regular counts of waterbirds have been made, including Langebaan Lagoon (Underhill, 1987) and the Swartkops estuary (Martin & Baird, 1987). This is reflected in a high avian biomass per unit intertidal area at the Berg River (Table 1.7). With regard to the migrant

Table 1.7. A comparison of the summer and winter biomass and energy demands of three feeding guilds of waterbirds at three South African coastal waterbirds. In calculating DEI per unit area, piscivores were assumed to feed entirely subtidally and other guilds to feed intertidally. Figures for Langebaan Lagoon and Swartkops estuary are calculated from data in Underhill (1987) and Martin & Baird (1987), respectively.

	Berg River	Langebaan Lagoon	Swartkops Estuary
Intertidal area (ha^{-1})	608	2530	173
Subtidal area (ha^{-1})	232	627	154
		SUMMER	
HERBIVORES			
Ave-daily biomass (kg)	819.0	25.6	-
Biomass (kg ha^{-1} d^{-1})	1.3	0.01	-
DEI (kJ d^{-1})	1 190.2 * 10^3	20.0 * 10^3	-
DEI (kJ ha^{-1} d^{-1})	1 957.6	8.5	-
INVERTEBRATE FEEDERS			
Ave-daily biomass (kg)	3 292.0	5 450.3	842.9
Biomass (kg ha^{-1} d^{-1})	5.4	2.3	4.9
DEI (kJ d^{-1})	4 245.2 * 10^3	10 151.3 * 10^3	1 320.5 * 10^3
DEI (kJ ha^{-1} d^{-1})	6 982.2	4 319.7	7 633.1
ALL INTERTIDAL FEEDERS			
DEI (kJ ha^{-1} d^{-1})	8 939.8	4 328.2	7 633.1
PISCIVORES			
Ave-daily biomass (kg)	1 432.0	244.8	95.6
Biomass (kg ha^{-1} d^{-1})	6.2	0.4	0.6
DEI (kJ d^{-1})	1 286.1 * 10^3	388.9 * 10^3	174.4 * 10^3
DEI (kJ ha^{-1} d^{-1})	5 543.7	620.2	1 132.4
		WINTER	
HERBIVORES			
Ave-daily biomass (kg)	1 340.0	604.1	-
Biomass (kg ha^{-1} d^{-1})	2.2	0.3	-
DEI (kJ d^{-1})	2 122.9 * 10^3	494.5 * 10^3	-
DEI (kJ ha^{-1} d^{-1})	3 491.6	210.4	-
INVERTEBRATE FEEDERS			
Ave-daily biomass (kg)	1 382.0	16 674.9	747.9
Biomass (kg ha^{-1} d^{-1})	2.3	7.1	4.3
DEI (kJ d^{-1})	1 754.7 * 10^3	12 371.4 * 10^3	986.0 * 10^3
DEI (kJ ha^{-1} d^{-1})	2 886.0	5 264.4	5 699.2
ALL INTERTIDAL FEEDERS			
DEI (kJ ha^{-1} d^{-1})	6 377.6	5 474.9	5 699.2

Table 1.7 (cont.)

PISCIVORES			
Ave-daily biomass (kg)	1 613.0	59.6	93.9
Biomass (kg ha^{-1} d^{-1})	6.9	0.1	0.6
DEI (kJ d^{-1})	1 200.8 * 10^{3}	84.8 * 10^{3}	126.3 * 10^{3}
DEI (kJ ha^{-1} d^{-1})	5 176.0	135.2	729.9
		ANNUAL AVERAGE	
INTERTIDAL FEEDERS			
Biomass (kg ha^{-1})	6.0	4.0	4.7
DEI (KJ ha^{-1} d^{-1})	8 076.3	4 714.6	6 981.4
PISCIVORES			
Biomass (kg ha^{-1})	6.4	0.3	0.6
DEI (KJ ha^{-1} d^{-1})	5 419.8	456.8	1 027.1

wader component of this density, the Berg River intertidal mudflats support one of the highest densities reported from the entire east Atlantic seaboard (Zwarts, 1988). Densities of waders on intertidal mudflats at European estuaries range between 0.4 birds ha^{-1} at the Danish Wadden Sea (Smit, 1982) and 18.0 birds ha^{-1} at the Vendée, France (Spitz, 1964). Densities of migrant waders on the west African coastline range between 5.2 birds ha^{-1} at Yawri Bay, Sierra Leone (Tye & Tye, 1987) and 41.6 birds ha^{-1} at the Banc d'Arguin, Mauritania (Engelmoer *et al.*, 1984). Densities of migrant waders at other sites in Southern Africa are lower than at the Berg River, ranging from 9.9 birds ha^{-1} at Walvis Bay, Namibia (Whitelaw *et al.*, 1978) to 19.7 birds ha^{-1} at Langebaan Lagoon (Underhill, 1987) and 24.0 birds ha^{-1} at the Swartkops estuary (Martin & Baird, 1987).

Although >5% of the national coastal populations of 34 species occur at the Berg River, this list is reduced dramatically when inland habitats, for which few survey data exist, are taken into consideration. It is likely that, at the national (rather than purely coastal) level, the Berg River supports, at times, more than 5% of the national populations of nine species: White Pelican, Greenshank, Curlew Sandpiper, Bartailed Godwit, Curlew, Hartlaub's Gull and Caspian, Swift and Sandwich Terns. In a national perspective, the breeding population of Caspian Terns is probably the single population of greatest importance (Velasquez *et al.*, 1990). For Palearctic migrant species, it is likely that only Curlew Sandpiper would satisfy the international 1% criterion.

Differences in arrival and departure times between Palearctic shorebird species have been linked with differences in the latitudes at which they breed and with timing of breeding (Underhill, 1987; Martin & Baird, 1988). Species which breed in the steppe and forest regions of the USSR, such as Marsh Sandpiper, complete their clutches by early June (Cramp & Simmons, 1983) and are among the first to leave African estuaries. In general, species which breed at higher latitudes and complete their clutches later remain until April. Examples from the Berg River include Ruff, Grey Plover and Little Stint. Patterns of arrival and departure of migratory waders from the Swartkops estuary differ slightly from those at the Berg River. At the Swartkops estuary the majority of Curlews, Curlew Sandpipers and Greenshanks left before March (Martin & Baird, 1987) whereas, at the Berg River, these species remained in numbers until April.

The February peak in wader abundance at the Berg River in both years, coupled with an increase in abundance of certain species in late April (Ringed and Grey Plovers, Ruff), suggest that some migratory waders may use the Berg River as a site at which to accumulate pre-migratory fat reserves. The bimodal pattern of wader abundance during the summer months suggests that birds may stop at the Berg River to feed on their southward migration. However, the fall in bird numbers during December and January coincides with the peak deposition of *Cladophora* on intertidal mudflats (Chapter 2), and emigration from the estuary at this time may simply be local movement in response to temporarily unfavourable feeding conditions.

Interannual fluctuations in the abundance of migrant waders have been reported at the Swartkops estuary (Martin & Baird, 1987) and Langebaan Lagoon (Underhill, 1987). These fluctuations have been linked to cycles of lemming *Dicrostonyx torquatus* and *Lemmus sibiricus* abundance at breeding grounds in the Taimyr Peninsula. In years when lemmings are scarce, Arctic Foxes *Alopex lagopus* prey heavily on the eggs and young of waders (Summers & Underhill, 1987). The austral summer of 1988/89 followed a breeding season in which lemmings were abundant on the Taimyr Peninsula, explaining the high numbers of Palearctic waders on the Berg River relative to the summer of 1987/88, which followed a 'poor' lemming year (Tomkovich, 1989). Given that most of the migrant waders which remain in South Africa during the austral winter are mostly first-year birds (Underhill, 1987), it can be predicted that winter numbers of most species would represent a greater proportion of the summer population in years following high breeding production than was the case in the 1988 winter. The small numbers of flamingos at the Berg River in 1988/89 relative to the previous summer may also be due to breeding failure at Etosha Pan, Namibia, which dried up in the preceding breeding season before chicks had fledged. However, there is no firm evidence of linkage between the two populations. There are no records of attempted breeding by Greater Flamingos at the Berg River, but Lesser Flamingos made an unsuccessful attempt to breed in 1974 (Winterbottom, 1979). During the study period, in September 1987, Lesser Flamingos built five nests in the salt pans, but there is no evidence that eggs were laid.

Patterns of seasonal abundance of resident species at the Berg River are similar to those at other coastal wetlands in South Africa. For the majority of resident species, seasonal fluctuations in numbers may be linked to breeding phenology and post-breeding movements from inland sites to the coast (Winterbottom, 1960; Berruti, 1983). This may be related to the drying up of ephemeral inland wetlands, and probably explains influxes of 1 000 to 3 500 Kittlitz's Plovers to the Berg River during the summer months (this study; Summers *et al.*, 1976). Generally, southern African estuaries do not support large numbers of waterfowl (Anseriformes), although some estuaries are important sites for the post-breeding moult of South African Shelducks (Siegfried, 1981). The most abundant ducks at the Berg River are Cape Teal, Yellowbilled Duck, Cape Shoveller, South African Shelduck and Egyptian Goose. However, there is no evidence that the estuary is an important moulting site for any of these species.

Habitat selection

Intertidal mudflats not only supported by far the greatest densities of birds throughout the year, but also were the favoured feeding habitat of most bird species (except diving and aerial piscivores which utilized predominantly subtidal habitats). Saltmarshes supported a low density of birds, and the highest selectivity index for this habitat (Redbilled Teal; 0.83) was low relative to the selection shown by most species for mudflats (Table 1.5). Saltmarshes were not important feeding grounds for any waterbird populations of national importance. Differences in the intensity of utilization of mudflats and saltmarshes are due largely to differences in the abundance of invertebrate prey in the two habitats, saltmarshes being relatively depauperate (Velasquez, unpubl. data). Saltpans were the favoured feeding habitat of eight species during the summer, but of only four species during winter. Saltpans do, however, support some of the important breeding populations at the estuary, including Cape Teals, Kelp and Hartlaub's Gulls, Caspian Terns and Kittlitz's and Chestnutbanded Plovers.

Densities of benthic invertebrates in salt pans of <60 ppt salinity are high: densities of chironomid fly larvae alone may reach 120 000 per m^2 (Velasquez, unpubl. data). However, the salt pans do not experience a tidal regime and the majority of invertebrates are unavailable to most birds for most of the time because of water depth. When the water level in low salinity pans is lowered artificially, very large numbers of waders move into the pans to exploit this temporarily superabundant food supply. During one such experiment, more than 50% of the entire estuarine population of Curlew Sandpipers moved to feed in a single salt pan (Velasquez, in prep.). Considerable potential thus exists for managing the salt pans in such a way as to make them a more attractive habitat for waterbirds.

Energy consumption

Relative to other coastal wetlands in South Africa, predation intensity by waterbirds (energy removal per unit area per unit time) at the Berg River is high. On an annual basis, predation intensity by intertidal feeders is approximately twice that at Langebaan Lagoon and 16% higher than at the Swartkops estuary: these differences are accounted for largely by the greater energy consumption by herbivores, principally Lesser Flamingos and Redknobbed Coots, at the Berg River (Table 1.7). During summer, energy consumption by invertebrate feeders is higher at the Swartkops estuary than at the Berg River. This reflects differences in the sizes of predators and prey at the two estuaries. Mudprawns dominate the benthic invertebrate fauna of the Swartkops estuary and are preyed on by large birds, principally Grey Plovers, Whimbrels and Kelp Gulls (Martin & Baird, 1987). At the Berg River, prey are much smaller, being mainly small polychaetes and gastropods (Chapter 2), and Kelp Gulls, rather than being true predators, predominantly scavenge on fish factory offal and other byproducts of man's activities. Energy transfer to piscivores at the Berg River is an order of magnitude greater than at either Langebaan Lagoon or the Swartkops estuary (Table 1.7).

The seasonal pattern of predation intensity at the Berg River and Langebaan Lagoon is reversed. At Langebaan Lagoon, predation is maximal during the winter, due mainly to large numbers of Greater Flamingos (Underhill, 1987). At the Berg River, predation intensity is slightly lower during winter than summer. The relatively small difference between the two seasons, in the absence of large numbers of Greater Flamingos, is due largely to winter influxes of Redknobbed Coots and Kelp Gulls. As a result, the overall contribution of invertebrate feeders to the total energy consumption at the Berg River is less than at Langebaan Lagoon.

Conservation perspectives

Because of its small size, the Berg River estuary supports few birds relative to some of the large wetlands on the west coast of Africa, such as the Banc d'Arguin in Mauritania (Zwarts, 1988). However, the unusually high densities of birds, particularly of migrant waders, are of considerable ecological interest. These high densities strongly suggest that the benefits derived by individual migrants which opt to spend the nonbreeding season at the Berg River at least offset any risks inherent in long distance migration. The most important benefit which these birds obtain should be a high nonbreeding survivorship. This, in turn, is almost certainly related to some predictable attribute of the estuary, presumably food availability. Prey production (88 g m^{-2} y^{-1}) is high relative to most other temperate estuaries (Chapter 2). The combination of high bird density and species richness at the Berg River, coupled with its geographical isolation from other comparable wetlands, and the scarcity of wetlands on the west coast of southern Africa generally, makes it a site of considerable conservation importance.

The Berg River estuary is of sufficient subregional importance for waterbirds to qualify for registration with the RAMSAR Convention. However, it does not qualify for registration on the grounds of being hydrologically pristine, and, whereas registration is desirable, more immediate attention should be given to affording the estuary protection at the national level. Such protection is of immediate importance in view of developments that have taken place at the estuary during the last 25 years and which threaten its ecological integrity. The present canalized mouth of the river is artificial and was completed in 1966. Prior to that time the river flowed out through the lagoon which lies to the south of the new mouth. Construction of the new mouth led to increased salt penetration upstream and to bank erosion due to high water velocities. Since its construction, dredging has been necessary to maintain the navigation channel at the mouth. This has resulted, among other things, in increased turbidity and contamination by released trace elements and nutrients (van Wyk, 1983). Dredging spoil which is deposited on saltmarshes reduces vegetation cover and diversity and increased surface salinity and desiccation potential (van Wyk, 1983). Several of these effects have been compounded by the construction of a marina upstream from the mouth. Saltmarshes are further susceptible to damage from hypersaline water originating in the commercial saltpans. Whereas some of this contamination probably originates as seepage, additional damage is almost certainly caused by the deposition of windblown hypersaline spume (pers. obs.).

Although the impacts of dredging have been assessed (van Wyk, 1983), other potentially negative impacts on the estuary's hydrology have not. These include the influence of upstream water abstraction on river flow patterns; changes in nutrient status of river water effected by runoff of agricultural fertilizers within the catchment area; and, erosion resulting from recreational activities, principally boating and waterskiing.

This study has shown clearly that intertidal mudflats are the most important feeding habitat for most birds in the estuary and that saltmarshes are the least important feeding habitat during low tide although they are important as high tide roosting areas and as feeding sites when tidal and weather conditions result in short periods of mudbank exposure. However, in view of the negative impacts of commercial and recreational development on water quality, especially on turbidity, conservation of the saltmarshes may be critical to the survival of the estuary as a prime waterbird habitat. By virtue of being vegetated, saltmarshes have the potential to act as sediment traps, thus reducing siltation rates on the mudflats, and also to reduce streambank erosion. Siltation of wetlands is a major concern at other sites in South Africa, including Walvis Bay (Hockey & Bosman, 1983) and Lake St Lucia, the largest estuarine system in Africa (Begg, 1978).

It is very likely that there is a substantial interchange of waterbirds between the Berg River estuary and Langebaan Lagoon, 40km to the southwest. Langebaan Lagoon is protected within a national park. If the conservation status of the Berg River estuary could be improved, this would be a first step towards providing a network of coastal wetland reserves for waterbirds in the western Cape Province.

REFERENCES

Baird, D., Evans, P. R., Milne, H. & Pienkowski, M. W. 1985 Utilization by shorebirds of benthic invertebrate production in intertidal areas. *Oceanogrphy Marine Biology Annual Review* **23**, 573-597.

Begg, G. 1978 The estuaries of Natal. *Natal Town and Regional Planning Rpt* **4**, 1-657.

Berruti, A. 1983 The biomass, energy consumption and breeding of waterbirds relative to hydrological conditions at Lake St. Lucia. *Ostrich* **54**, 65-82.

Carp, E. 1972 *Proceedings of the International Conference on Conservation of Wetlands and Waterfowl.* Ramsar, Iran, 30 January - 3 February 1971. International Waterfowl Research Bureau, Slimbridge.

Cooper, J. 1978 Energetic requirements for growth and maintenance of the Cape Gannet (Aves: Sulidae). *Zoology of Africa* **13**: 305-317.

Cooper, J. & Hockey, P. A. R. 1981 The atlas and site register of South African coastal birds. Part 2: The Atlas. Unpubl. Report to SANCOR. pp 324.

Cooper, J. Summers, R. W. & Pringle, J. S. 1976 Conservation of coastal habitats of waders in the south-western Cape, South Africa. *Biology Conservation* **10**, 239-247.

Cramp, S. & Simmons, K. E. L. (eds). 1983 *The Birds of the Western Palearctic.* Vol. 3. Oxford University Press, Oxford.

Engelmoer, M. T., Piersma, T., Altenburg, W. & Mes, R. 1984 The Banc d'Arguin (Mauritania). In: *Coastal waders and wildfowl in winter* (Evans, P. R., Goss-Custard, J. D. & Hale, W. G., eds). Cambridge University Press, Cambridge, pp 293-310.

Fairall, N. 1981 A study of the bioenergetics of the Redknobbed Coot *Fulica cristata* on a South African estuarine lake. *South African Journal of Wildlife Research* **11**, 1-4.

Halse, S. A. 1984 Food intake, digestive efficiency, and retention time in spurwinged geese *Plectropterus gambensis*. *South African Journal of Wildlife Research* **14**, 106-110.

Hockey, P. A. R. 1984 Growth and energetics of the African Black Oystercatcher *Haematopus moquini*. *Ardea* **72**, 111-117.

Hockey, P. A. R. & Bosman, A. L. 1983 Conservation-management of the Walvis Bay lagoon with special reference to its importance as a bird habitat. Report to the Association of Round Tables of South Africa, pp 33.

Jacobs, J. 1974 Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia* **14**, 413-417.

Le Roux, P.J. 1972 Wetlands and waterfowl in South Africa. In: *Proceedings of the International Conference on Conservation of Wetlands and Waterfowl*. Ramsar, Iran, 30 January - 3 February 1971 (Carp, E., ed). International Waterfowl Research Bureau, Slimbridge, pp 235-238.

Maclean, G. L. 1985 *Roberts' Birds of Southern Africa*. John Voelcker Bird Book Fund, Cape Town.

Martin, A. P. & Baird, D. 1987 Seasonal abundance and distribution of birds on the Swartkops estuary, Port Elizabeth. *Ostrich* **58**, 123-135.

Martin, A. P. & Baird, D. 1988. Lemming cycles - which Palearctic migrants are affected? *Bird Study* **35**, 143-145.

Nagy, K. A. 1987 Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* **57**, 111-128.

Pringle, J. S. & Cooper, J. 1975 The Palearctic wader population of Langebaan Lagoon. *Ostrich* **46**, 213-218.

Puttick, G. M. 1980 Energy budgets of Curlew Sandpipers at Langebaan Lagoon, South Africa. *Estuarine Coastal and Marine Science* **11**, 207-215.

Robertson H. G. 1981 Annual summer and winter populations of Palearctic and resident waders (Charadrii) at Langebaan Lagoon, South Africa, 1975-1979. In: *Proceedings of the Symposium on Birds of the Sea and Shore, 1979* (Cooper, J., ed). African Seabird Group, Cape Town, pp 335-345.

Ryan, P. G., Cooper, J., Hockey, P. A. R. & Berruti, A. 1986 Waders (Charadrii) and other waterbirds on the coast and adjacent wetlands of Natal, 1980-81. *Lammergeyer* **36**, 1-33.

Ryan, P. G., Underhill, L. G., Cooper, J. & Waltner, M. 1988 Waders (Charadrii) and other waterbirds on the coast, adjacent wetlands and offshore islands of the southwestern Cape Province, South Africa. *Bontebok* **6**, 1-19.

Siegfried, W. R. 1970 Wildfowl distribution, conservation and research in Southern Africa. *Wildfowl* **21**, 89-98.

Siegfried, W. R. 1981 The estuarine avifauna of southern Africa. In: *Estuarine Ecology, with Particular Reference to Southern Africa* (Day, J. H., ed). A.A. Balkema, Cape Town, pp 223-250.

Smit, C. J. 1982 Wader and waterfowl counts in the international Wadden Sea area: the results of the 1981-1982 survey. *Wader Study Group Bulletin* **35**, 14-19.

Smit, C. J. & Piersma, T. 1989 Numbers, midwinter distribution, and migration of wader populations using the East Atlantic Flyway. In: *Flyways and reserve networks for waders* (Boyd, H. & Pirot, J. Y., eds). *IWRB Special Publication* **9**, 24-63.

Spitz, F. 1964 Répartition écologique des anatides et limicoles de la zone maritime du sud de la Vendée. *Terre et Vie* **18**, 452-488.

Stewart, B. A. & Bally, R. 1985 The ecological role of the Redknobbed Coot *Fulica cristata* Gmelin at the Bot River estuary, South Africa: a preliminary investigation. *Transactions of the Royal Society of South Africa* **45**, 419-426.

Summers, R. W. 1977 Distribution, abundance and energy relationships of waders (Aves: Charadrii) at Langebaan Lagoon. *Transactions of the Royal Society of South Africa* **42**, 483-495.

Summers, R. W. & Underhill, L. G. 1987 Factors related to the breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. *Bird Study* **34**, 161-171.

Summers, R. W., Cooper, J. & Pringle, J. S. 1977 Distribution and numbers of coastal waders (Charadrii) in the south-western Cape, South Africa, summer 1975-76. *Ostrich* **48**, 85-97.

Summers, R. W., Pringle, J. S. & Cooper J. 1976 The status of coastal waders in the south-western Cape, South Africa. Western Cape Wader Study Group, Cape Town.

Tomkovich, P. S. 1989 Nesting conditions of waders in the tundras of the Soviet Union in 1988. *Information, Working Group on Waders*. Magadan, pp 51-58. (In Russian).

Tye, A. & Tye, H. 1987 The importance of Sierra Leone for wintering waders. *Wader Study Group Bulletin* 49, *Suppl. / IWRB Special Publication* **7**, 71-75.

Underhill, L. G. 1987 Waders (Charadrii) and other waterbirds at Langebaan Lagoon, South Africa, 1975-1986. *Ostrich* **58**, 145-155.

van Wyk, A. C. 1983 Effects of dredging on the Berg River estuary. Unpubl. MSc Thesis. University of Cape Town, Cape Town, South Africa.

Velasquez, C. R., Kalejta, B. & Turner, E. 1990. The Berg River estuary: an important wetland for Caspian Terns *Sterna caspia* in South Africa. *Marine Ornithology* **18**, 65-68.

Whitelaw, D. A., Underhill, L. G., Cooper, J. & Clinning, C. F. 1978 Waders (Charadrii) and other birds on the Namib coast: counts and conservation priorities. *Madoqua* **11**, 137-150.

Winterbottom, J. M. 1960 Report on the Cape Bird Club vlei counts, 1952-58. *Ostrich* **31**, 135-168.

Winterbottom, J. M. 1979 A guide to the birds of the S.W. Cape. Cape Bird Club, Cape Town.

Zwarts, L. 1988 Numbers and distribution of coastal waders in Guinea-Bissau. *Ardea* **76**, 42-55.

APPENDIX 1.1.

Feeding guilds and scientific names of species mentioned in the text and tables. Codes 1-4 identify the habitats in which each species foraged (1= intertidal mudflats; 2= saltmarshes; 3= saltpans; 4= subtidal).

HERBIVORES		HABITATS
Lesser Flamingo	*Phoenicopterus minor*	1,2,3
Egyptian Goose	*Alopochen aegyptiacus*	1,2,3
Spurwinged Goose	*Plectropterus gambensis*	1,2
Purple Gallinule	*Porphyrio porphyrio*	1,2,3
Redknobbed Coot	*Fulica cristata*	1,2,3
INVERTEBRATE FEEDERS		
Cattle Egret	*Bubulcus ibis*	2
Blacknecked Grebe	*Podiceps nigricollis*	3,4
Sacred Ibis	*Threskiornis aethiopicus*	1,2,3
Glossy Ibis	*Plegadis falcinellus*	1,2,3
African Spoonbill	*Platalea alba*	1,2,3
Greater Flamingo	*Phoenicopterus ruber*	1,2,3
South African Shelduck	*Tadorna cana*	1,2,3
African Rail	*Rallus caerulescens*	2
Black Crake	*Amaurornis flavirostris*	2
African Black Oystercatcher	*Haematopus moquini*	1
Ringed Plover	*Charadrius hiaticula*	1,2,3
Whitefronted Plover	*C. marginatus*	1,2,3
Chestnutbanded Plover	*C. pallidus*	1,2,3
Kittlitz's Plover	*C. pecuarius*	1,2,3
Threebanded Plover	*C. tricollaris*	1,2,3
Mongolian Plover	*C. mongolus*	1,2,3
Sand Plover	*C. leschenaultii*	1,2,3
Grey Plover	*Pluvialis squatarola*	1,2,3
Crowned Plover	*Vanellus coronatus*	3
Blacksmith Plover	*V. armatus*	1,2,3
Turnstone	*Arenaria interpres*	1,2,3
Terek Sandpiper	*Xenus cinereus*	1,2,3
Common Sandpiper	*Tringa hypoleucos*	1,2,3
Wood Sandpiper	*T. glareola*	1,2,3
Redshank	*T. totanus*	1,2,3
Marsh Sandpiper	*T. stagnatilis*	1,2,3
Greenshank	*T. nebularia*	1,2,3
Knot	*Calidris canutus*	1,2,3
Curlew Sandpiper	*C. ferruginea*	1,2,3
Little Stint	*C. minuta*	1,2,3
Pectoral Sandpiper	*C. melanotos*	2,3
Sanderling	*C. alba*	1,3
Broadbilled Sandpiper	*Limicola falcinellus*	1,2,3
Ruff	*Philomachus pugnax*	1,2,3
Blacktailed Godwit	*Limosa limosa*	1,2,3
Bartailed Godwit	*L. lapponica*	1,2,3
Curlew	*Numenius arquata*	1,2,3
Whimbrel	*N. phaeopus*	1,2,3
Rednecked Phalarope	*Phalaropus lobatus*	3
Avocet	*Recurvirostra avosetta*	1,2,3

Blackwinged Stilt	*Himantopus himantopus*	1,2,3
Spotted Dikkop	*Burhinus capensis*	1,2,3
Water Dikkop	*Burhinus vermiculatus*	2
Greyheaded Gull	*Larus cirrocephalus*	1,2,3
Hartlaub's Gull	*L. hartlaubii*	1,2,3
Franklin's Gull	*L. pipixcan*	3
Whitewinged Tern	*Chlidonias leucopterus*	1,2,3
PISCIVORES		
Great Crested Grebe	*Podiceps cristatus*	3,4
Dabchick	*Tachybaptus ruficollis*	3,4
White Pelican	*Pelecanus onocrotalus*	3,4
Whitebreasted Cormorant	*Phalacrocorax carbo*	3,4
Cape Cormorant	*P. capensis*	3,4
Reed Cormorant	*P. africanus*	3,4
Darter	*Anhinga melanogaster*	4
Grey Heron	*Ardea cinerea*	1,2,3
Blackheaded Heron	*A. melanocephala*	1,2,3
Purple Heron	*A. purpurea*	1,2
Great White Egret	*Egretta alba*	1,2
Little Egret	*E. garzetta*	1,2,3
Yellowbilled Egret	*E. intermedia*	1,2
Blackcrowned Night Heron	*Nycticorax nycticorax*	1,2,3
Little Bittern	*Ixobrychus minutus*	2
African Fish Eagle	*Haliaeetus vocifer*	1,2,3,4
Osprey	*Pandion haliaetus*	3,4
Caspian Tern	*Sterna caspia*	3,4
Swift Tern	*S. bergii*	3,4
Sandwich Tern	*S. sandvicensis*	3,4
Common Tern	*S. hirundo*	3,4
Little Tern	*S. albifrons*	3,4
Pied Kingfisher	*Ceryle rudis*	2,3,4
Giant Kingfisher	*C. maxima*	4
Malachite Kingfisher	*Alcedo cristata*	3,4
SCAVENGER		
Kelp Gull	*Larus dominicanus*	1,2,3,4
OMNIVORES		
Yellowbilled Duck	*Anas undulata*	1,2,3
Cape Teal	*A. capensis*	1,2,3
Redbilled Teal	*A. erythrorhyncha*	1,2,3
Cape Shoveller	*A. smithii*	1,2,3
Moorhen	*Gallinula chloropus*	2
RAPTORS		
African Fish Eagle	*Haliaeetus vocifer*	1,2,3,4
African Marsh Harrier	*Circus ranivorus*	1,2
Osprey	*Pandion haliaetus*	3,4
OTHERs		
Marabu Stork	*Leptoptilos crumeniferus*	?

CHAPTER 2

DISTRIBUTION, ABUNDANCE AND PRODUCTIVITY OF BENTHIC INVERTEBRATES AT THE BERG RIVER ESTUARY, SOUTH AFRICA

with P. A. R. Hockey,

Estuarine, Coastal and Shelf Science (1991)

SUMMARY

Twenty-five benthic invertebrate species were identified from samples taken monthly over 17 months at four sites on the Berg River estuary, South Africa. Gastropods and polychaetes dominated the macrofauna in terms of both numbers and biomass. Abundance of the dominant species fluctuated in response to seasonal growth of eelgrass *Zostera capensis* and filamentous alga *Cladophora* sp.. Differences in distributions of invertebrates on the estuary were attributed to differences in physical properties of the substratum and in vegetation cover. *Hydrobia* sp., *Ceratonereis erythraeensis* and *C. keiskama* were the most important species in terms of biomass and accounted for an average of 75% of total biomass at all study sites. Biomass peaked during the austral winter, early spring and again in autumn. An increase in biomass in winter was due to somatic production, whereas spring and autumn increases were attributed to recruitment of juveniles following reproduction. Mean annual biomass for the whole estuary was 19.36 g m^{-2}, and mean annual production 87.58 g m^{-2} y^{-1}, yielding a net P/B ratio of 4.52. Production and P/B ratios of invertebrates in estuaries and coastal lagoons at temperate and subtropical latitudes are correlated positively with mean annual ambient temperature and negatively with distance from the equator. Production data are lacking from tropical estuaries.

INTRODUCTION

The production of single species or restricted taxonomic groups of invertebrates inhabiting estuarine mudflats has been estimated by various authors, but there are few studies which consider entire benthic invertebrate assemblages (Knox, 1986; McLusky, 1989). Furthermore, most estimates of production have been made in the northern hemisphere and there are few data available on the production of benthic macrofauna in tropical, subtropical and south temperate estuaries.

In several studies, benthic productivity has been calculated in order to assess the availability of food to higher trophic level consumers (Hibbert, 1976; Wolff & de Wolf, 1977). The most conspicuous secondary consumers in estuarine ecosystems are shorebirds (Aves: Charadriiformes). The majority of shorebirds utilizing southern African estuaries during the austral summer are migratory species which breed in the Holarctic region. The Berg River estuary in the southwestern Cape, South Africa (32°47'S, 18°10'E), supports one of the highest densities of migrant shorebirds found at any estuary on the East Atlantic seaboard (Chapter 1).

The aims of this study are to quantify the distribution, abundance and productivity of benthic invertebrate species and assemblages at the Berg River estuary, and to assess whether the high densities of shorebirds reflect unusually high benthic productivity relative to more northerly estuaries.

STUDY AREA AND METHODS

Sampling area

The study area extended from 5.5 km upstream of the Berg River mouth to the river mouth itself. This area contains 144 ha of intertidal mudflats, bordered by 242 ha of saltmarsh and 222 ha of commercial saltpans. Four study sites A, B, C, and D, each of 2 000 m^2 (25 x 80 m), were established at the decreasing distance from the river mouth (Fig 2.1).

Substratum particle size, penetrability and organic content

Surface sediment characteristics at the four sites were determined. Four 50 mm deep cores were collected from each site. Animals and vegetation were removed before clay and silt fractions were separated from the coarse fractions in the wet sieving process. Both the residuals were dried to constant mass at 60°C. Size distribution of coarse particles was obtained by sieving the residuals. Size fractions were expressed as a percentage and plotted as cumulative percentages using the Phi-scale. Mdø (median particle size), QDø (phi quartile deviation) and Skqø (phi quartile skewness) were obtained directly from the curves. To determine organic content of the substrata all sediment fractions were mixed thoroughly and burned in a muffle furnace at 450°C for 4 hours.

An index of sediment penetrability was obtained by dropping a 400 mm metal rod of 5 mm diameter weighing 150 g onto the sediment down a 1.5 m long PVC pipe, and recording the depth to which the rod was buried. At each site, penetrability was measured at hourly intervals over the 4 hours of mudflat exposure.

Vegetation cover

Vegetation cover (%) was determined monthly at each site in 25 randomly-positioned quadrants, each of 0.25 m^2. The quadrants contained 81 intercepts and the proportion of intercepts covering green vegetation on the ground was recorded.

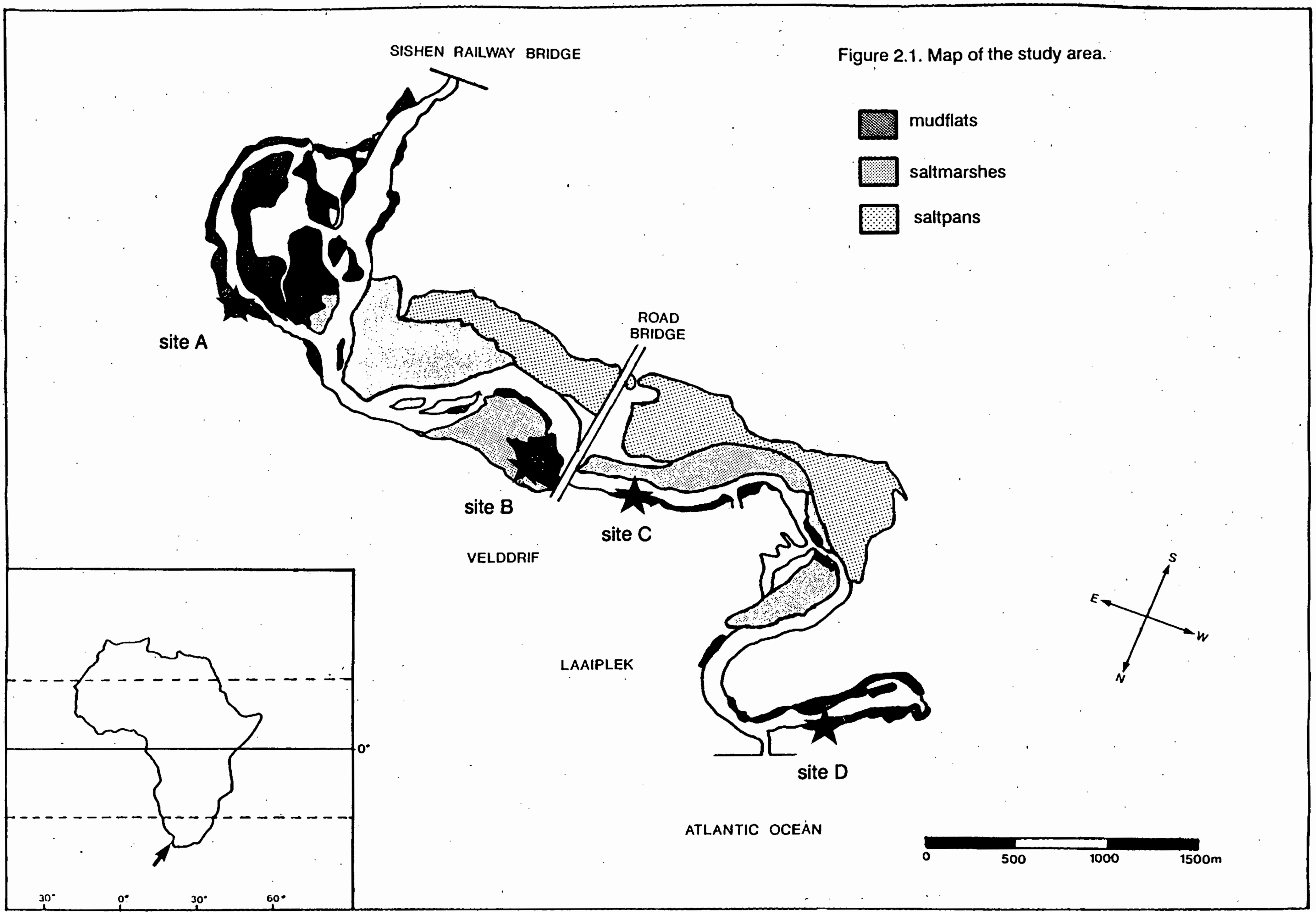


Figure 2.1. Map of the study area.

Dry weight of vegetation was determined monthly by removing green vegetation from every core used for invertebrate sampling. Vegetation was dried at 60°C for 24 hours and weighed.

Infaunal sampling

Invertebrates were sampled in each plot, at the same tidal state, once a month from December 1987 to April 1989. Ten randomly-positioned cores of 69 mm diameter (0.0037 m^2) and 300 mm depth were removed from the substratum. Samples were washed through a 500 um mesh sieve within 24 hours of collection and animals recovered were preserved in 10% formalin. Animals were identified to species or genus level and, except for two polychaete species, maximum lengths were measured to the nearest 0.1 mm using a binocular microscope and graticule. Gastropods *Hydrobia* sp., which occurred in high numbers, were divided into five size classes - very large ($\geqslant$4.6 mm), large (3.6-4.5 mm), medium (2.6-3.5 mm), small (1.6-2.5 mm) and very small ($\leqslant$1.5 mm). Three hundred animals from each class were used to determine mean individual dry flesh biomass per class. Because polychaete worms often were broken during the sieving process, only jaw length was measured. Jaw length was converted to body length and whole animal dry mass using conversion equations calculated from whole polychaetes collected specifically for this purpose (Table 2.1). Similar correlations between dry mass and total animal length were derived for isopods and amphipods (Table 2.1). Dry masses of crabs and prawns were established individually after drying them at 60°C for 24 hours. It was difficult to establish length-weight relationships for small, soft-bodied animals which were broken during the sieving process and lacked hard parts (*Capitella capitata*, *Boccardia* sp.). In these cases, mean dry mass of an individual animal was determined from pooled samples of unbroken animals.

Table 2.1. Relationships between body length (mm), dry mass (g) and body parameters of some invertebrate species at the Berg River estuary.

SPECIES	REGRESSION EQUATION	r	N
Ceratonereis erythraeensis			
Body length(L)/jaw length(J)	$L=60.63J - 11.31$	0.82	35
Dry mass(M)/jaw length(J)	$M=4.57*10^{-3}\ J^{2.79}$	0.72	20
Ceratonereis keiskama			
Body length(L)/jaw length(J)	$L=24.51J - 2.15$	0.91	30
Dry mass(M)/jaw length(J)	$M=1.7*10^{-3}\ J^{2.31}$	0.82	22
Perinereis nuntia subsp. *vallata*			
Body length(L)/jaw length(J)	$L=41.57J - 10.21$	0.98	15
Dry mass(M)/jaw length(J)	$M=0.3*10^{-2}\ J^{3.32}$	0.99	15
Exosphaeroma hyloecetes			
Dry mass(M)/body length(L)	$M=0.12*10^{-3}\ L^{2.33}$	0.89	20
Melita zeylanica			
Dry mass(M)/body length(L)	$M=0.85*10^{-5}\ L^{2.61}$	0.80	29

Biomass and production estimates

Mean biomass of the entire benthic community was calculated for each month at each site over the 17 month study period. Mean annual biomass was determined, including taking an average for those months which were sampled in more than 1 year (December - April). In order to extrapolate data from the study plots to the entire estuary, the estuary was divided into four sections (Fig 2.1). It has been assumed that study sites A, B, C and D were representative of each section. From the estimates of mean annual invertebrate biomass and total annual production of each section, and the percentage contribution of each section of the estuary to the total intertidal area, mean annual biomass and total annual production for the whole estuary were calculated. Direct determination of production was made for the two *Ceratonereis* species (Chapter 3). Mean annual biomass and P/B ratios were used to calculate total annual production for the remaining species. P/B ratios for the majority of species were taken from Bennett and Branch (1990), who used the relationship:

$$P/B = 0.65\ M^{-0.37}$$ (Banse & Mosher, 1980).

This equation allows calculation of P/B ratios from body mass at maturity (M).

RESULTS

Physical factors and vegetation cover

Coarse sediments predominated at the mouth of the river, becoming finer further upstream, although silt content was highest at site C and lowest at B (Table 2.2). Organic content was highest at site C and lowest at site D, mirroring high and low silt contents at these sites.

Substratum penetrability varied between sites, being greatest in the mid-reaches of the estuary (sites B and C) and least in the upper and lower reaches. In the mid-

Table 2.2. Sediment characteristics of the substratum at the four study sites. Wentworth scale.

Site	Mdø	QDø	Skqø	Percent organics
A	2.37	0.70	-0.13	0.69
	(0.09)	(0.07)	(0.10)	(0.05)
B	2.80	0.50	-0.07	1.71
	(0.29)	(0.10)	(0.05)	(1.19)
C	2.80	0.79	-0.27	5.14
	(0.19)	(0.33)	(0.29)	(0.73)
D	0.66	1.17	0.62	0.36
	(0.11)	(0.36)	(0.30)	(0.21)

reaches, *Zostera* cover either decreased penetrability (site B) or did not affect it (site C), whereas at sites A and D where penetrability was least, *Zostera* cover markedly increased penetrability. There was no significant change in the penetrability of sediments with *Zostera* cover during the 4 hours of exposure at sites A, B, C and D respectively: $F=1.22$, $df=4, 31$, $p>0.25$; $F=2.19$, $df=4, 32$, $p>0.05$; $F=2.72$, $df=3, 28$, $p>0.05$; $F=1.75$, $df=4, 50$, $p>0.1$) (Table 2.3). However, at all sites where the sediment was bare, a significant decrease in penetrability occurred during tidal exposure. A significant decrease in penetrability occurred after one hour of exposure at sites C and D ($F=45.29$, $df=3, 28$, $p<0.00001$; $F=29.68$, $df=4, 50$, $p<0.00001$, respectively), where sediments were relatively coarse. A significant decrease in penetrability occurred after 2 hours of exposure at site B ($F=7.83$, $df=4, 32$, $p<0.0002$) and after 3 hours at site A ($F=8.08$, $df=4, 31$, $p<0.0001$) where fine sediments predominated.

Vegetation cover varied seasonally at all four stations, with biomass and cover peaking during summer (November-March) (Fig 2.2). Two species were dominant: eel-grass *Zostera capensis* and the filamentous alga *Cladophora* sp.. Overall, site B had the highest vegetation cover throughout the year, dominated by *Zostera capensis*; Site A had the lowest average cover, with minimal *Zostera* growth but seasonal eruptions of *Cladophora*.

There were considerable differences in vegetation cover between years, particularly at sites A and D. These differences were accounted for almost entirely by differences in *Cladophora* cover. In January 1989 *Cladophora* at site A decayed and was flushed from the estuary.

Table 2.3. Penetrability (cm) (±SE) of different sediment types during four hours of exposure.

	Penetrability (cm)									
	Mudflat with *Zostera*					Bare mudflat				
	Exposure time (hrs)					Exposure time (hrs)				
Site	0	1	2	3	4	0	1	2	3	4
A	7.00 (0.01)	7.25 (0.17)	7.75 (0.31)	8.21 (0.26)	7.60 (0.59)	4.06 (0.08)	3.92 (0.08)	3.50 (0.18)	3.21 (0.10)	3.26 (0.16)
B	11.50 (0.35)	10.50 (0.26)	10.39 (0.55)	10.83 (0.55)	9.74 (0.28)	16.00 (0.29)	15.03 (0.15)	14.03 (0.32)	14.43 (0.30)	14.71 (0.15)
C	13.87 (0.07)	13.53 (0.14)	12.43 (0.10)	13.55 (0.12)	-	15.73 (0.14)	13.22 (0.24)	12.53 (0.29)	13.06 (0.78)	-
D	9.84 (0.15)	9.29 (0.30)	9.00 (0.33)	9.19 (0.28)	9.05 (0.70)	7.04 (0.16)	4.86 (0.35)	3.59 (0.32)	3.87 (0.32)	3.18 (0.16)

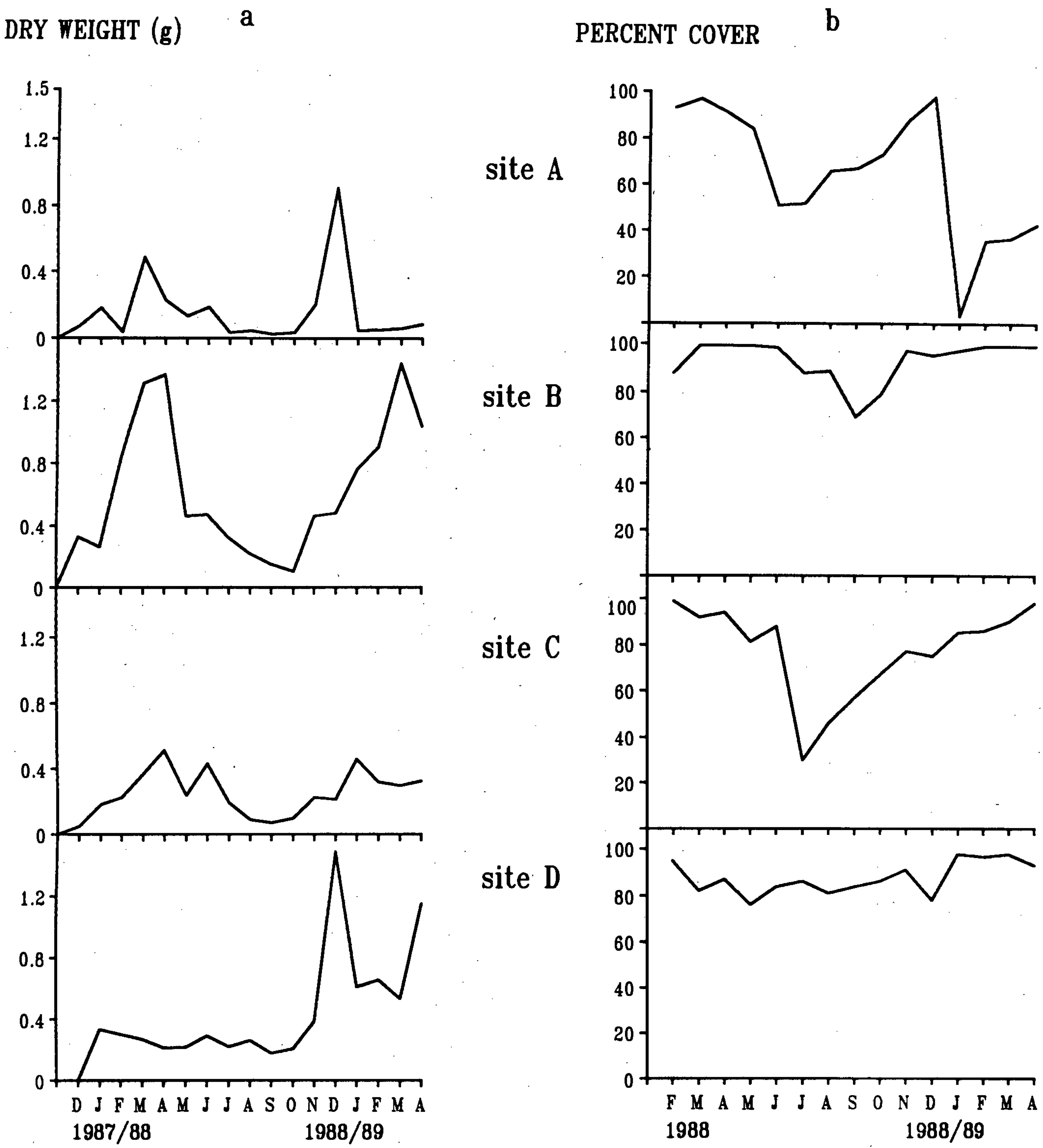


Figure 2.2. Mean dry mass of vegetation (g per 10 cores) (a) and percent vegetation cover (b) at the four study sites.

Invertebrate distribution and abundance

Twenty-five species of benthic macrofauna were recorded at the Berg river intertidal mudflats. Arthropods were most diverse, being represented by 14 species. Of the remaining phyla, annelids were represented by eight species and molluscs by three species (Table 2.4).

Seven species were numerically dominant, and the five most abundant of these (*Hydrobia* sp., *Capitella capitata*, *Boccardia* sp., *Ceratonereis erythraeensis* and *C. keiskama*) constituted 79% (site A) to 98% (site C) of the total invertebrate numbers. *Hydrobia sp.* was the most abundant species.

Highest invertebrate densities were recorded at site B (Table 2.4) and ranged between 38 400 and 197 000 animals m^{-2}. Site A supported the lowest density but the highest diversity (H') of invertebrates (Table 2.4).

Of the seven commonest species, densities of *Exosphaeroma hyloecetes*, *Hydrobia*, *Capitella capitata*, *Melita zeylanica* and *Ceratonereis keiskama* were positively correlated with vegetation biomass (Table 2.5). By contrast, densities of *Ceratonereis erythraeensis* and *Boccardia* were negatively correlated with vegetation biomass.

Seasonal variations in invertebrate abundance

There was considerable seasonal variation in species abundance within and between sites. *Boccardia* increased in numbers during late spring and summer at all four study sites. *Capitella capitata* followed a similar pattern, reaching peaks in the summer and autumn months at all sites except site D (Fig 2.3).

Table 2.4. Mean densities (per m^2) and, in parentheses, the percentage contribution to the total density of benthic invertebrates at each site at the Berg River estuary between December 1987 (*Hydrobia* sp. from January 1988 and April 1989). Diversities (H') and eveness (J') of benthic macrofauna at four study sites are calculated from Shannon's Diversity Index (Zar, 1977).

		Study site			
Rank	Species	A	B	C	D
ANNELIDA					
	Polychaeta				
4	*Ceratonereis erythraeensis* Fauvel	1795.1 (10.4)	2402.3 (2.7)	3736.5 (12.3)	3271.0 (6.1)
5	*Ceratonereis keiskama* Day	5402.5 (31.2)	1346.7 (1.5)	0	0
11	*Perinereis nuntia* subsp. *vallata* (Grube)	0	0	0	310.7 (0.6)
3	*Boccardia* sp.	3485.8 (20.1)	3371.3 (3.8)	2582.6 (8.5)	4586.8 (8.5)
2	*Capitella capitata* (Fabricius)	1560.7 (9.0)	3841.8 (4.3)	4461.7 (14.7)	4164.8 (7.7)
12	*Prionospio sexoculata* Augener	22.0 (0.1)	18.9 (<0.1)	1.6 (<0.1)	197.2 (0.4)
19	*Schistomeringos neglecta* Fauvel	0	0	0	28.4 (0.1)
22	*Desdemona ornata* Banse	4.7 (<0.1)	9.4 (<0.1)	0	1.7 (<0.1)
ARTHROPODA					
	Isopoda				
8	*Leptanthura* sp.	695.4 (4.0)	80.2 (0.1)	0 0	0 0
7	*Exosphaeroma hyloecetes* Barnard	347.7 (2.0)	668.6 (0.7)	391.0 (1.3)	309.2 (0.6)
20	*Paridotea ungulata* (Pallas)	9.4 (0.1)	6.3 (<0.1)	1.6 (<0.1)	6.7 (<0.1)
14	Unidentified	166.8 (1.0)	0	0	0
	Amphipoda				
6	*Melita zeylanica* Stebbing	1522.9 (8.8)	1808.4 (2.0)	185.6 (0.6)	367.7 (0.7)

Table 2.4 (cont.)

15	*Orchestia* sp.	59.8 (0.3)	26.7 (<0.1)	7.9 (<0.1)	1.7 (<0.1)
9	*Grandidierella lutosa* Barnard	656.9 (3.8)	18.9 (<0.1)	7.9 (<0.1)	23.4 (<0.1)
	Anomura				
18	*Callianassa kraussi* Stebbing	25.2 (0.1)	0	11.0 (<0.1)	10.2 (<0.1)
21	*Upogebia capensis* Krause	1.6 (<0.1)	0	9.4 (<0.1)	5.1 (<0.1)
	Brachyura				
10	*Hymenosoma orbiculare* Desmarest	85.0 (0.5)	66.1 (0.1)	108.6 (0.4)	113.7 (0.2)
25	*Thaumastoplax spiralis* Barnard	0	0	1.6 (<0.1)	0
	Insecta				
24	unidentified	0	1.6 (<0.1)	0	0
7	Tabanid larvae	23.6 (0.1)	55.1 (0.1)	0	0
13	Chironomid larvae	88.1 (0.5)	132.2 (0.1)	15.7 (0.1)	3.3 (<0.1)
MOLLUSCA					
	Gastropoda				
1	*Hydrobia* sp.	1369.0 (7.9)	75561.6 (84.5)	18823.6 (62.0)	40504.6 (75.0)
16	*Nassarius kraussianus* (Duncker)	0	0	0	80.2 (0.1)
23	unidentified	0	0	0	3.3 (<0.1)
	S	19	17	15	19
Density (m^{-2})		17322	89416	30346	53990
	H’	2.936	1.025	1.685	1.359
	J’	0.691	0.251	0.431	0.320

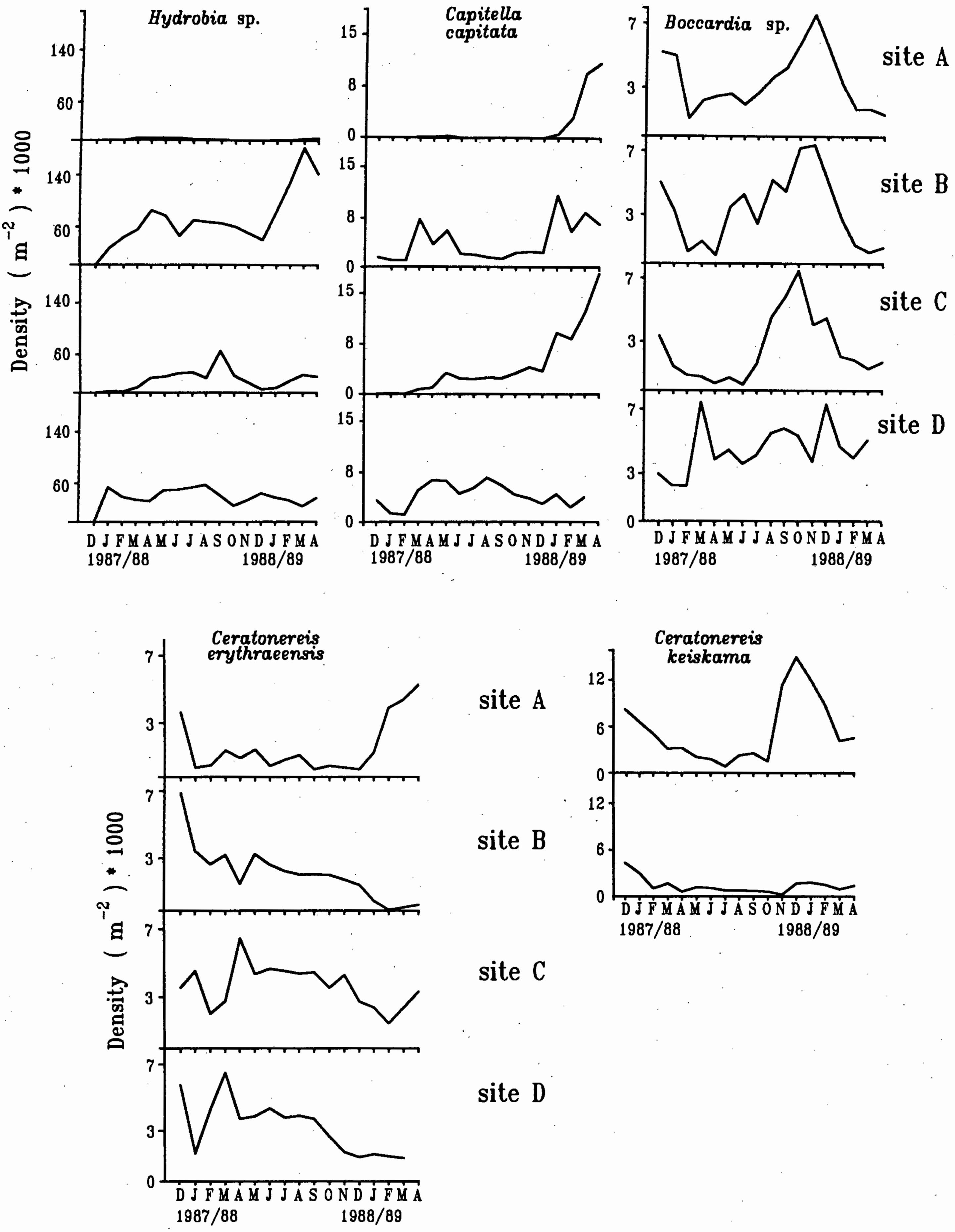


Figure 2.3. Seasonal abundance of the five commonest species of benthic macrofauna at the four study sites from December 1987 to April 1989.

Seasonal patterns in the abundance of *Hydrobia* and the two *Ceratonereis* species were less clear. *Hydrobia* generally was most abundant during the summer months, corresponding with peak vegetation biomass. Seasonal abundance of *Ceratonereis erythraeensis* differed considerably between the sites, although there was a tendency for densities to be highest during the summer months (Fig 2.3).

There were some marked interannual differences in invertebrate abundance. Generally, increases in numbers of all species in the summer and autumn of 1988/89 were greater than in 1987/88. This might be associated with differences in algal abundance between the years, algal biomass being greater in 1988/89 than in 1987/88. *Ceratonereis erythraeensis* was negatively associated with algae (Table 2.5) and this may explain its decrease at sites B and D in the summer and autumn of 1989. *Capitella capitata* and *Hydrobia*, which were positively associated with algae, increased in abundance following the algal proliferation in 1988/89. *Capitella capitata* was absent from site A until a settlement of algae occurred in summer 1988/89.

Invertebrate biomass

Molluscs and annelids made the greatest contribution to invertebrate biomass at the estuary (Fig 2.4). *Hydrobia* and *Ceratonereis erythraeensis* were the most important species, contributing on average 75% to the total biomass at the four study sites. At site A, *Ceratonereis* spp. alone constituted *ca* 70% of the total biomass.

There were marked seasonal changes in invertebrate biomass within and between the sites (Fig 2.4). Generally, maximum biomass was attained during winter and early spring and again in autumn, with marked reductions during the summer. This pattern is most clearly seen if the biomass contribution of Decapoda is ignored. In particular, the sandprawn *Callianassa kraussi* and mudprawn *Upogebia capensis* are rare relative to other invertebrates, but are large. One or two individuals in a series

Table 2.5. Relationship between invertebrate density (per m^2) and dry weight (g per 0.037 m^2) of vegetation at the Berg River estuary. In all cases df=59.

Species	r	p
Exosphaeroma hyloecetes	+0.68	< 0.000001
Hydrobia sp.	+0.60	< 0.000001
Capitella capitata	+0.54	< 0.00001
Melita zeylanica	+0.38	< 0.003
Ceratonereis keiskama	+0.32	< 0.09
Ceratonereis erythraeensis	-0.39	< 0.003
Boccardia sp.	-0.29	< 0.03

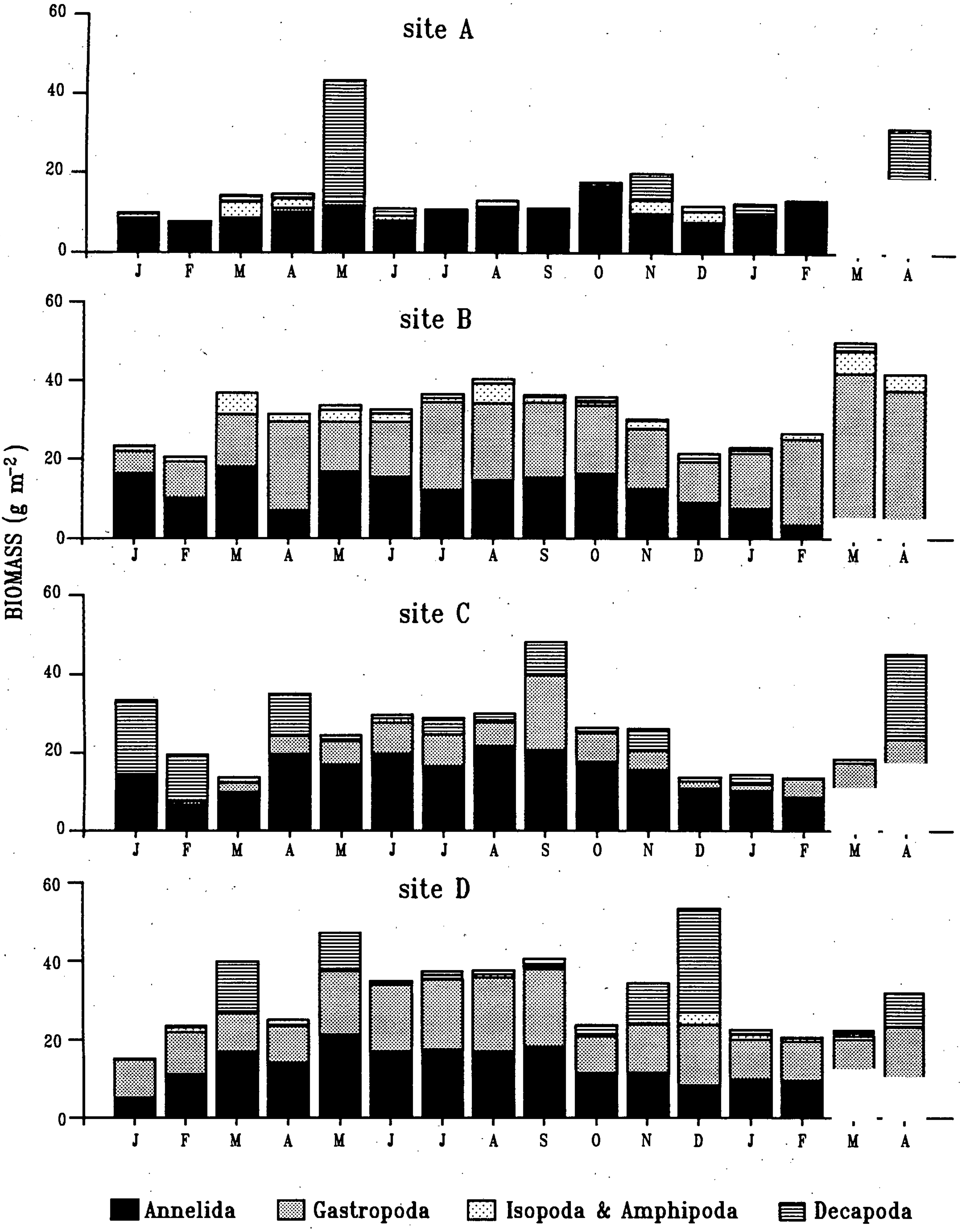


Figure 2.4. Mean biomass (m^{-2}) of the major phyla of invertebrates at the study sites from January 1988 to April 1989.

of core samples has an effect on total sample biomass which is disproportionate to their abundance. Exceptionally high densities of *Hydrobia* at site B in autumn 1989 contributed significantly to the increase in total biomass at this site.

Overall, the highest biomass was supported at site B, ranging between 23.34 and 49.93 g m^{-2} with an average annual biomass of 33.02 g m^{-2} (Table 2.6). Site A supported the lowest biomass. Mean annual biomass over the whole estuary was calculated to be 19.39 g m^{-2} for the 12 dominant species (Table 2.6). The remaining species were scarce, and, because of their small body size, contributed little to the total biomass.

Invertebrate production

Total annual production ranged from 66.7 ($\pm$1.4) (SE) g m^{-2} y^{-1} at site A to 146.9 ($\pm$7.0) (SE) g m^{-2} y^{-1} at site B (Table 2.7). Total annual production for the whole estuary (calculated in the same way as biomass) was 87.58 g m^{-2} y^{-1}, yielding a P/B ratio of 4.52 for the benthic community as a whole. Four species contributed 67% to the total annual production at site A (Table 2.7). At the other three sites, *Ceratonereis erythraeensis* and *Hydrobia* contributed, on average, 62% of annual production.

DISCUSSION

Invertebrate distribution and abundance

Sediment characteristics and the amount of vegetation cover was important in determining the distribution and seasonal abundance of invertebrate macrofauna at the Berg River estuary. Species such as *Ceratonereis keiskama* and *Perinereis nuntia vallata* occurred in a restricted range of sediment types. *C. keiskama*, the smallest of the nereid species at the Berg River estuary, was absent from coarse sediments,

Table 2.6. Mean annual biomass (dry weight g m^{-2}) estimates for intertidal invertebrates at the Berg River estuary.

Site	% of intertidal area	(A) Calculated mean annual biomass at the study site (g m^{-2})	Contribution of A to the mean annual biomass for the whole estuary (g m^{-2})
A	63.05	16.72	10.54
B	12.25	33.02	4.04
C	8.56	27.04	2.31
D	12.32	20.29	2.50

Therefore, mean annual biomass
of 12 dominant species
for the whole estuary = 19.39

Table 2.7. Total annual production ($g\ m^{-2}\ y^{-1}$) of dominant invertebrate species at the four study sites. Production obtained from: [1] Bennett & Branch (in press), [2] Puttick (1977), [3] Chapter 3 [4] P/B = 1.64, the average P/B of *C. erythraeensis* at the Berg River.

	Annual production ($g\ m^{-2}\ y^{-1}$)			
	Site			
Species	A	B	C	D
Ceratonereis erythraeensis	12.2[3]	20.4[4]	16.1[3]	17.5[4]
Ceratonereis keiskama[3]	8.7	1.8	0	0
Perinereis nuntia subsp. *vallata*[4]	0	0	0	3.9
Boccardia sp.[1]	7.2	11.9	7.5	14.1
Capitella capitata[1]	1.5	10.7	12.3	14.0
Melita zeylanica[1]	7.2	10.3	0.4	1.3
Grandidierella lutosa[1]	0.9	0	0	0
Exosphaeroma hyloecetes[1]	0.8	5.6	3.8	2.5
Hymenosoma orbiculare[1]	14.4	2.5	5.9	7.8
Callianassa/Upogebia[1]	9.3	0.0	10.0	10.2
Hydrobia sp.[2]	4.5	83.7	30.3	66.9
Total annual production	66.7	146.9	86.3	138.2

whereas *Perinereis nuntia*, the largest of the nereids, occurred only at the site where sediment was coarsest (Tables 2.2 & 2.4). In addition to particle size, sediment penetrability and water content may also be important in determining the distribution of burrowing species. Wharfe (1977) demonstrated that fine-grained sediments have a greater water retention capacity than coarse sediments and are associated with a richer bacterial flora and higher organic fractions. This study additionally has shown that the penetrability of coarse sediments decreases during exposure more rapidly than that of the finer sediments, and that penetrability of bare sediments decreases more than that of vegetated sediments, presumably because of differences in water retention capacity. On the basis of this, we predict that there would be reduced vertical migration of invertebrates during the tidal cycle in *Zostera* and *Cladophora*-covered mudflats relative to bare mudflats, the former should thus be suitable as a foraging habitat for birds for longer following initial exposure.

The distribution of some species was independent of sediment characteristics but was closely tied to vegetation cover, especially to irruptive growth of filamentous algae. Algae have important effects on the physical properties of the sediment. The oxygenated layer of a sediment may be considerably reduced in the presence of an algal layer, resulting in anoxia immediately below the algae; algae also retain water locally and, therefore, reduce desiccation and salinity stresses; they also impair the access of invertebrates to the surface but increase the amount of food available to herbivores and other deposit feeders (Woodin, 1977).

In the present study, species adversely affected by algal cover, such as *Ceratonereis erythraeensis*, fell in numbers when algal deposits were large, whereas opportunistic species (*Hydrobia* sp. and *Capitella capitata*) and surface-dwelling mobile species increased in abundance. Changes in polychaete abundance in response to changes in algal cover have been reported elsewhere. In the Lower Medway estuary, U.K., colonization of new sites by *Capitella capitata* took place during the warmer months when algae grew most rapidly (Wharfe, 1977). By contrast, a population of *Australonereis ehlersi* (Augener) was eliminated by algal deposition at the Werribee sewage-treatment farm, Australia (Dorsey, 1982).

Several factors may be responsible for the growth of green algae on the estuarine mudflats. Increase in algal biomass at the Avon-Heathcote estuary, New Zealand, has been associated with the discharge of increasing amounts of sewage effluent into the estuary (Knox, 1986). Extensive studies of the growth of *Cladophora* at the Peel-Harvey estuary, Western Australia, revealed that algae were sensitive to several environmental factors, especially nutrient supply, light and temperature (Hodgkin *et al.*, 1980). Reproduction of several estuarine algae is suppressed at low salinities (Wilkinson, 1981). The opening of an artificial mouth of the Berg River in 1966 led to increased upstream penetration of salt water, this effect being most pronounced in summer when river levels are low (van Wyk, 1983). Over much of the estuary, therefore, the seasonal salinity regime is more extreme than it was historically. This may stimulate the growth of algae, which, according to local landowners, has increased considerably in recent years.

The species richness of invertebrates at the Berg River estuary is low. Similarly low values have been reported from other South African estuaries such as the Bot River (27 species - Decker & Bally, 1985) and the Palmiet River (28 species - Branch & Day, 1984). In contrast to this, the Knysna estuary supports over 360 species (Day, 1967) and the Klein River 134 species (Scott *et al.*, 1952). At the Werribee sewage-treatment farm in Australia, where benthic invertebrate densities ranged between 300 000 and 400 000 individuals m^{-2} (one of the densest macrofaunal communities reported to date - Dorsey, 1982) mean species diversity H'(1.6) and evenness J'(0.53) were similar to the Berg River. Physiological stresses resulting from algal deposition or increased salinity, which at certain times of year may exceed the tolerance of several species, might be a direct cause of the low species richness of invertebrates at the Berg River estuary.

Low species diversity may reflect high numerical abundance of individual species (Boyden & Little, 1973). The Berg River compares favourably with northern estuaries with regard to the densities (measured as the numbers of individuals m^{-2}) of dominant species. Densities of *Hydrobia* at the Berg River range between 27 and 182 500. The maximum density of *H. ulvae* (Pennant) at European estuaries range from 11 500 at the Thames River, U.K. to 90 000 at the Medway estuary, (Howells, 1965; Newell, 1965; Wolff & de Wolf, 1977; Wharfe, 1977). The status of *Hydrobia* in Southern African estuaries is not well known, due to confusion in the past with *Assiminea* spp. However, at the Bot River it reaches a maximum density of only 4 000 (Koop *et al.*, 1983).

Densities of *Capitella capitata* at the Berg River range from 27 to 18 909. *Capitella capitata* is a cosmopolitan species which occurs in a wide range of habitats and increases rapidly in abundance under favourable conditions (Grassle & Grassle, 1974). Densities worldwide range from 6 at the River Mersey, U.K. (James & Gibson, 1980) to 400 000 at the Wild Harbor River, Massachusetts, U.S.A. (Grassle & Grassle, 1974).

The maximum density of 6 550 *Ceratonereis erythraeensis* per m^2 at the Berg River is high in comparison with other South African sites, such as the Bot River (1 140 - Koop *et al.*, 1983) and Langebaan Lagoon (600 - Puttick, 1977). A much higher density of *C. erythraeensis* (15 430) was recorded at the Werribee sewage-treatment farm (Dorsey, 1982).

Biomass and production

The high total invertebrate biomass at the Berg River in autumn 1989 was due to changes in the physical conditions of the estuary caused by algal deposition. These changes are believed to have enhanced the reproductive success of certain species, reflected in increased biomass and abundance. Increases in biomass during winter were due largely to the growth of mature individuals, whereas biomass increases in early spring and autumn were due to recruitment of juveniles following reproduction. Post-spawning mortality of *Ceratonereis* spp. in early summer may have contributed significantly to the drop in overall biomass during that period.

Seasonal fluctuations in invertebrate biomass at the Berg River differ slightly from those reported from other localities at similar latitudes. At Langebaan Lagoon, South Africa and Westernport Bay, Victoria, Australia, peaks of invertebrate biomass occurred in spring and autumn and there were significant reductions in biomass in winter and again in summer (Puttick, 1977; Robertson, 1977, cited by NOME, 1982). Invertebrate biomass in north temperate estuaries fluctuates differently to that in south temperate estuaries. Invertebrate biomass at the former sites peaks in early spring and summer and is lowest during autumn and the boreal winter (Beukema, 1974; Wolff & de Wolf, 1977). Seasonal fluctuations in biomass at these latitudes are more extreme than at the south temperate Berg River.

Invertebrate biomass, production and P/B ratio at the Berg River estuary are high in relation to many other sites (Table 2.8). Differences in the productivity of benthic primary consumers between estuaries are likely to be determined largely by the abundance and sources of food material available to them. In North American estuaries, adjacent saltmarshes provide a major input of organic material to mudflats, river input is considered only of secondary importance as a source of organic matter (Nichols, 1977). In the majority of European estuaries, on the other

Table 2.8. Mean annual biomass (dry weight g m^{-2}), production (dry weight g m^{-2} y^{-1}) and P/B ratios of macrobenthic communities at some intertidal mudflats.

Area	Latitude	Dominant invertebrates	Mean biomass g m^{-2}	Production g m^{-2} y^{-1}	P/B	Source
Forth estuary, Scotland	57°N	Oligochaeta/Bivalvia	10.50	12.90	1.23	McLusky, 1987
Humber estuary, UK	54°N	Bivalvia	24.00	27.00	1.12	McLusky, 1989
Grevelingen estuary, The Netherlands	53°N	Mollusca	25.70	41.30	1.60	Wolff & de Wolf, 1977
Wadden Sea, The Netherlands	53°N	Bivalvia/Polychaeta	27.00*	30.00*	1.1*	Beukema, 1981
Lynher estuary, UK	51°N	*Macoma*	13.24	13.31	1.01	Warwick & Price, 1975
Southampton Water, UK	51°N	Bivalvia	140.00	188.50	1.35	Hibbert, 1976
Petpeswick Inlet, Canada	44°N	Bivalvia/Gastropoda	16.22	21.20	1.31	Burke & Mann, 1974
San Francisco Bay, USA	37°N	Bivalvia	16.64*	74.93*	4.50*	Nichols, 1977
Banc d'Arguin, Mauritania	11°N	Bivalvia/Polychaeta	3.20*	6.00-12.00*	3.30*	NOME, 1982
Westernport Bay, Australia	32°S		10.00-15.00*	43.00*	3.40*	NOME, 1982
Berg River estuary, S. Africa	32°S	Gastropoda/Polychaeta	19.35	87.58	4.52	This study
Langebaan Lagoon, S. Africa	33°S	Gastropoda/Amphipoda	19.21	95.25	4.96	Puttick, 1977
Swartkops estuary, S. Africa	34°S	Decapoda	69.30	77.70	1.12	Muller, 1984; Emmerson, 1986; Baird, 1988
Upper Waitemata Harbour, N. Zealand	35°S		17.90	27.30	1.53	Knox, 1986

* gAFDWm^{-2}

hand, much of the detritus and nutrients are derived by import from tidal currents in the adjacent seas, and 90-95% of the intertidal areas are bare mud (McLusky, 1989). At the Berg River, eel-grass *Zostera capensis* and green algae *Cladophora* form a thick layer on intertidal mudflats throughout much of the year and are certainly a major food source for primary consumers within the estuary. High nutrient concentrations and high rates of plankton production in the Southern Benguela upwelling region (Shannon & Pillar, 1986) presumably provide an additional source of food material for invertebrates.

Estuarine productivity in relation to latitude: consequences for avian carrying capacity

If the production of benthic primary consumers within an estuary depends on food availability, one might expect that, in an area where food is abundant, production of invertebrates should be concomitantly high. Mild weather conditions and the absence of extreme temperatures may further promote high production levels.

The production of invertebrate communities is positively and significantly correlated with mean annual ambient temperature ($r=0.72$, $p<0.01$ - Fig 2.5A). Because mean temperature is negatively correlated with latitude ($r=-0.87$, $p<0.01$), production is also negatively correlated with latitude, decreasing with increasing distance from the equator ($r=-0.72$, $p<0.01$ - Fig 2.5B). Two sites included in Table 2.8, the Hamble Spit, U.K. and the Banc d'Arguin, Mauritania are excluded. Total macrofaunal biomass and production values at the former site refer to a selected small area within the estuary and do not represent mean values as is the case in other studies. Values from the Banc d'Arguin are based only on the production of a dominant bivalve, *Anadara senilis* (L.), a long-lived species with a slow turnover. More than 100 invertebrate species have been recorded over the entire intertidal area of the

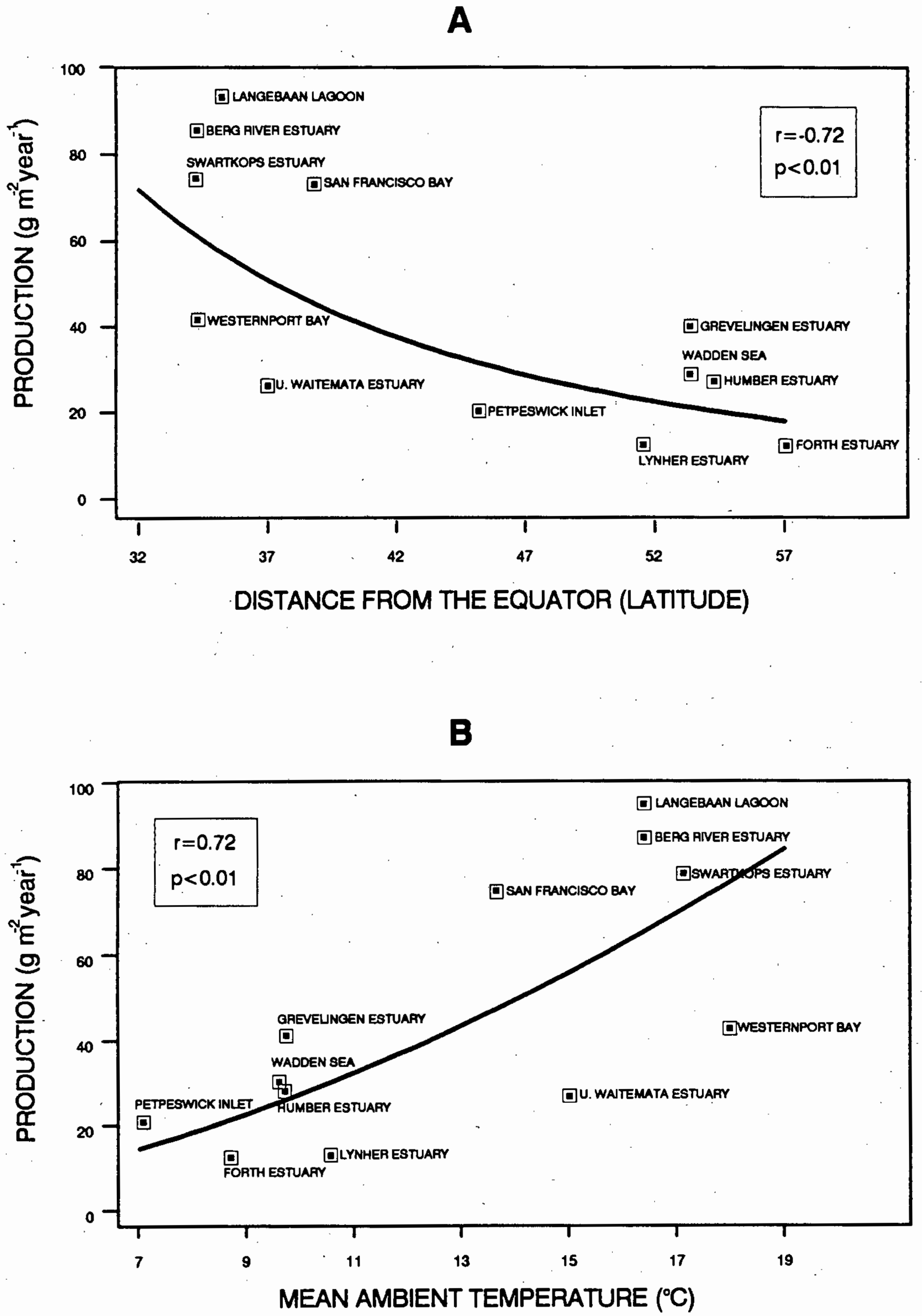


Figure 2.5. Relationship between estuarine invertebrate production and, (A) mean annual ambient temperature, (B) distance from the equator. Mean temperature calculated from tables in Pearce and Smith, 1984.

Banc d'Arguin, of which 52 are molluscs and 59 polychaetes and oligochaetes (NOME, 1982).

The correlation between temperature and production suggests that a lack of extreme temperatures, especially cold temperatures, might allow prolonged reproduction of invertebrates and a continuous supply of food for their maintenance. Goss-Custard *et al.* (1977) demonstrated that densities of estuarine-feeding shorebirds within a limited geographic area were linked to prey availability. If this pattern holds true throughout the nonbreeding range of Holarctic breeding migrant shorebirds, and shorebird density is linked to estuarine productivity, it can be predicted that warm temperate and tropical estuaries will support higher shorebird densities than cold temperate estuaries. High densities of shorebirds at the Berg River, and at other warm temperate and tropical sites on the east Atlantic seaboard (Zwarts, 1988) support this prediction. Studies of invertebrate productivity in tropical estuaries are now required to determine the relationship between production and latitude at latitudes of less than 30° (Fig 2.5B).

REFERENCES

Baird, D. 1988 Synthesis of ecological research in the Swartkops estuary. In *The Swartkops Estuary* (Baird, D., Marais, J. F. K. & Martin, A. P., eds). *South African Natural Scientific Progress Report* **156**, 41-56.

Banse, K. & Mosher, S. 1980 Adult body mass and annual production/biomass relationships of field populations. *Ecological Monographs* **50**, 355-379.

Bennett, B. A. & Branch, G. M. (1990) Relationships between production and consumption of prey species by resident fish in the Bot, a cool temperate South African estuary. *Estuarine, Coastal and Shelf Science* **30**, 139-155.

Beukema, J. J. 1974 Seasonal abundance in the biomass of the macro-benthos of a tidal flat area in the Dutch Wadden Sea. *The Netherlands Journal of Sea Research* **8**, 94-107.

Beukema, J. J. 1981 Quantitative data on the benthos of the Wadden sea In: *Invertebrates of the Wadden Sea* (Dankers, H. K. & Wolff, W. J., eds). Balkema, Rotterdam, pp 125-133.

Boyden, C. R. & Little C. 1973 Faunal distribution in soft sediments of the Severn Estuary. *Estaurine, Coastal and Shelf Science* **1**, 203-223.

Branch, G. M. & Day, J. A. 1984 Ecology of South African estuaries: Part XIII. The Palmiet River estuary in the south-western Cape. *South African Journal of Zoology* **19**, 63-77.

Burke, M. W. & Mann K. H. 1974 Productivity and production: biomass ratios of bivalve and gastropod populations in an eastern Canadian estuary. *Journal of the Fisheries Research Board of Canada* **31**, 167-177.

Day, J. H. 1967 The biology of Knysna Lagoon, South Africa. In: *Estuaries* (Lauff, G. H., ed). Washington. American Association of Advanced Science, pp. 397-407.

Decker, H. P. & Bally R. 1985 The benthic macrofauna of the Bot River estuary, South Africa, with a note on its meiofauna. *Transactions of the Royal Society* *of South Africa* **45**, 379-395.

Dorsey, J. H. 1982 Intertidal community offshore from the Werribee Sewage-treatment Farm: an opportunistic infaunal assemblage. *Australian Journal of Marine and Freshwater Research* **33**, 45-54.

Emmerson, W. D. 1986 The ecology of *Palaemon pacificus* (Stimpson) associated with *Zoostera capensis* Setchell. *Transactions of the Royal Society of South Africa* **46**, 79-97.

Goss-Custard, T. D., Kay D. G. & Blindell R. M. 1977 The density of migratory and overwintering Redshank, *Tringa totanus* (L.) and Curlew, *Numenius arquata* (L.), in relation to the density of their prey in south-east England. *Estuarine and Coastal Marine Science* **5**, 497-510.

Grassle, J. F. & Grassle, J. P. 1974 Opportunistic life histories and genetic systems in marine benthic polychaetes. *Journal of Marine Research* **32**, 253-284.

Hibbert, C. J. 1976 Biomass and production of a bivalve community on an intertidal mud-flat. *Journal of Experimental Marine Biology and Ecology* **25**, 249-261.

Hodgkin, E.P., Birch, P. B., Black, R. E. & Humphries, R. B. 1980 The Peel-Harvey estuarine system study (1976-1980). *Report No 9.* Department of Conservation and Environment. Perth, Western Australia.

Howells, W. R. 1965 The macrofauna of the intertidal soils of the Towy Estuary, Carmarthenshire. *Annual Magazine of Natural History* **7**, 577-607.

James, C. J. & Gibson, R. 1980 The distribution of the Polychaete *Capitella capitata* (Fabricius) in dock sediments. *Estuarine and Coastal Marine Science* **10**, 671-683.

Koop, K., Bally, R. & McQuaid, C. D. 1983 The ecology of South African estuaries. Part XII: The Bot River, a closed estuary in the south-western Cape, South Africa. *South African Journal of Zoology* **18**, 1-10.

Knox, G. A. 1986 *Estuarine Ecosystems: a systems approach.* Vol. I & II. CRC Press, INC. Boca Raton, Florida.

Longbottom, M. R. 1979 The distribution of *Arenicola maritima* (L.) with particular reference to the effects of particle size and organic matter of the sediments. *Journal of Experimental Marine Biology and Ecology* **5**, 138-157.

McLusky, D. S. 1987 Intertidal habitats and benthic macrofauna of the Forth estuary, Scotland. *Proceeding of the Royal Society of Edinburgh* **93B**, 389-399.

Mclusky, D. S. 1989 *The Estuarine Ecosystem*. Blackie & Son Ltd.

Muller, I. 1984 The occurrence and abundance of polychaetes in the Swartkops estuary. Unpubl. B.Sc. project. University of Port Elizabeth, Port Elizabeth, South Africa.

Newell, R. C. 1965 The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proceedings of the Zoological Society of London* **144**, 25-45.

Nichols, F. H. 1977 Infaunal biomass and production on a mudflat, San Francisco Bay, California. In: *Ecology of Marine Benthos* (Coull, B. C., ed). University of South Carolina Press, Columbia, pp. 339-357.

NOME, 1982 *Wintering waders on the Banc d'Arguin*. Communication No **6**, Wadden Sea Working Group. The Netherlands.

Pearce, E. A. & Smith, C. G. 1984 *The World Weather Guide*. Hutchinson, London.

Puttick, G. 1977 Spatial and temporal variations in intertidal animal distribution at Langebaan Lagoon, South Africa. *Transactions of the Royal Society of South Africa* **42**, 403-430.

Scott, K. M. F., Harrison, A. P. & Macnae, W. 1952 The ecology of South African estuaries. Part II- The Klein River Estuary, Hermanus, Cape. *Transactions of the Royal Society of South Africa* **33**, 283-331.

Shannon, L. V. & Pillar, S. C. 1986 The Benguela ecosystem. Part III. Plankton. *Oceanography and Marine Biology. An Annual Reviev* **24**, 65-170.

van Wyk, A. C. 1983 Effect of dredging on the Berg River estuary. Unpubl. M.Sc. Thesis. University of Cape Town, Cape Town, South Africa.

Warwick, R. M. & Price, R. 1975 Macrofauna production in an estuarine mud-flat.

Journal of the Marine Biological Association of the United Kingdom **55**, 1-18.

Wharfe, J. R. 1977 An ecological survey of the benthic invertebrate macrofauna of the Lower Medway Estuary, Kent. *Journal of Animal Ecology* **46**, 93-113.

Wilkinson, M. 1981 Survival Strategies of attached algae in estuaries. In: *Feeding and Survival Strategies of Estuarine Organisms* (Jones, N. V. & Wolff W. J., eds). Plenum Press, New York, pp 29-38.

Wolff, W. J. & de Wolf, L. 1977 Biomass and production of zoobenthos in the Grevelingen Estuary, The Netherlands. *Estuarine and Coastal Marine Science* **5**, 1-24.

Woodin, S. A. 1977 Algal "gardening" behaviour by nereid polychaetes: effects on soft-bottom community structure. *Marine Biology* **44**, 39-42.

Zar, B. 1977 *Field and Laboratory Methods for General Ecology*. Wm. C. Brown Company Publishers, Dubuque.

Zwarts, L. 1988 Numbers and distribution of coastal waders in Guinea-Bissau. *Ardea* **76**, 42-55.

CHAPTER 3

DISTRIBUTION, BIOMASS AND PRODUCTION OF <u>CERATONEREIS</u> <u>ERYTHRAEENSIS</u> (FAUVEL) AND <u>CERATONEREIS</u> <u>KEISKAMA</u> (DAY) AT THE BERG RIVER ESTUARY, SOUTH AFRICA

SUMMARY

Population dynamics of the polychaetes *Ceratonereis keiskama* and *C. erythraeensis* were studied at the Berg River estuary, South Africa, from December 1987 to April 1989. There was marked size-related depth stratification of both species, with small worms being concentrated in the upper layer of the substratum and larger ones deeper down. Reproduction of both species occurred in summer. Three cohorts were distinguished in both populations. Recruitment of *C. keiskama* peaked in December whereas that of *C. erythraeensis* varied between years and sites (December - April). The population biomass of *C. keiskama* peaked in mid summer and was lowest during the winter and spring. *C. erythraeensis* maintained a high population biomass during winter and reached its lowest biomass during January-February. The total annual production of *C. keiskama* in the restricted area of the estuary were it occurred was 7.58 g m^{-2} y^{-1}, with a mean annual biomass of 4.11 g m^{-2}, making P/B = 1.84. Total annual production of *C. erythraeensis* for the whole estuary was 14.42 g m^{-2} y^{-1}, mean annual biomass was 7.59 g m^{-2}, and P/B = 1.90.

INTRODUCTION

Studies of the production and biomass of estuarine benthic communities are essential in establishing energy budgets for these systems. The importance of macrobenthos in the production of intertidal areas has well been studied in the northern hemisphere but there are very limited data available south of the equator. Several studies have been made in South African estuaries but these are concerned largely with composition, abundance, biomass and distribution of benthic macrofauna, rather than with their production. A brief report on the production of most important components of macrobenthic fauna exist in South Africa for Langebaan Lagoon (Puttick, 1977) and the Swartkops estuary (Muller, 1984; Baird, 1988). There are, however, no detailed studies of the seasonal production of estuarine intertidal invertebrates in South Africa. Such information is essential when interactions between prey populations and their predators are considered. Although shorebirds (Aves: Charadriiformes) are the most conspicuous secondary consumers on the estuaries there are no published studies to date which demonstrate a relationship between them and their prey populations on the seasonal basis in the southern hemisphere.

Twenty-five benthic invertebrate species have been recorded from intertidal mudflats at the Berg River estuary (Chapter 2). Of these, polychaetes of the family Nereidae are the most important prey of shorebirds (Chapter 4) which feed in high densities at the estuary, particularly during the austral summer.

Three species of nereid worms occur in the estuary: *Ceratonereis erythraeensis* Fauvel (1919), *C. keiskama* Day (1953) and *Perinereis nuntia* subsp. *vallata* Grube (1857). The last of these species is confined to an area near the mouth of the river, where it is scarce (Chapter 3). The two *Ceratonereis* species are abundant in the estuary and their distribution is correlated with sediment characteristics. *Ceratonereis* *erythraeensis* is most abundant in coarse sediments, whereas *C. keiskama* is confined to fine sediments (Chapter 2).

The aim of this study was to investigate seasonal patterns in the demography and biomass of *Ceratonereis* species, and to determine their annual production.

STUDY SITE AND METHODS

Four study sites A, B, C and D, each of 2 000 m^2 (25 x 80 m) were established at decreasing distances from the river mouth (Fig 2.1). Each month, between December 1987 and April 1989, ten randomly-positioned core samples were taken to a depth of 300 mm at each site. The core was 69 mm in diameter and was divided into two sections, 0-50 mm and 50-300 mm, to determine depth distribution of nereids. Samples were washed through a 500 um sieve and all nereids retained were preserved in 10% formalin. All samples were taken at low tide.

The bodies of the nereids often were damaged during the sieving process and consequently only their jaws were measured - using a binocular microscope and graticule. Jaw lengths were converted to dry body mass and body length using conversion equations calculated from intact worms collected specifically for this purpose.

Ceratonereis erythraeensis:

Body length = 60.63 Jaw length - 11.31 ($r=0.82$, $N=35$)

Dry mass = $4.57*10^{-3}$ Jaw length$^{2.79}$ ($r=0.72$, $N=20$)

C. keiskama:

Body length = 24.51 Jaw length - 2.15 ($r=0.91$, $N=30$)

Dry mass = $1.70*10^{-3}$ Jaw length$^{2.31}$ ($r=0.82$, $N=22$)

The size cohorts of the populations were separated from each other by using probability paper (Harding, 1949; Cassie, 1954). Production of both *Ceratonereis* species was estimated using mean numbers and weight increment of each cohort as described by Crisp (1971). Production was calculated separately for each cohort in each month for the whole study period (17 months). The total annual production was determined by taking an average of those months which were sampled in more than one year (December-April) and summing the production in each month over the 12 month period. The mean annual biomass was calculated in the same way. Both biomass and production are expressed in dry g.

RESULTS

Life cycle and population structure

Ceratonereis keiskama occurred only at sites A and B. Three cohorts were present at both sites during the study period (Figs 3.1 & 3.2). Cohort 1 was present at the beginning of the study period and contained mature individuals, assumed to have originated from a major spawning peak during summer of the previous year. A second cohort, of immature animals, was also present at the start of the study and remained through the winter until the following summer when a third cohort, consisting of small individuals, appeared.

Ceratonereis erythraeensis occurred at all four study sites, but recruitment patterns differed at each site. Cohorts at sites B and D could not be separated because small animals were present throughout the year and the whole population decreased in numbers towards the end of the study period. This decrease indicates either emigration or death of mature individuals, but which of these took place is unknown. Populations of *C. erythraeensis* at the other two sites, A and C, were represented by three cohorts during the study period (Figs 3.3 & 3.4). Cohort 1 contained mature individuals and was present through the summer and autumn of

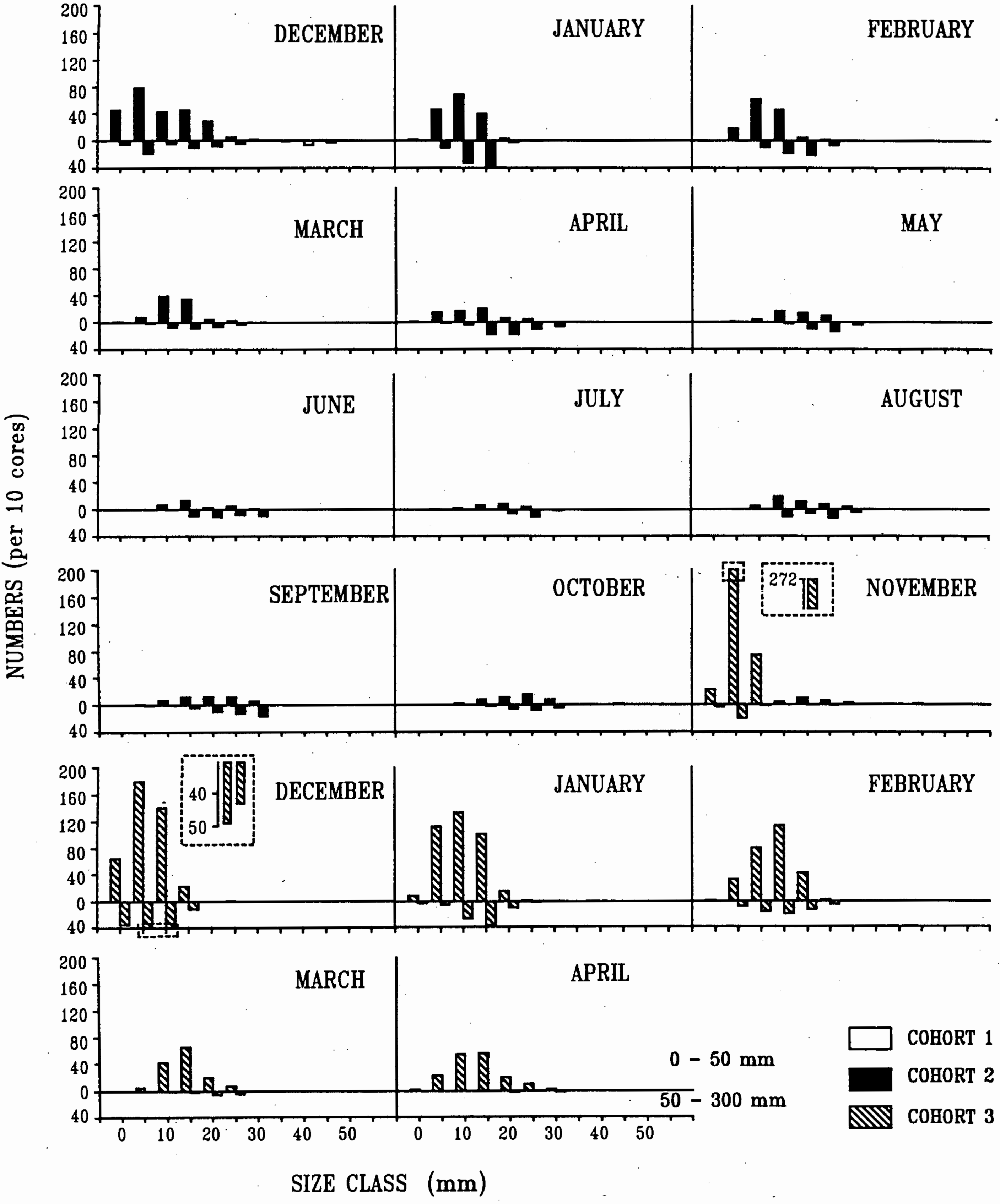


Figure 3.1. Size distribution of *Ceratonereis keiskama* at 0-50 and 50-300 mm depths at site A from December 1987 to April 1989.

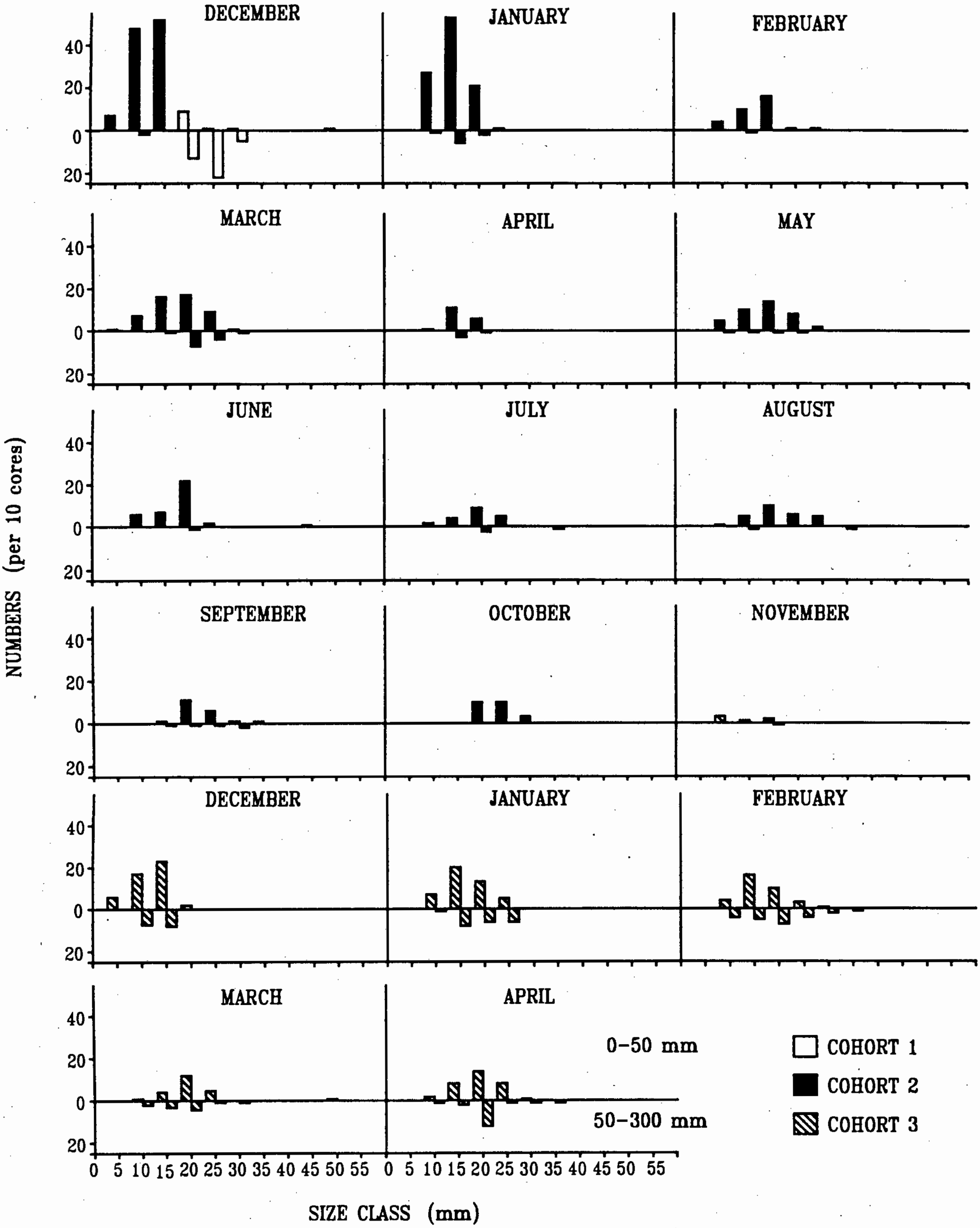


Figure 3.2. Size distribution of *Ceratonereis keiskama* at 0-50 and 50-300 mm depths at site B from December 1987 to April 1989.

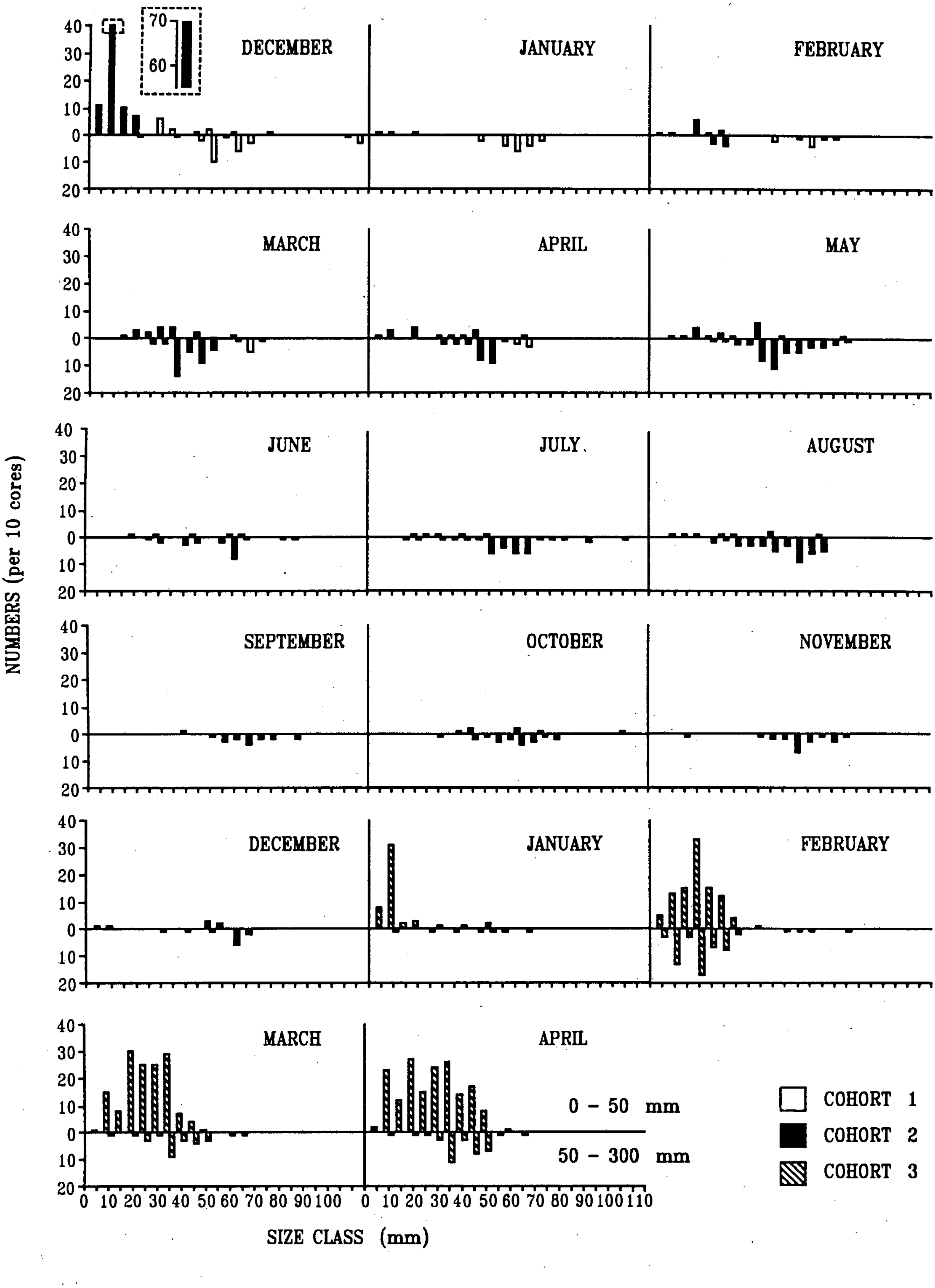


Figure 3.3. Size distribution of *Ceratonereis erythraeensis* at 0-50 and 50-300 mm depths at site A from December 1987 to April 1989.

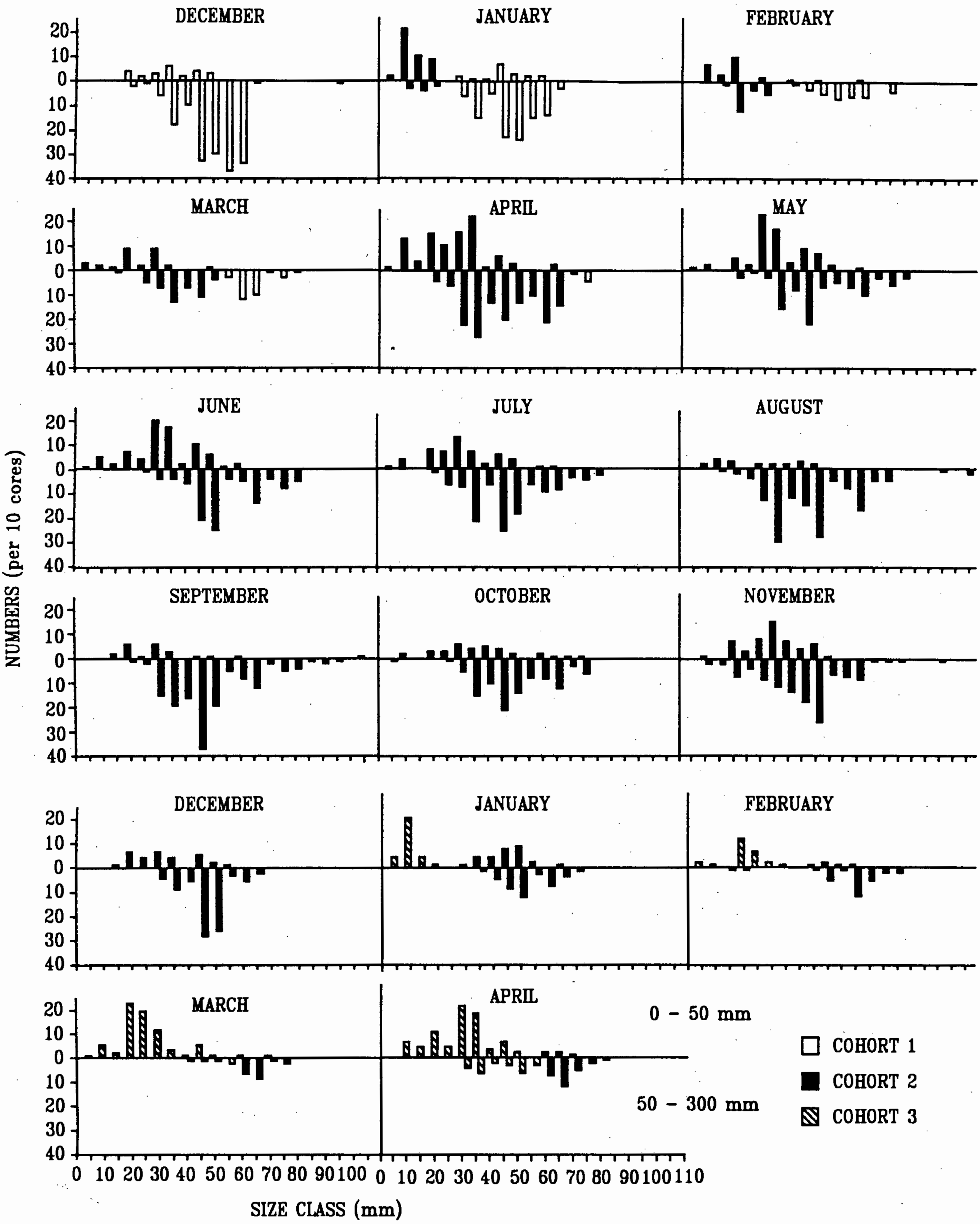


Figure 3.4. Size distribution of *Ceratonereis erythraeensis* at 0-50 and 50-300 mm depths at site C from December 1987 to April 1989.

1988. Cohort 2 was present at the start of the study period at site A and appeared one month later at site C, remaining until the following summer. By this time, newly-settled individuals of cohort 3 entered the population. Recruitment was spread over the period January to April at site C in both years. There was a difference in the recruitment pattern at site A between years with a later recruitment peak in the summer of 1988/89 (April) than in 1987/88 (December) (Figs 3.3 & 3.4). Despite these differences, all recruitment was consistently concentrated in summer and early autumn (December-April).

Density

The average density of *C. keiskama* varied between 6 258 ± 1 958 (SE) m^{-2} in December 1987 and 788 ± 93 m^{-2} in July 1989. The highest density of 14 897 m^{-2} was reached in December 1989 at site A. The density of cohort 2 decreased steadily at site A and more rapidly at site B, where 60% of the December 1987 stock had disappeared by February 1988 (Fig 3.5a). An increase in density at both sites in summer 1989 was due to newly recruiting individuals of cohort 3.

The average density of *C. erythraeensis* over the whole estuary (including sites B and D) varied between 5 088 ± 809 (SE) m^{-2} in December 1987 and 1 585 ± 483 m^{-2} in December 1989. The highest density of 7 034 m^{-2} was recorded at site B in December 1987. At site C, cohort 2 was numerically dominant throughout the study period (Fig 3.6a). After a peak in abundance in April, the population remained stable throughout the winter and spring, but had fallen by 87% by February of the following year. At site A, cohort 2 was never as abundant as at site C, but seasonal patterns of density at the two sites were similar. Due to earlier recruitment, cohort 3 was more abundant at site A than at site C at the end of the study period.

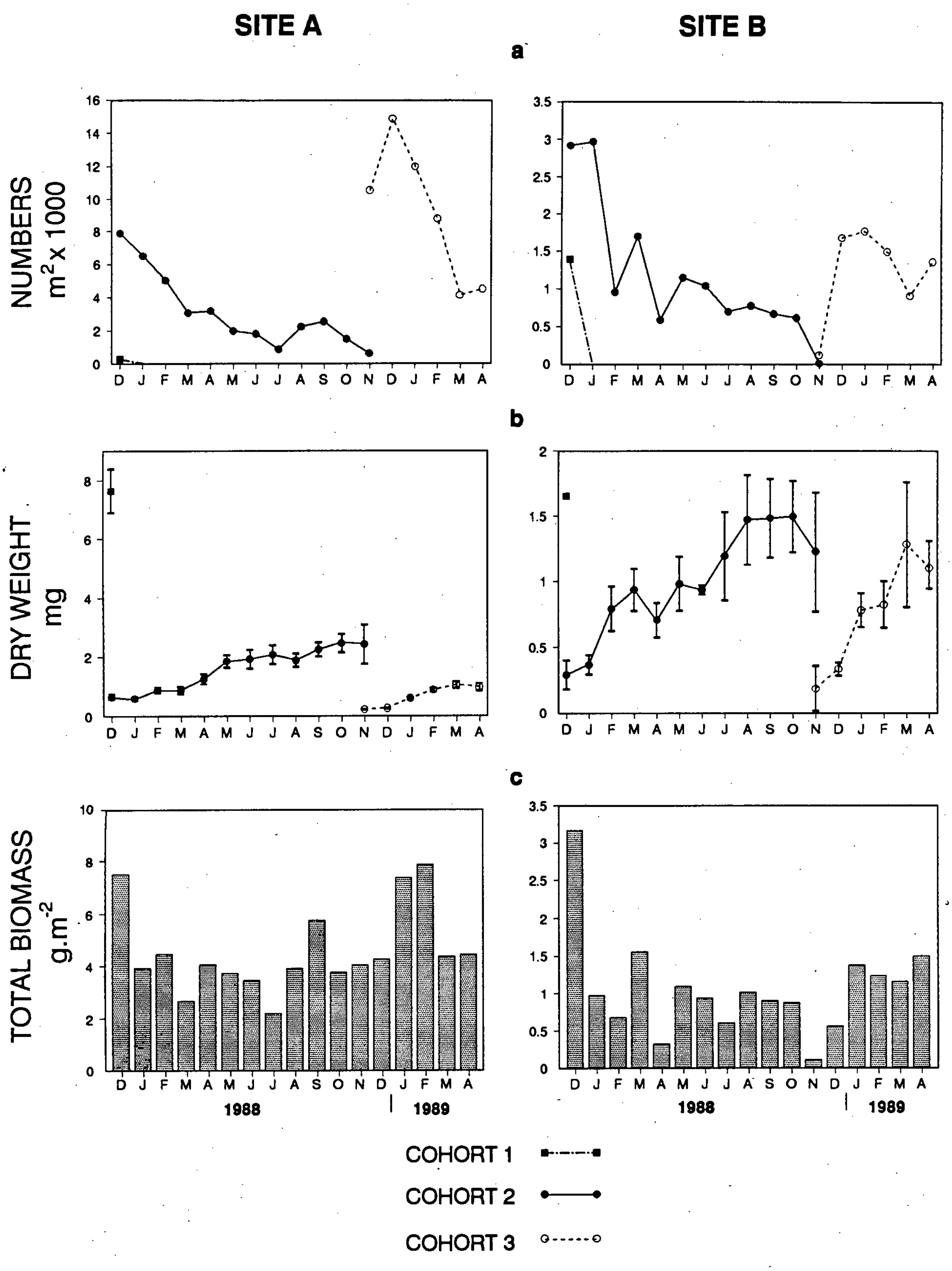
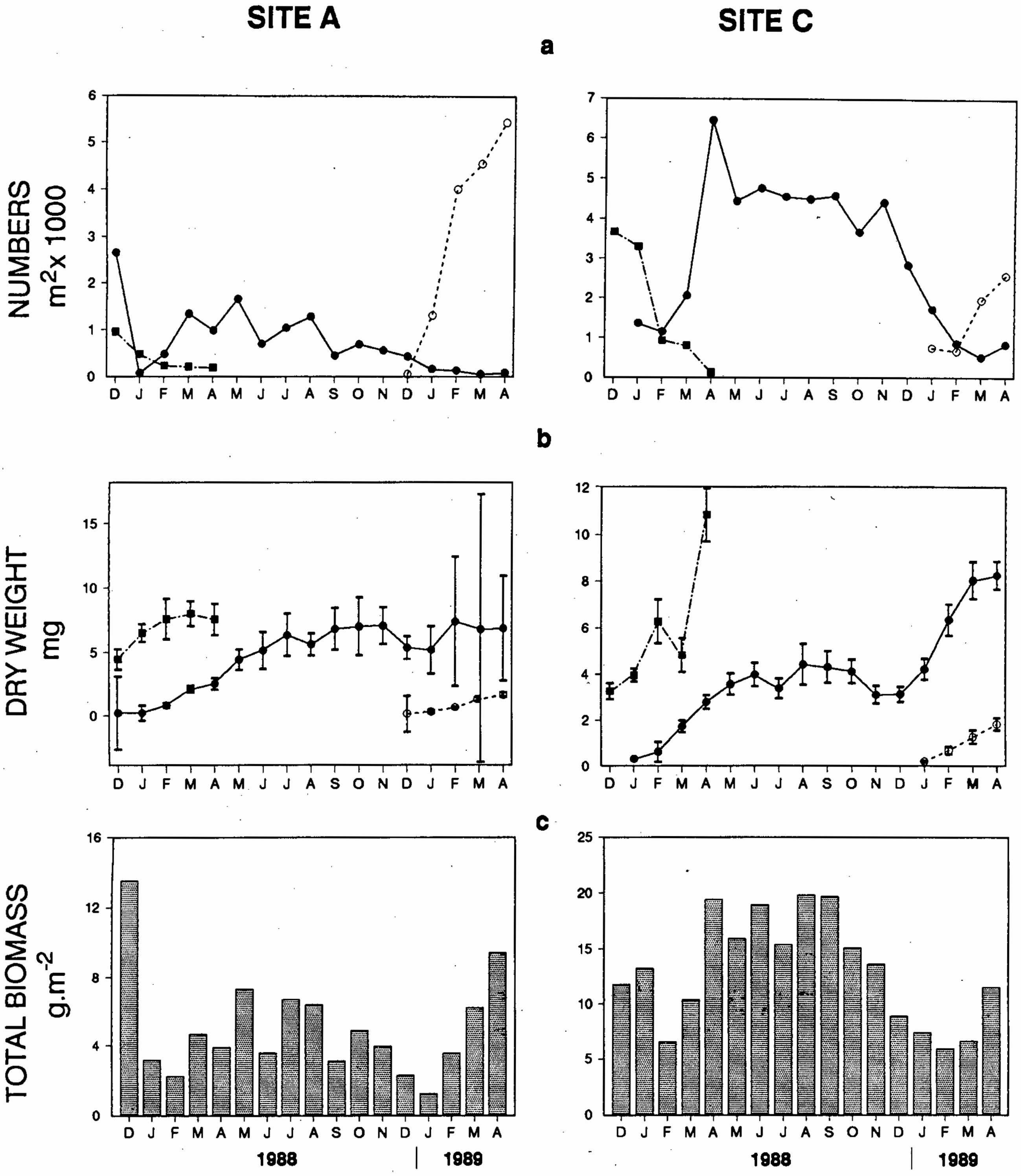


Figure 3.5. *Ceratonereis keiskama* at sites A and B; a - numbers (m^{-2}) of individuals in the three cohorts; b - mean dry weight (mg) of three cohorts (± 95% confidence limits); c - biomass (g m^{-2}) of the total population.



COHORT 1 ■-·-■

COHORT 2 ●—●

COHORT 3 ○----○

Figure 3.6. *Ceratonereis erythraeensis* at sites A and C; a - numbers (m^{-2}) of individuals in the three cohorts; b - mean dry weight (mg) of three cohorts (± 95% confidence limits); c - biomass ($g\ m^{-2}$) of the total population.

Biomass

The biomass of *C. keiskama* peaked in summer due to rapid settlement and growth of recruits (Figs 3.5a, b & c). The fall in total biomass at site A occurred in winter due to mortality of the dominant cohort (2). Lowest biomass at site B occurred in spring (November). This can be attributed to the disappearance of mature individuals of cohort 2 and the low biomass of recruits of cohort 3 entering the population (Fig 3.5b). Mean annual biomass of *C. keiskama* for the two sites was 4.11 g m^{-2}.

Ceratonereis erythraeensis showed different patterns of biomass fluctuation to *C. keiskama.* The lowest biomass was reached in late summer (January-February) due to the disappearance of the overwintering cohort 1 and to low numbers and biomass of recruits (Figs 3.6a, b & c). The high biomass during winter and spring at both sites was maintained by the growth and high abundance of cohort 2. Despite the drop in numbers of cohort 2 in summer 1989 at site A, total biomass continued to rise due mainly to the rapid increase in abundance of cohort 3. Mean annual biomass of *C. erythraeensis* for the whole estuary was 7.59 g m^{-2}.

Biomass stratification

A greater proportion of the biomass of *C. erythraeensis* occurred in the 50-300 mm layer than in the 0-50 mm layer of the substratum (Fig 3.7). This pattern was reversed only in autumn 1989 at sites A and D. At the former site, where the pattern was most pronounced, this was due to recruitment of small individuals close to the surface. An increase in biomass in the deeper layer of the substratum during the winter months probably is due to growth and downward movement of older individuals.

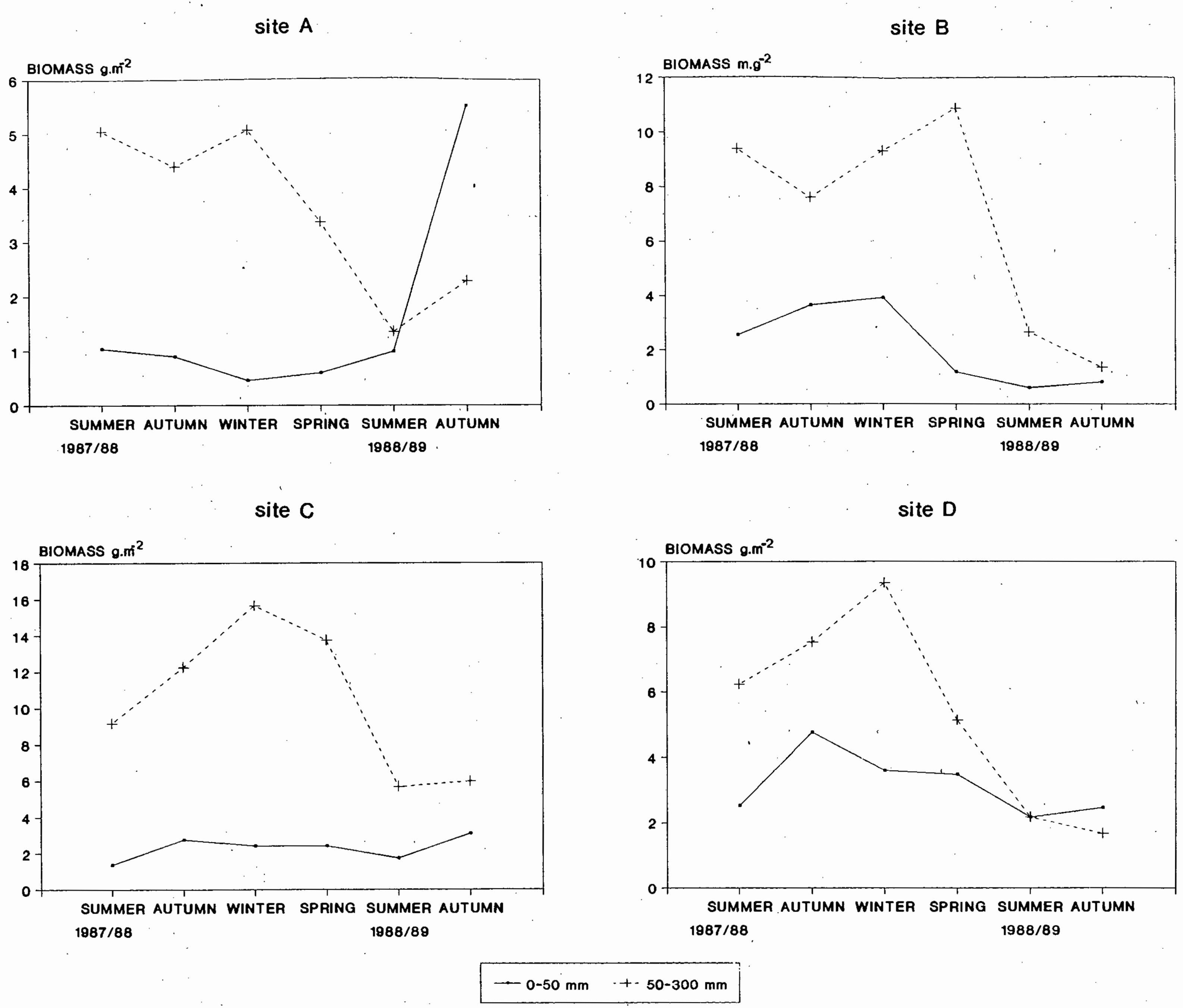


Figure 3.7. Seasonal variations in the biomass of *Ceratonereis erythraeensis* at 0-50 and 50-300 mm depths at the four study sites.

On average, 26% (2.26 g m^{-2}) of the total biomass of *C. erythraeensis* was present in the upper layer of the substratum (Table 3.1). By contrast, the biomass of *C. keiskama* in the upper layer of the substratum was greater than in the deeper layer (Fig 3.8). On average, 69% (2.06 g m^{-2}) of the total biomass of this species was in the upper layer: this is close to the average biomass of *C. erythraeensis* at the same depth. A marked increase in the biomass of *C. keiskama* in the upper layer at site A during the spring and summer of 1989 was due to recruitment occurring in this layer. This recruitment occurred slightly later at site B than at site A (Figs 3.1, 3.2 & 3.8).

Small individuals of both species predominated in the upper layer of the substratum and larger individuals in the lower layer (Figs 3.9A & B).

Production

Table 3.2 shows the computation used to calculate the annual production of *C. keiskama* as exemplified by site B. In cases where a sudden drop in numbers or mean weight of individuals in a cohort occurred in only one month, data were interpolated using values for the preceding and following months. Total annual production of *C. keiskama* for the two sites (A & B) was 7.58 g m^{-2} y^{-1}, mean annual biomass was 4.11 g m^{-2} and the P/B ratio was 1.84 (Table 3.3).

The production of *C. erythraeensis* was calculated at only two sites (Table 3.3). An annual production of this species for the entire estuary was established as follows. The measured production of *C. erythraeensis* at sites A and C contributed 9.04 g m^{-2} y^{-1} to the total production of the estuary (Table 3.3). The mean annual biomass for these areas was 4.76 g m^{-2} and the P/B ratio calculated from these values was 1.90. Using this ratio and annual mean biomass for the whole estuary (7.59 g m^{-2} - Table 3.3) the total annual production was calculated as 14.42 g m^{-2} y^{-1} (Table 3.3).

Table 3.1. Average biomass (g m^{-2}) and percentage of the total biomass of *Ceratonereis erythraeensis* and *C. keiskama* at 0-50 and 50-300 mm depths from December 1987 to April 1989.

Ceratonereis erythraeensis

	Average biomass (g m^{-2}) and % of the total biomass at each site					
	A	B	C	D	Mean	SD
Depth 0-50						
Biomass	1.396	2.167	2.243	3.231	2.259	0.752
(%)	(27.6)	(23.5)	(17.5)	(35.7)	(26.1)	(7.6)
Depth 50-300						
Biomass	3.658	7.041	10.658	5.824	6.795	2.931
(%)	(72.4)	(76.5)	(83.1)	(64.3)	(74.1)	(7.9)

Ceratonereis keiskama

	A	B	Mean	SD
Depth 0-50				
Biomass	3.347	0.768	2.058	1.824
(%)	(66.7)	(71.8)	(69.3)	(3.6)
Depth 50-300				
Biomass	1.673	0.301	0.987	0.969
(%)	(33.3)	(28.2)	(30.8)	(3.6)

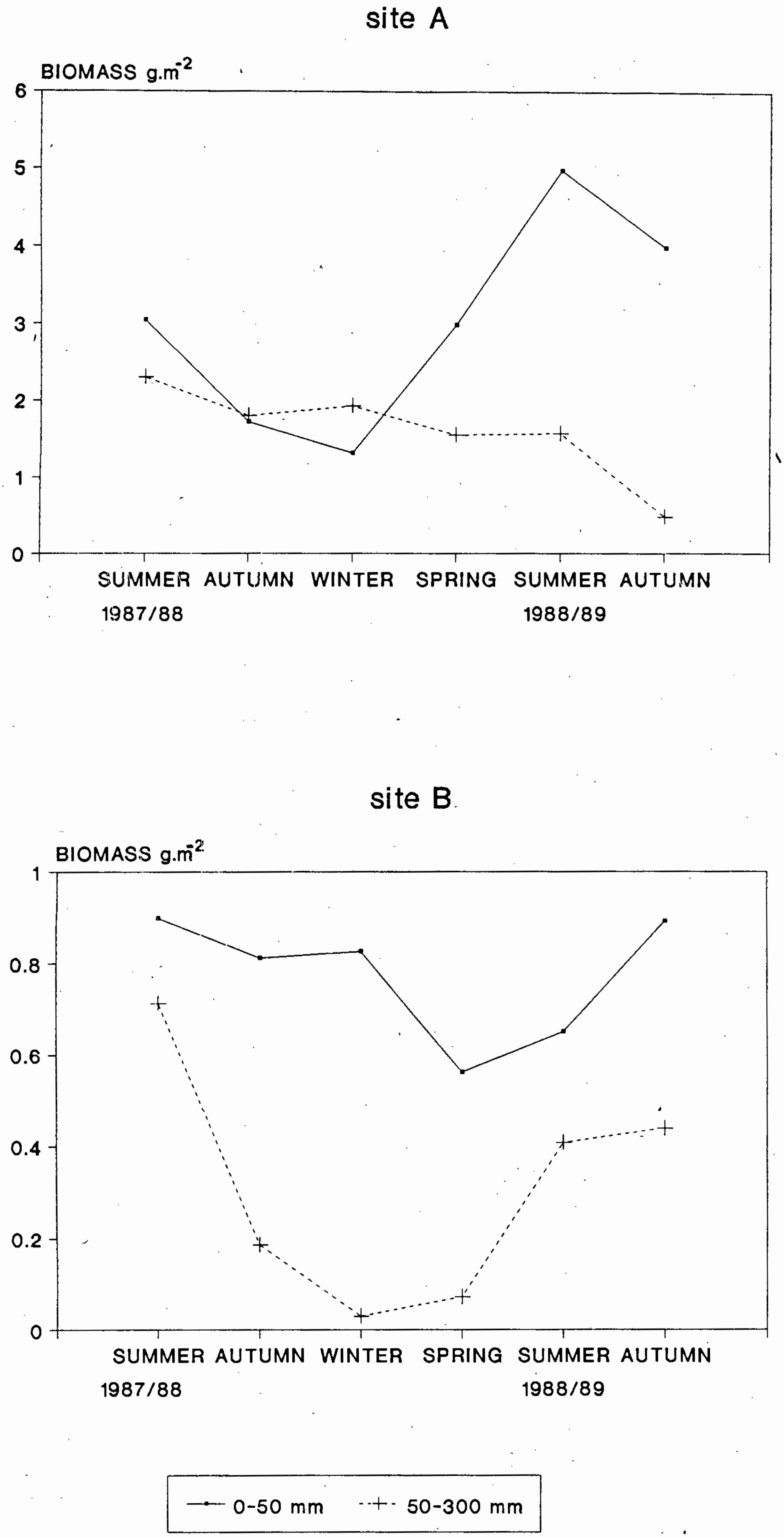


Figure 3.8. Seasonal variations in the biomass of *Ceratonereis keiskama* at 0-50 and 50-300 mm depths at sites A and B.

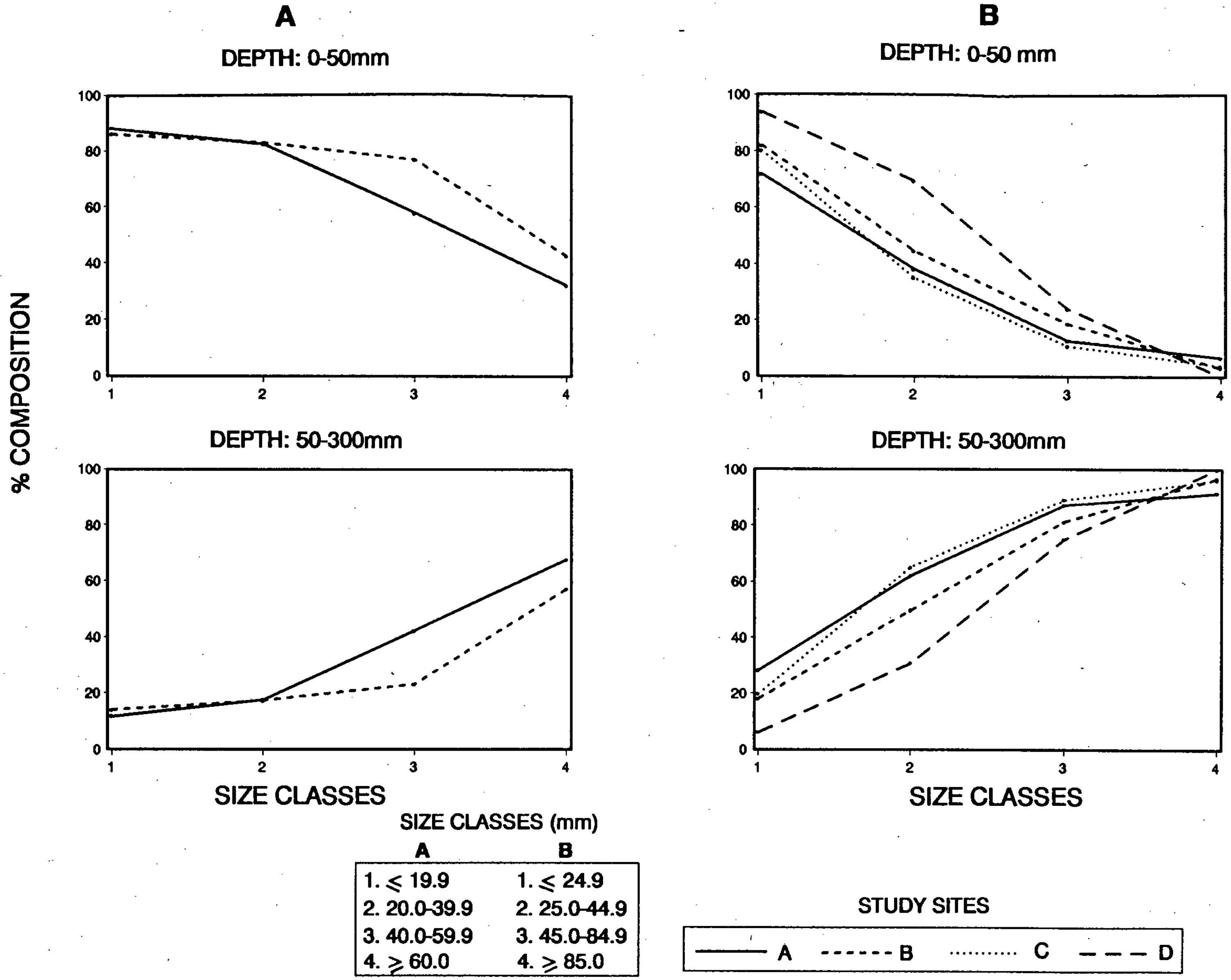


Figure 3.9. The percentage distribution of four size classes of *Ceratonereis keiskama* (A) and *C. erythraeensis* (B) at 0-50 and 50-300 mm depths from December 1987 to April 1989.

Table 3.2. Summary of data used to calculate total annual production (g m^{-2} y^{-1}) and P/B ratio of *Ceratonereis keiskama* at site B.

Date	Age class	Numbers N (m^{-2})	Mean weight $\bar{w}$ (mg)	Mean numbers $\bar{N}$ (m^{-2})	weight increment Δw (mg)	Production increment $\bar{N} x \Delta w$ (mg m^{-2})	Total biomass (mg m^{-2})	Month	Mean monthly production (mg m^{-2} $month^{-1}$)	Mean monthly biomass (mg m^{-2})
Dec 1987	1	1390.7	1.678	-	-	-	2333.6			
Dec	2	2915.2	0.293	-	-	-	854.2	D	130.8	1877.0
Jan	2	2968.7	0.369	2942.0	0.076	223.6	1095.5	J	497.3	1238.9
Feb	2	2340.2*	0.793	2654.5	0.424	1125.5	1855.8	F	596.2	1545.0
Mar	2	1711.7	0.938	2026.0	0.145	293.8	1605.6	M	423.7	1386.6
Apr	2	1430.9*	0.961*	1571.3	0.023	36.1	1375.1	A	-85.4	1439.1
May	2	1150.0	0.983	1290.5	0.022	28.4	1130.5	M	28.4	1130.5
Jun	2	1043.1	0.937	1096.6	-0.046	-50.4	977.4	J	-50.4	977.3
Jul	2	695.4	1.194	869.3	0.257	223.4	830.3	J	223.4	830.3
Aug	2	775.6	1.473	735.5	0.279	205.2	1142.5	A	205.2	1142.5
Sep	2	668.6	1.485	722.1	0.012	8.7	992.9	S	8.7	992.9
Oct	2	615.1	1.497	641.9	0.012	7.7	920.8	O	7.7	920.9
Nov	2	80.2	1.230	347.7	-0.267	-92.8	98.7	N	-92.8	119.0
Nov	3	107.0	0.190	-	-	-	20.3			
Dec 1988	3	1684.9	0.336	896.0	0.146	130.8	566.1			
Jan	3	1765.2	0.783	1725.1	0.447	771.1	1382.2			
Feb	3	1497.7	0.824	1631.5	0.041	66.9	1234.1			
Mar	3	909.3	1.284	1203.5	0.460	553.6	1167.5			
Apr	3	1364.0	1.102	1136.7	-0.182	-206.9	1503.1			

*interpolated data (See text)

Total annual production (P): 1.89 (g m^{-2} y^{-1})
Mean annual biomass (B): 1.13 (g m^{-2})
P/B ratio: 1.67

Table 3.3. Mean annual biomass (m.a.b.) (g m^{-2}) and total annual production (t.a.p.) (g m^{-2} y^{-1}) of *Ceratonereis erythraeensis* and *C. keiskama* at each study site and over all intertidal areas.

Ceratonereis erythraeensis

Site	% of intertidal area	m.a.b. of the site (g m^{-2})	t.a.p.of the site (g m^{-2} y^{-1})	P/B	Contribution of the m.a.b. of the site to the m.a.b. for all intertidal areas (g m^{-2})	Contribution of the t.a.p. of the site to the t.a.p. for all intertidal areas (g m^{-2} y^{-1})
A	63.05	5.58	12.15	2.17	3.52	7.66
B	12.25	12.41	-	-	1.52	-
C	8.56	14.43	16.09	1.11	1.24	1.38
D	12.32	10.65	-	-	1.31	-
					A+C=4.76	A+C=9.04

For all intertidal areas (see text):
B = 7.59
P/B = 1.90
P = 14.42

Ceratonereis keiskama

Site	% of intertidal area	m.a.b. of the site (g m^{-2})	t.a.p.of the site (g m^{-2} y^{-1})	P/B	Contribution of the m.a.b. of the site to the m.a.b. for all intertidal areas (g m^{-2})	Contribution of the t.a.p. of the site to the t.a.p. for all intertidal areas (g m^{-2} y^{-1})
A	83.70	4.69	8.68	1.85	3.93	7.27
B	16.30	1.13	1.89	1.67	0.18	0.31

For the intertidal areas where it occurs:
P = 7.58
B = 4.11
P/B = 1.84

Most of the annual production of *C. keiskama* occurred during January-March (57% at site A and 86% at the B) whereas that of *C. erythraeensis* peaked between February and May (73% at site A and 94% at site B) (Figs 3.10a & 3.10b). There was little or no production during the winter and spring months by either species.

DISCUSSION

The P/B ratios of both *Ceratonereis* species are within the range of those recorded for other nereid species. The P/B ratio of *Nereis diversicolor* at the Ythan estuary, Scotland, is 3.0 (Chambers & Milne, 1975), and a value of 2.5 was reported from Belgium (Heip & Herman, 1979). Kay & Bradfield (1973) reported a P/B ratio of 1.6 for *Nereis virens*. The biomass, annual production and P/B ratio of *C. erythraeensis* at the Berg River estuary were lower than at Werribee, Australia ($B = 31.0$ g m^{-2}, $P = 92.0$ g m^{-2} y^{-1}, $P/B = 2.9$ - Dorsey, 1981).

The reproductive cycle of *C. erythraeensis* at the Berg River varied in different parts of the estuary. Similar local variability in the population structure of *C. erythraeensis* was reported from Australia by Dorsey (1981). Populations with distinctive cohorts also reproduced during summer (January and February). Similarly, the life cycle of *Nereis diversicolor*, a common nereid worm in European estuaries, differs widely between sites (Heip & Herman, 1978; Chambers & Milne, 1975).

The differences in the population structure of *C. erythraeensis* at the Berg River estuary may be influenced by differential predation pressure between the sites. Predation by birds in particular may be responsible for size-related vertical stratification of worms in the substratum. A low proportion of size classes 3 (40.0 - 59.9 mm) and 4 (>60.0 mm) of *C. keiskama* in the upper layer at site A (Fig 3.9) coincided with a much higher predation pressure by birds at this site than at the site B. The relatively high proportion of the biomass of *C. erythraeensis* in the upper

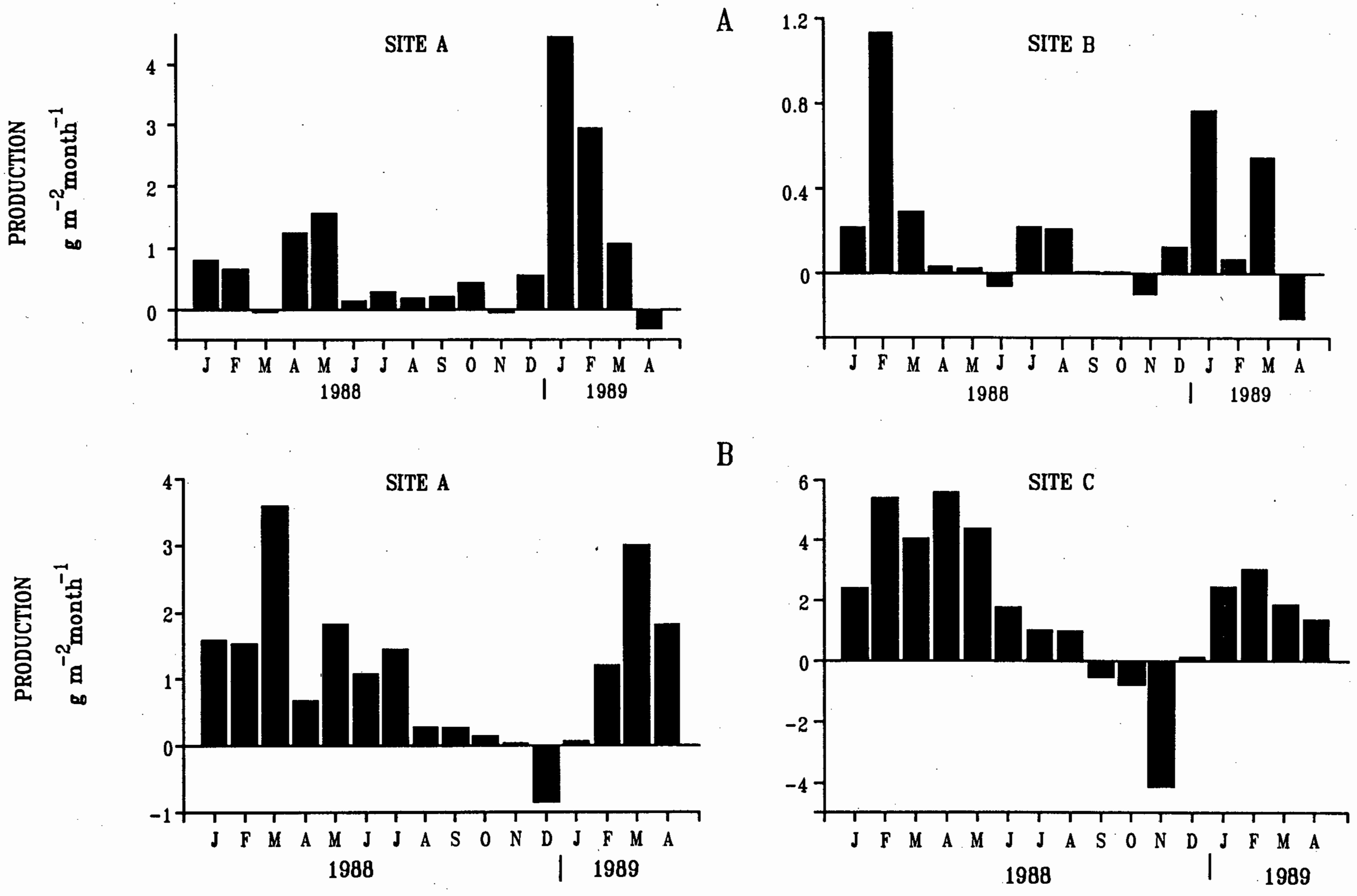


Figure 3.10. Production (g m^{-2}month^{-1}) of the total population of *Ceratonereis keiskama* (A) and *C. erythraeensis* (B).

layer of the substratum at site D (Table 3.1) may be due to the relatively low avian predation pressure at this site. It is difficult to estimate how much of the annual production of nereids is utilized by predators, since an unknown proportion is released in form of spawned gametes. About 40% of the total production of *Nereis diversicolor* (Chambers & Milne, 1975) and almost half of that of *Scobicularia plana* (Hughes, 1970) is estimated to be in form of gametes. The large worms, which make up high proportion of the worms in the deeper layer of the substratum, are unavailable to all but a few avian predators. During winter the proportion of larger individuals of both *Ceratonereis* species increased considerably in the deeper layer of the substratum. Nereid abundance is also lowest at this time of the year. The above factors create poor feeding conditions for invertebrate feeders which, however, are at their lowest density at this time of the year. The productivity of estuarine invertebrates peaks at the warmest time of year and is thus asynchronous in the northern and southern hemispheres. The period of maximum predation pressure by shorebirds, however, is synchronous in the two hemispheres, occurring during the boreal winter (austral summer). Thus, in the southern hemisphere, peaks of production and predation coincide, whereas in the north, predation peaks at the time of year when invertebrate productivity is at its lowest. These differences are likely to have profound implications for the carrying capacity of estuaries for shorebird predators.

REFERENCES

Baird, D. 1988 Synthesis of ecological research in the Swartkops estuary. In: *The Swartkops estuary* (Baird, D., Marais, J. F. K. & Martin, A.P. S., eds). *African Natural Scientific Progress Report* **156**, 41-56.

Cassie, R. M. 1954 Some uses of probability paper in the analysis of size frequency distributions. *Australian Journal of Marine and Freshwater Research* **5**, 513-522.

Chambers, M. R. & Milne, H. 1975 Life cycle and production of *Nereis diversicolor* O. F. Muller in the Ythan Estuary, Scotland. *Estuarine and Coastal Marine Science* **3**, 133-144.

Crisp, D. J. 1971 Energy flow measurements. In: *Methods for the Study of Marine Benthos, I. B. P. Handbook* **16** (Holme, N. A. & McIntyre, A. D., eds). Blackwell, Oxford, pp 197-279.

Dorsey, J. H. 1981 The ecology of *Australonereis ehlersi* (Augener, 1913) and *Ceratonereis erythraeensis* Fauvel, 1919 (Polychaeta, Nereidae) living offshore from the Werribee sewage-treatment farm, Port Phillip Bay, Victoria, Australia. Unpubl. Ph.D thesis. University of Melbourne, Melbourne, Australia.

Harding, J. P. 1949 The use of probability paper for the graphical analysis of polymodal frequency distributions. *Journal of the Marine Biological Association of the United Kingdom* **28**, 141-153.

Heip, C. & Herman, R. 1979 Production of *Nereis diversicolor* O. F. Muller (Polychaeta) in a shallow brackish-water pond. *Estuarine and Coastal Marine Science* **8**, 297-305.

Hughes, R. N. 1970 An energy budget for a tidal population of the bivalve *Scrobicularia plana* (da Costa). *Journal of Animal Ecology* **39**, 357-381.

Kay, D. G. & Bradfield, A. E. 1973 The energy relations of the polychaete *Neanthes* (=*Nereis*) *virens* (Sars). *Journal of Animal Ecology* **42**, 673-692.

Muller, I. 1984 The occurrence and abundance of polychaetes in the Swartkop estuary. Unpubl. B.Sc. project. University of Port Elizabeth, Port Elizabeth, South Africa.

Puttick, G. M. 1977 Spatial and temporal variations in inter-tidal animal distribution at Langebaan Lagoon, South Africa. *Transactions of the Royal Society of South Africa* **42**, 403-440.

CHAPTER 4

DIETS OF SELECTED MIGRANT AND RESIDENT WADERS AT THE BERG RIVER ESTUARY, SOUTH AFRICA

SUMMARY

The diets of four common migrant waders; Curlew Sandpiper *Calidris ferruginea*, Grey Plover *Pluvialis squatarola*, Greenshank *Tringa nebularia* and Ringed Plover *Charadrius hiaticula*, and three resident species, Kittlitz's *Charadrius pecuarius*, Whitefronted *C. marginatus* and Blacksmith Plovers *Vanellus armatus*, were studied at the Berg River estuary, South Africa from December 1987 to April 1990. Direct observations of feeding were combined with analyses of stomach contents, pellets and droppings.

Nereid worms, *Ceratonereis erythraeensis* and *C. keiskama*, were the principal food of all species studied except Greenshanks, which fed mostly on crabs, *Hymenosoma orbiculare*. Despite considerable overlap in the diets of all bird species, there was clear separation in the size classes of nereids taken by birds. The smallest sizes, 1-5 mm, were avoided by all species. Visually foraging plovers (Charadriidae) fed on the largest nereids regardless of their abundance. Curlew Sandpipers, predominantly tactile foragers, were the only birds which consumed different sized worms in proportion to their occurrence in the substratum.

Seasonal variations in the diet of waders are linked to seasonal changes in the availability of prey species. The efficiency of various techniques used to examine shorebird diet is discussed.

INTRODUCTION

The majority of shorebirds (Aves: Charadrii) breed at high northern latitudes where the taxonomic diversity of food sources is limited and community structure are relatively simple (Holmes & Pitelka, 1968). Additionally, food shortages may occur during the Arctic summer as a consequence of severe weather conditions (Holmes, 1966). The majority of these birds migrate south of their breeding grounds before the boreal winter. The nonbreeding grounds, notably south temperate localities, support a more predictable and diverse food supply (Recher, 1966). On the nonbreeding grounds, shorebirds feed in relatively dense, mixed-species assemblages where competition for food resources is more likely to occur than on the breeding grounds (Recher, 1966). Birds therefore have to cope with these different feeding habitats and prey taxa by using different foraging behaviour and adopting different feeding techniques (Baker & Baker, 1973). In addition, migrant shorebirds during the nonbreeding season are often sympatric with resident congeners: the interactions occurring in such situations are poorly understood.

In this Chapter, an analysis of the diets of migratory Curlew Sandpipers and Grey Plovers and, to a lesser extent, Greenshanks and Ringed Plovers is presented. Diets of the resident Kittlitz's, Whitefronted and Blacksmith Plovers are also examined. Competition for food resources between the species is discussed. Finally, the efficiency of various techniques used to examine the diets of birds is summarized.

METHODS

Observations

Focal observations of shorebirds were made at four study sites A, B, C and D, each of 2 000 m^2 (25 x 80 m) (Fig 2.1). Shorebirds were distributed unevenly along the Berg River estuary (Chapter 7) and, therefore, observations of particular bird species were confined to those sites where these species were most abundant. Birds, selected at random, were observed through a 22 x telescope for periods of one minute and the number and type of prey taken were recorded. Prey taken by birds fell into three categories: nereid worms, crabs and others. The latter category comprised small prey which could not be identified in the field.

The following months are included in each season: December, January and February are the summer months; March, April and May the autumn; June, July and August the winter and September, October and November the spring. Sample sizes for data in Figures 4.5-4.9 are listed in Appendix 4.1. Sample sizes for Figures 4.10-4.14 are the same as in Figures 4.1-4.4.

Stomach contents

Birds were collected while feeding at different tidal stages throughout the year. Ten percent formalin was immediately injected into the stomachs and oesophagi to prevent post mortem digestion. Later the stomachs and oesophagi were removed and their contents preserved in 10% formalin. Stomach and oesophageal contents were examined under a binocular microscope and the numbers of each prey species were recorded. The numbers of each prey type were established either by counting whole specimens or fragments from which the original number of individuals could be determined. The sizes of nereid worms were determined by measuring either the whole body or the length of their left jaws, from which body length could be calculated (Chapter 2). The three species of nereids taken by birds, *Ceratonereis keiskama*, *C. erythraeensis* and *Perinereis nuntia* were easily separated by the colour and shape of their jaws. Analysis of stomachs was restricted to establishing the percentage of stomachs containing certain prey items. The stomach contents of 80 Curlew Sandpipers, six Kittlitz's Plovers, three Whitefronted Plovers, two Blacksmith Plovers and one Ringed Plover were analyzed. Since the oesophagi of birds seldom contained more than one or two prey items, their contents were lumped with stomach contents.

Pellets and droppings

Pellets and droppings were collected immediately after the focal observations were completed and were preserved in 75% alcohol. Later they were analyzed under a binocular microscope in the same way as stomach contents. Forty droppings of Grey Plovers, fourteen of Whitefronted Plovers and thirty of Blacksmith Plovers were collected. Five pellets regurgitated by Grey Plovers and six by Greenshanks were also analyzed.

RESULTS

Diet of birds - focal observations

Nereid worms were numerically the most important dietary component of all species except Greenshanks and Curlew Sandpipers at site B and Grey Plovers at site D (Figs 4.1-4.4). Crabs dominated the diet of Greenshanks (Fig 4.3) and were important in the diet of Grey Plovers at all sites except site A (Fig 4.2). Crabs were numerically unimportant in the diets of other birds, but together with nereids, they were important prey items in terms of biomass and energy content of all prey taken by the birds. In contrast, prey in the category of "others", although frequently taken by some bird species, contributed little to the total biomass and energy content of prey taken. Fish were important prey items in terms of both biomass and energy for Grey Plovers and Greenshanks at site D (Figs 4.2 & 4.3).

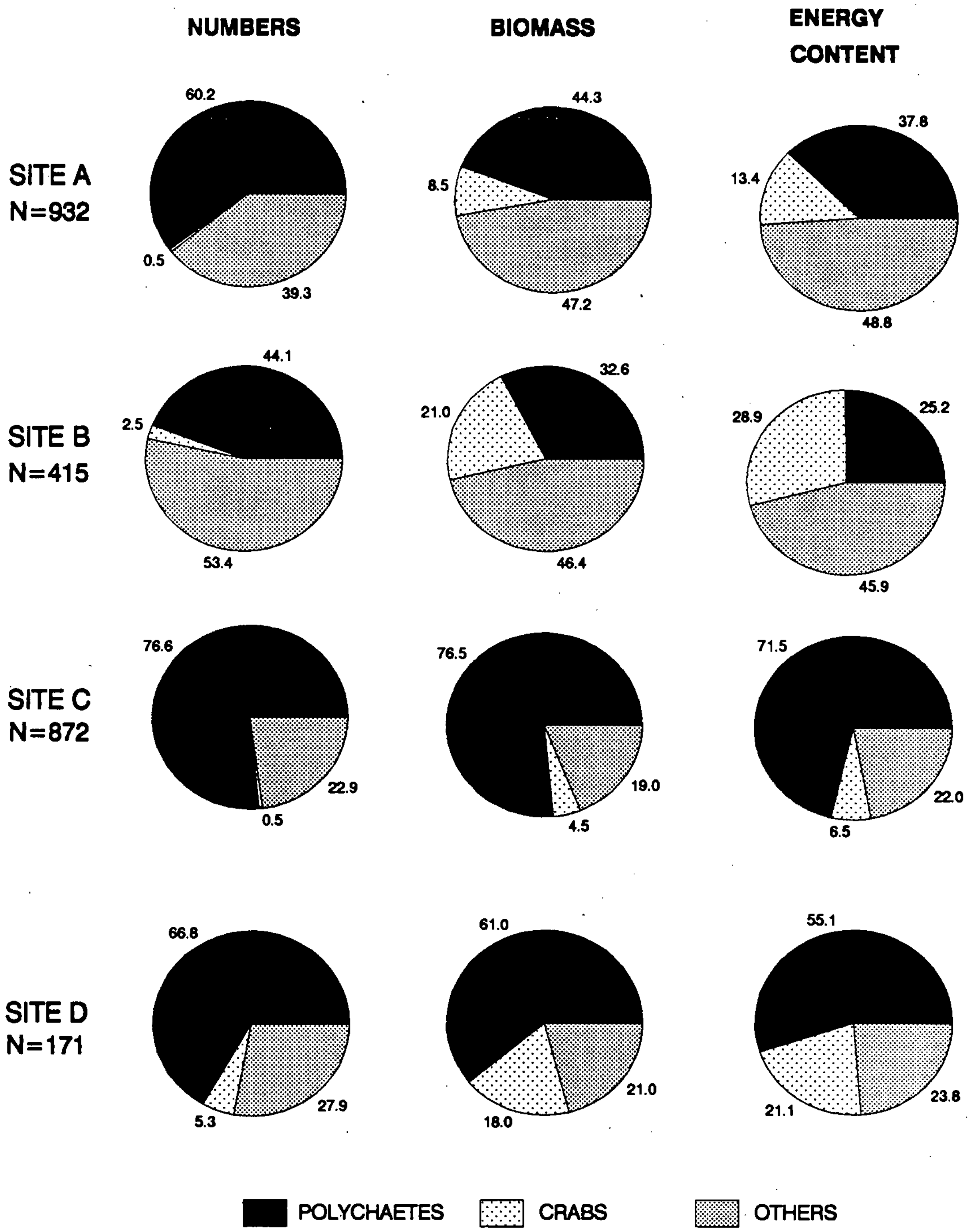


Figure 4.1. Curlew Sandpipers: proportion of food types in terms of numbers, biomass and energy content at the Berg River estuary.

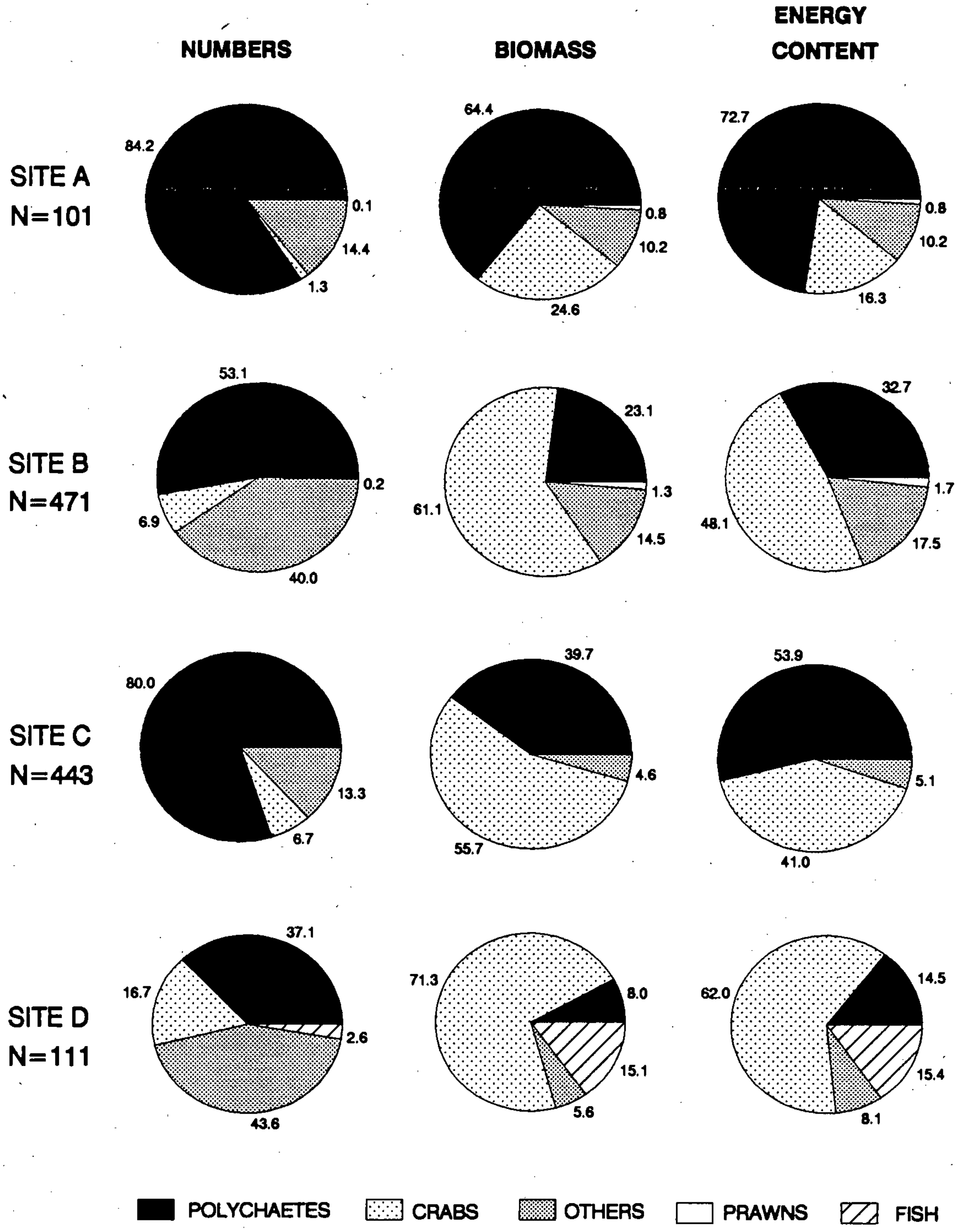


Figure 4.2. Grey Plovers: proportion of food types in terms of numbers, biomass and energy content at the Berg River estuary.

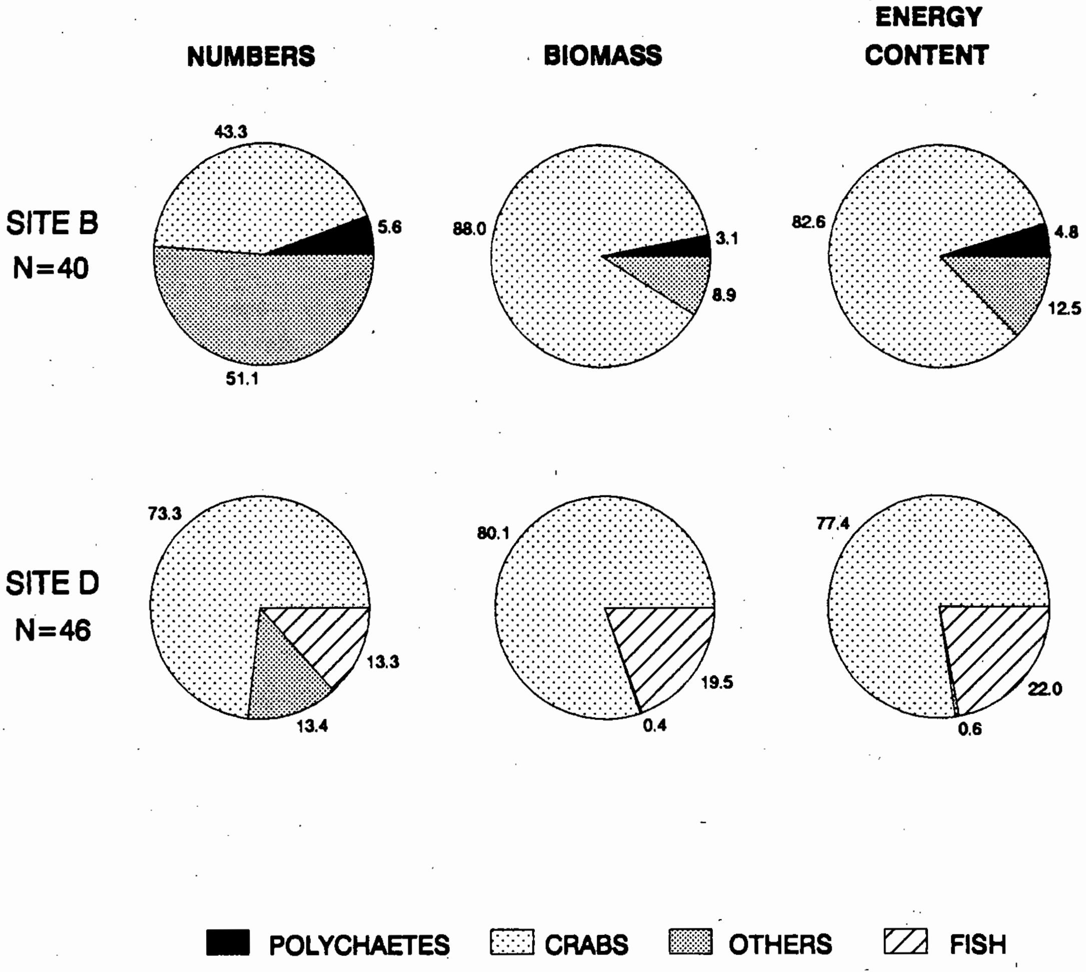


Figure 4.3. Greenshanks: proportion of food types in terms of numbers, biomass and energy content at the Berg River estuary.

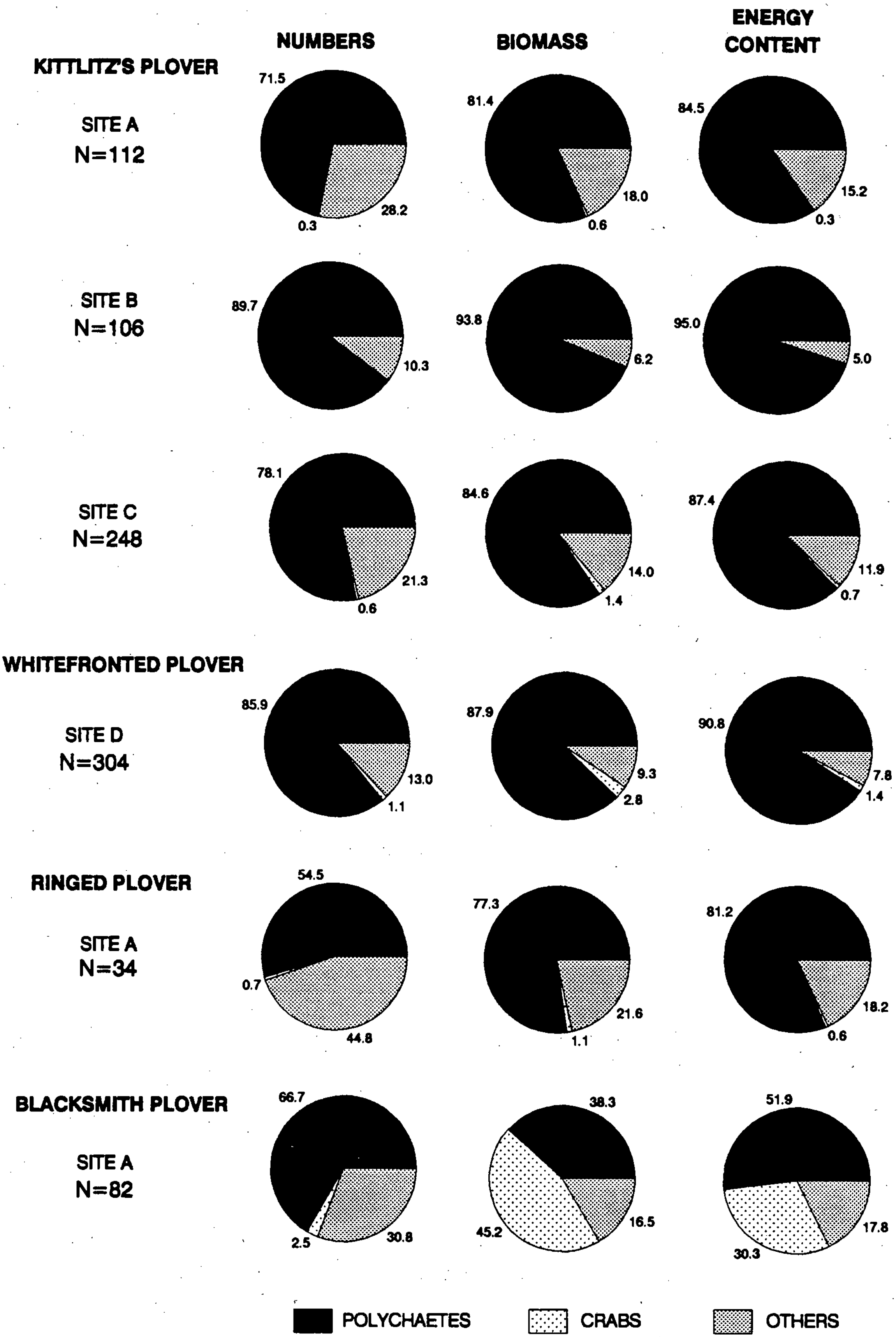


Figure 4.4. Kittlitz's, Ringed and Blacksmith Plovers: proportion of food types in terms of numbers, biomass and energy content at the Berg River estuary.

Diet of birds - analysis of stomach contents, droppings and pellets

Analysis of stomach contents, droppings and pellets confirmed the importance of nereids in the diet of all bird species (Tables 4.1-4.5). *Ceratonereis keiskama* was best represented in the stomachs of Curlew Sandpipers. This was mainly due to the fact that 91% of Curlew Sandpiper stomachs were collected at site A, where *C. keiskama* is a dominant invertebrate (Chapter 2). Nevertheless, on average, each Curlew Sandpiper stomach contained 181 jaws of *C. keiskama* and the maximum number recorded in one stomach was 1022. *Ceratonereis keiskama* occurs only at sites A and B and *Perinereis nuntia* only at site D (Chapter 2). The occurrence of their jaws in the stomachs of Kittlitz's Plovers collected at site C suggests that these birds do not feed on one mudflat continuously throughout the low tide but move between mudflats. Alternatively, jaws of polychaetes remain in the stomachs for longer than one day.

Gastropods, *Hydrobia* sp., and the larvae and adults of insects were important dietary components of Curlew Sandpipers, Ringed and Blacksmith Plovers. Isopods, *Exosphaeroma hyloecetes*, were well represented in the stomachs of all the above species and in droppings of Grey Plovers. Soft-bodied polychaetes, *Boccardia* spp. and *Capitella capitata*, and amphipods were found only in the oesophagi of Curlew Sandpipers. Crabs *Hymenosoma orbiculare* were well represented in the stomachs, droppings and pellets of all birds. However, it was impossible to quantify their numbers and sizes, especially in the pellets, since they were highly fragmented.

The presence of vegetable seeds in the diets of Curlew Sandpipers, Kittlitz's and Blacksmith Plovers indicates that these birds fed for some of the time on the adjacent saltmarshes.

Table 4.1. Curlew Sandpiper: occurrence (% in parentheses) of food items in 80 stomachs collected from intertidal mudflats at the Berg River estuary.

	Number of stomachs (%)	Amount of food
POLYCHAETA		
Ceratonereis keiskama	59 (74)	10 662 jaws
C. erythraeensis	27 (34)	600 jaws
Boccardia sp.	6 (8)	33 specimens
Capitella capitata	9 (11)	232 specimens
ISOPODA		
Exosphaeroma hyloecetes	16 (20)	46 specimens
AMPHIPODA		
Melita zeylanica	8 (10)	14 specimens
Orchestia sp.	1 (1)	1 specimen
Grandidierella lutosa	1 (1)	5 specimens
BRACHYURA		
Hymenosoma orbiculare	3 (4)	8 specimens
INSECTA		
Tabanid larvae	8 (10)	10 specimens
Chironomid larvae	8 (10)	10 specimens
Adult Coleoptera	1 (1)	3 specimens
Pupae	3 (4)	15 specimens
GASTROPODA		
Hydrobia sp.	22 (28)	182 complete specimens
VEGETABLE MATTER		
Seeds	24 (30)	73 specimens

Table 4.2. Grey Plover: occurrence of food items in 22 droppings collected at site A and 18 droppings and 5 pellets collected at site B at the Berg River estuary.

	Site A		Site B	
	Number of samples (%)	Amount of food	Number of samples (%)	Amount of food
POLYCHAETA				
Ceratonereis keiskama	19 (83)	74 jaws	4 (17)	20 jaws
C. erythraeensis	21 (91)	157 jaws	15 (65)	57 jaws
ISOPODA				
Exosphaeroma hyloecetes	5 (22)	5 specimens	23 (100)	23 specimens
BRACHYURA				
Hymenosoma orbiculare	4 (17)	3 specimens	7 (30)	3 specimens

Table 4.3. Occurrence of food items in 6 stomachs of Kittlitz's Plover and 1 stomach of Ringed Plover collected at site C at the Berg River estuary.

	Kittlitz's Plover		Ringed Plover	
	Number of samples (%)	Amount of food	Number of samples (%)	Amount of food
POLYCHAETA				
Ceratonereis erythraeensis	5 (100)	60 jaws	1 (100)	34 jaws
C. keiskama	3 (60)	11 jaws	-	-
Perinereis nuntia	1 (2)	1 jaw	-	-
ISOPODA				
Exosperoma hyloecetes	-	-	1 (100)	3 specimens
BRACHYURA				
Hymenosoma orbiculare	1 (2)	fragments	1 (100)	1 specimen
INSECTA				
Tabanid larvae	-	-	1 (100)	9 specimens
Adult Coleoptera	1 (2)	1 specimen	1 (100)	2 specimens
GASTROPODA				
Hydrobia sp.	-	-	1 (100)	9 specimens
VEGETABLE MATTER				
Seeds	1 (2)	2 specimens	-	-

Table 4.4. Blacksmith Plover: occurrence of food items in 2 stomachs and 30 droppings collected at site A at the Berg River estuary.

	Stomachs		Droppings	
	Number of samples (%)	Amount of food	Number of samples (%)	Amount of food
POLYCHAETA				
Ceratonereis erythraeensis	1 (50)	1 jaws	18 (60)	41 jaws
C. keiskama	-	-	22 (73)	63 jaws
ISOPODA				
Exosphaeroma hyloecetes	-	-	18 (60)	fragments
BRACHYURA				
Hymenosoma orbiculare	-	-	4 (13)	fragments
INSECTA				
Chironomid larvae	1 (50)	45 specimens	-	-
Tabanid larvae	1 (50)	12 specimens	-	-
Adult Coleoptera	-	-	6 (20)	many fragments
GASTROPODA				
Hydrobia sp.	1 (50)	10 specimens	-	-
VEGETABLE MATTER				
Seeds	2 (100)	10 whole specimens	2 (7)	11 whole specimens and many fragments

Table 4.5. Whitefronted Plover: occurrence of food items in 3 stomachs and 14 droppings collected at site D at the Berg River estuary.

	Stomachs		Droppings	
	Number of samples (%)	Amount of food	Number of samples (%)	Amount of food
POLYCHAETA				
Ceratonereis erythraeensis	3 (100)	38 jaws	11 (79)	32 jaws
Perinereis nuntia	2 (67)	2 jaws	2 (14)	4 jaws
BRACHYURA				
Hymenosoma orbiculare	1 (33)	1 specimen	3 (21)	many fragments
INSECTA				
Chironomid larvae	1 (33)	1 specimen	-	-
Unidentified larvae	1 (33)	1 specimen	-	-
Adult Coleoptera	-	-	7 (50)	many fragments

Seasonal changes in diet

There were marked seasonal and annual changes in the proportion of different prey consumed by birds at the four sites. There was an increase in the frequency of nereids in the diets of the majority of birds in spring (Figs 4.5-4.9), which probably reflects an increase in their abundance and availability following reproduction (Chapter 3). Nereids were important dietary components of Grey Plovers throughout the year of 1988 at site B. In contrast, nereids were never an important constituent of Curlew Sandpipers' diet at the same site. However, for both species at site B, the importance of nereids in the diet decreased after the spring of 1988. This reflects a decrease in abundance of *Ceratonereis erythraeensis* at this site, which began in December 1988 (Chapter 2). By April 1989 nereids had almost disappeared from the area and their contribution to the diet of Grey Plovers had dropped by 88%. There were no seasonal changes in the proportion of prey taken by Grey Plovers at site C where nereids remained a dominant prey item in both years (Fig 4.6). In contrast, at the same site, the proportion of nereids taken by Curlew Sandpipers increased in spring (Fig 4.5), whereas Kittlitz's Plovers fed almost exclusively on nereids in autumn and winter (Fig 4.8).

The proportion of small prey taken by birds at site B increased when the population of the preferred prey, nereids, decreased. The proportion of crabs taken by Greenshanks decreased from 69% in autumn to 29 and 24% in winter and spring respectively, being replaced by small prey and nereids (Fig 4.7). Curlew Sandpipers and Whitefronted Plovers, on the other hand, increased the proportion of crabs in their diets in summer 1988/89 at site D (Figs 4.5 & 4.9).

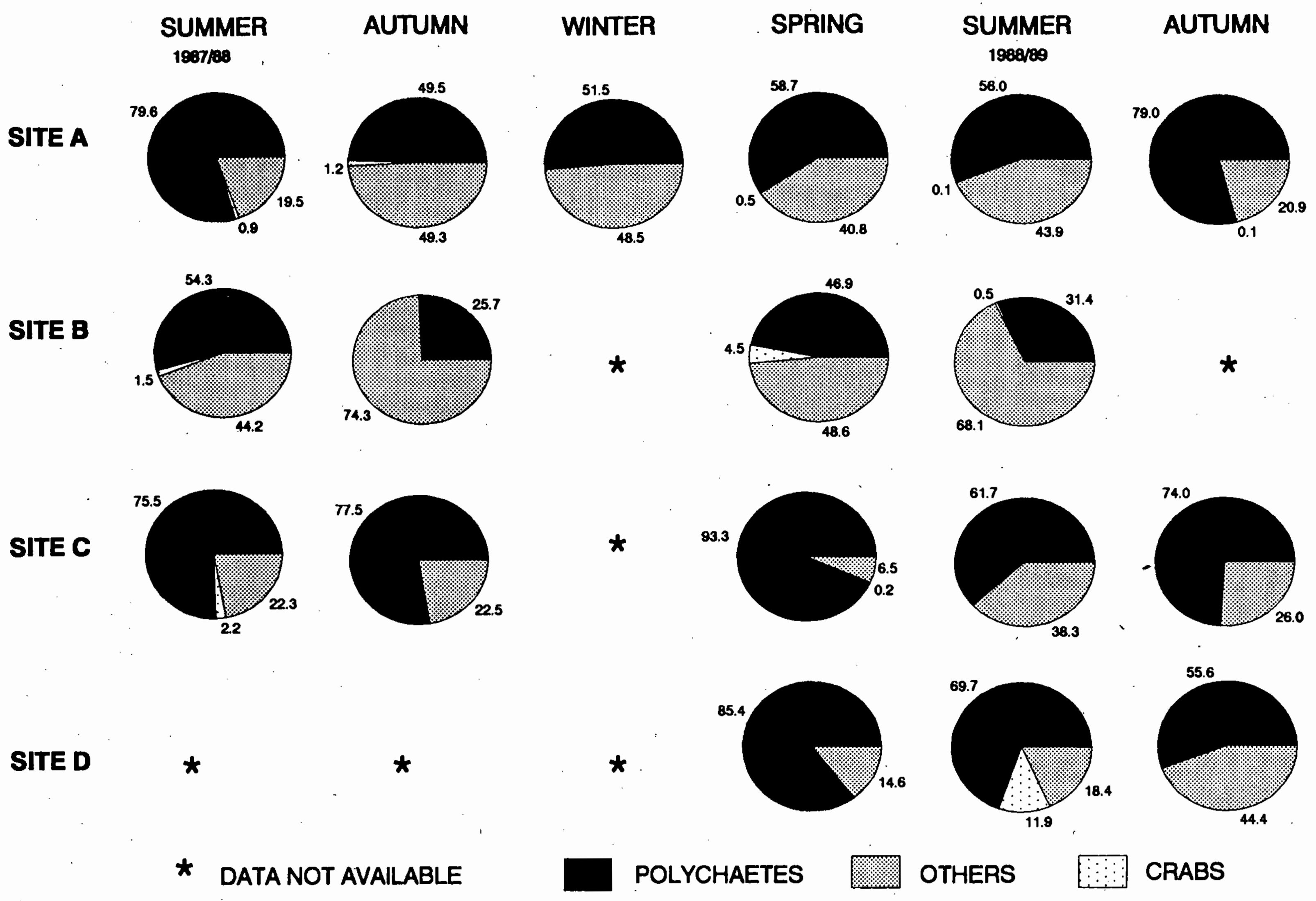


Figure 4.5. Seasonal changes in the diet of Curlew Sandpipers at the Berg River estuary.

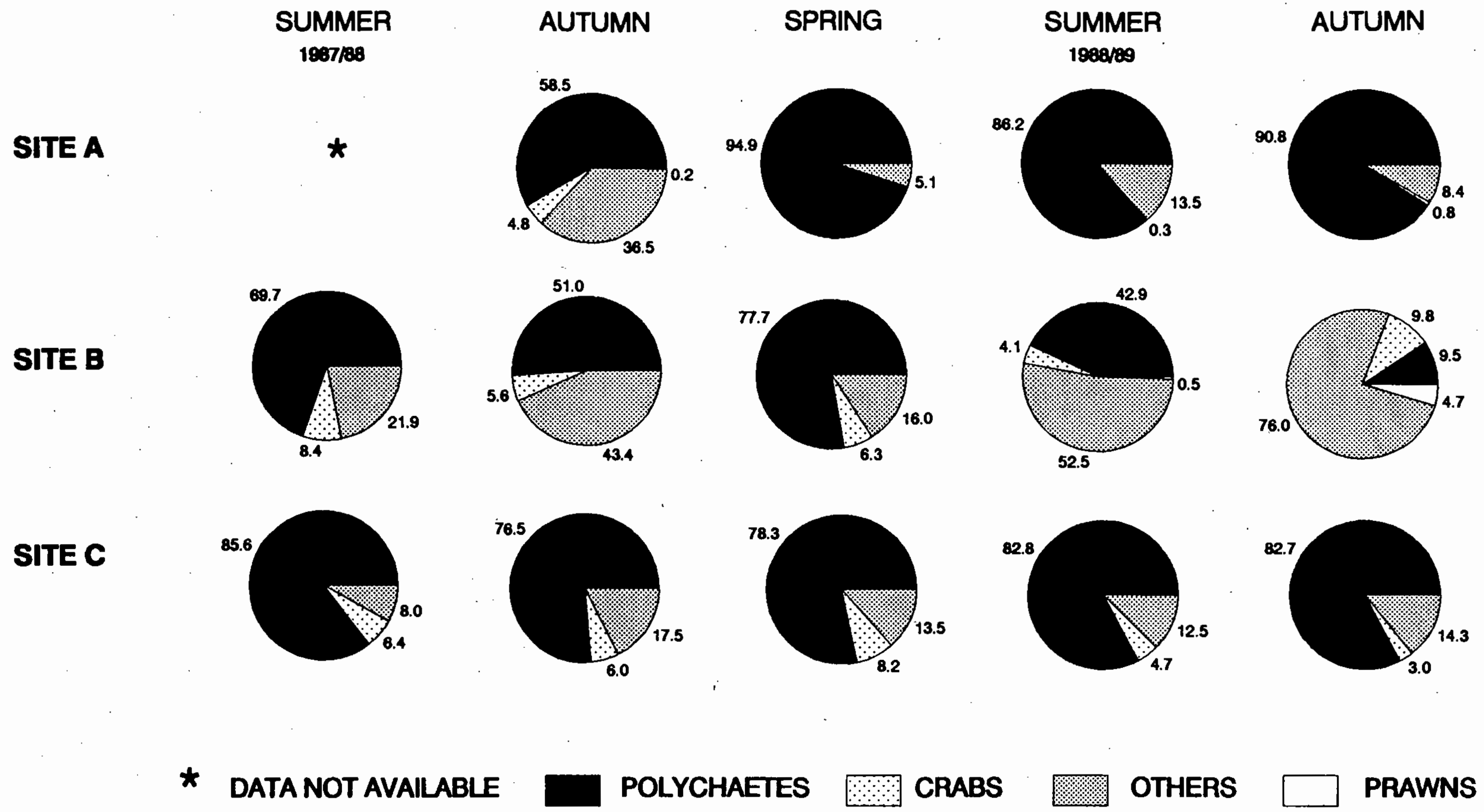


Figure 4.6. Seasonal changes in the diet of Grey Plovers at the Berg River estuary.

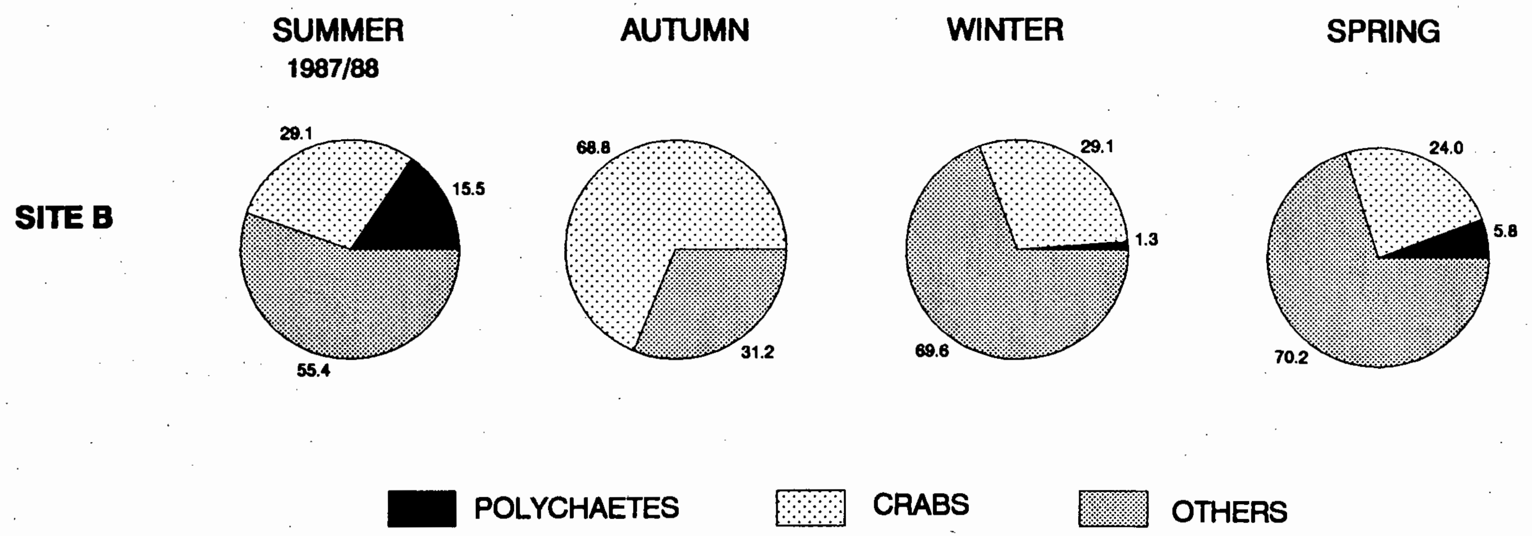


Figure 4.7. Seasonal changes in the diet of Greenshanks at the Berg River estuary.

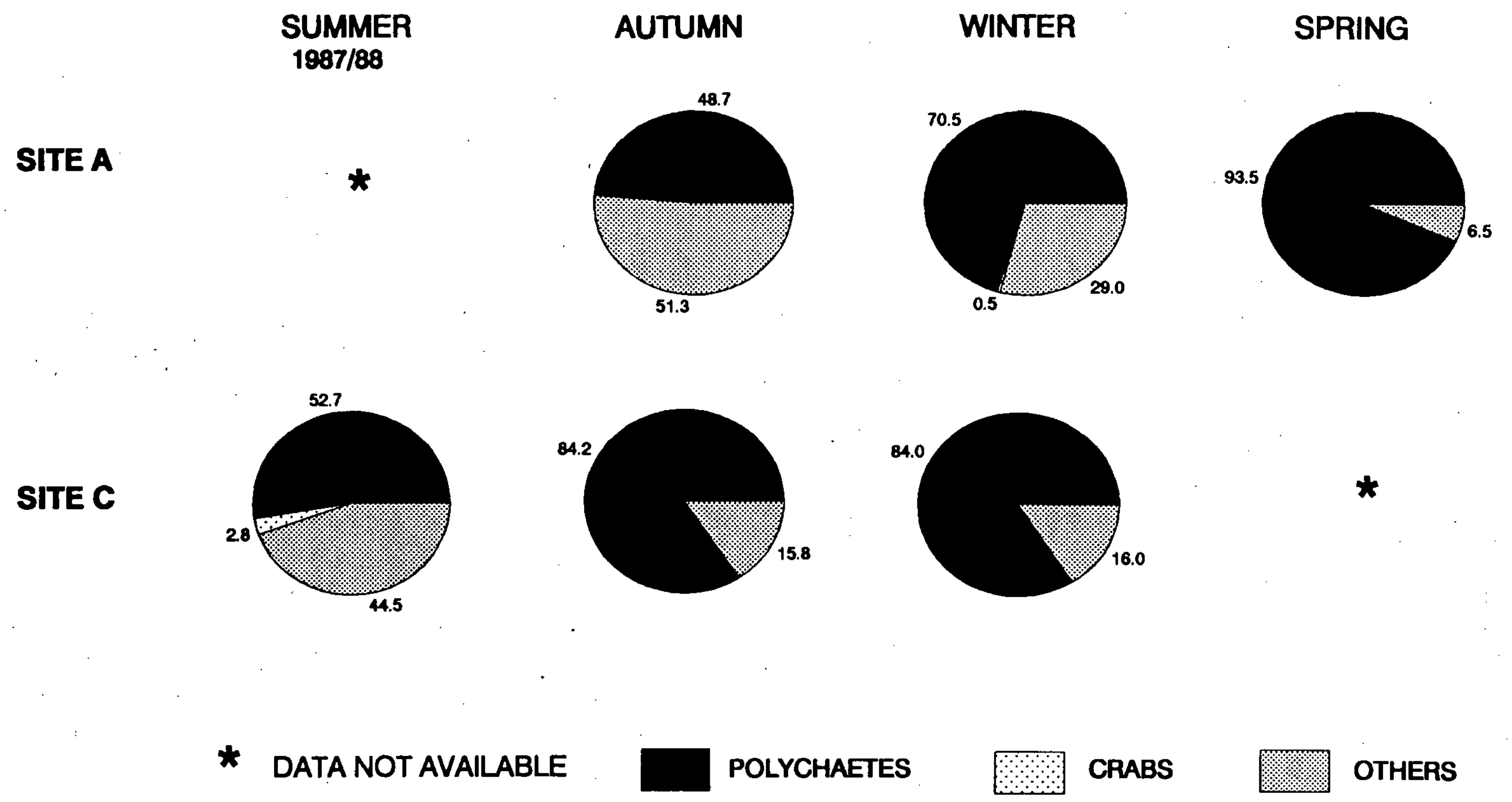


Figure 4.8. Seasonal changes in the diet of Kittlitz's Plovers at the Berg River estuary.

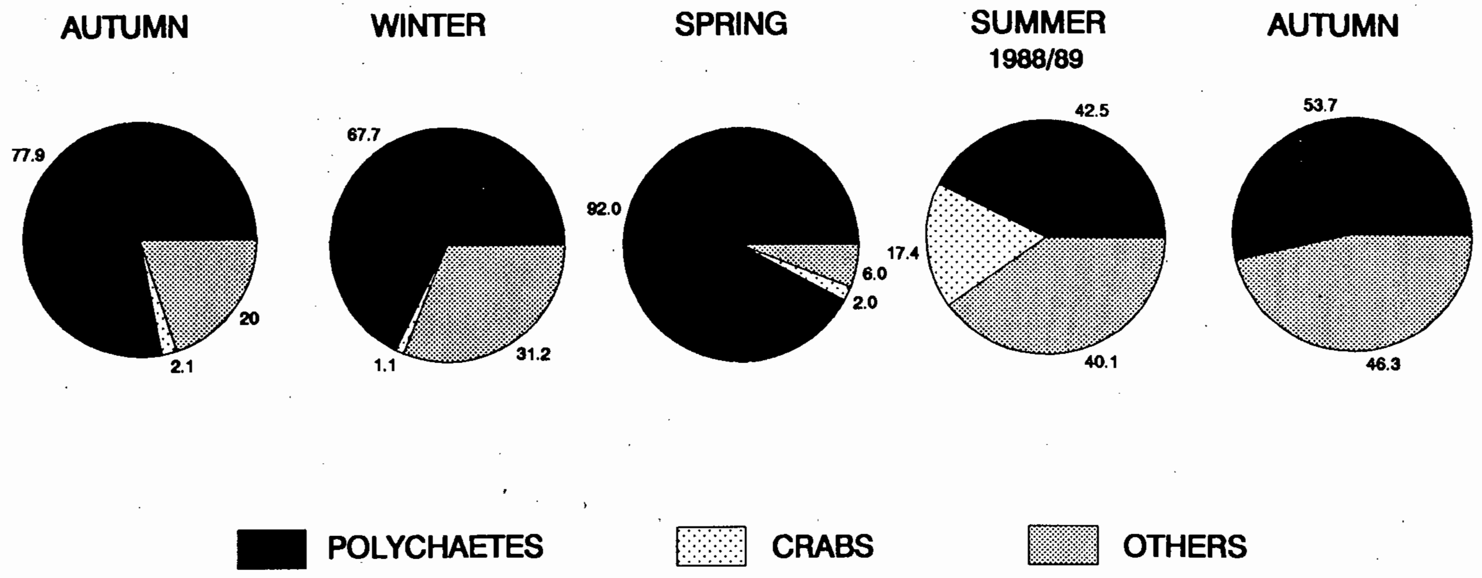


Figure 4.9. Seasonal changes in the diet of Whitefronted Plovers at the Berg River estuary.

Tidal changes in diet

For the majority of birds the proportion of nereids in the diet was lowest three or two hours before low tide and increased two or three hours after low tide, as determined by direct observations (Figs 4.10-4.14). There were marked but not significant fluctuations in the proportion of nereids taken by Curlew Sandpipers at site D (Kruskal-Wallis Test; $H=4.90$; $df=99$; $p>0.05$) (Fig 4.10) and Blacksmith Plovers at site A ($H=10.57$, $df=69$, $p>0.05$) (Fig 4.14). The proportion of nereids consumed by Greenshanks was at a maximum one hour after low tide at site B and at low tide at site D (Fig 4.12). There was a considerable but not significant increase in the proportion of crabs taken by Greenshanks two hours after low tide at site D (Student *t* test; $t=1.63$, $df=16$, $0.05<p<0.1$). The proportion of small prey in the diets of all species was highest before low tide and gradually decreased thereafter.

Prey size selection

Nereid worms were the dominant prey of the majority of birds. Their size frequencies in the birds' diets were reconstructed from jaws retained in the stomachs, droppings and pellets of birds.

All birds ignored the smallest nereids, 1-5 mm in length (Figs 4.15 & 4.18) and no jaws representing worms of between 5 and 10 mm in length were found in the stomachs or droppings of Grey, Kittlitz's and Whitefronted Plovers.

There were marked differences in the preferred size classes of nereids taken by different species and by the same species at different sites. Curlew Sandpipers fed on a very narrow range of nereid sizes at site A, where the preferred sizes ranged between 20 and 25 mm in winter and spring, and between 15 and 20 mm in summer and autumn (Fig 4.15). In all seasons, except spring, the most abundant size classes

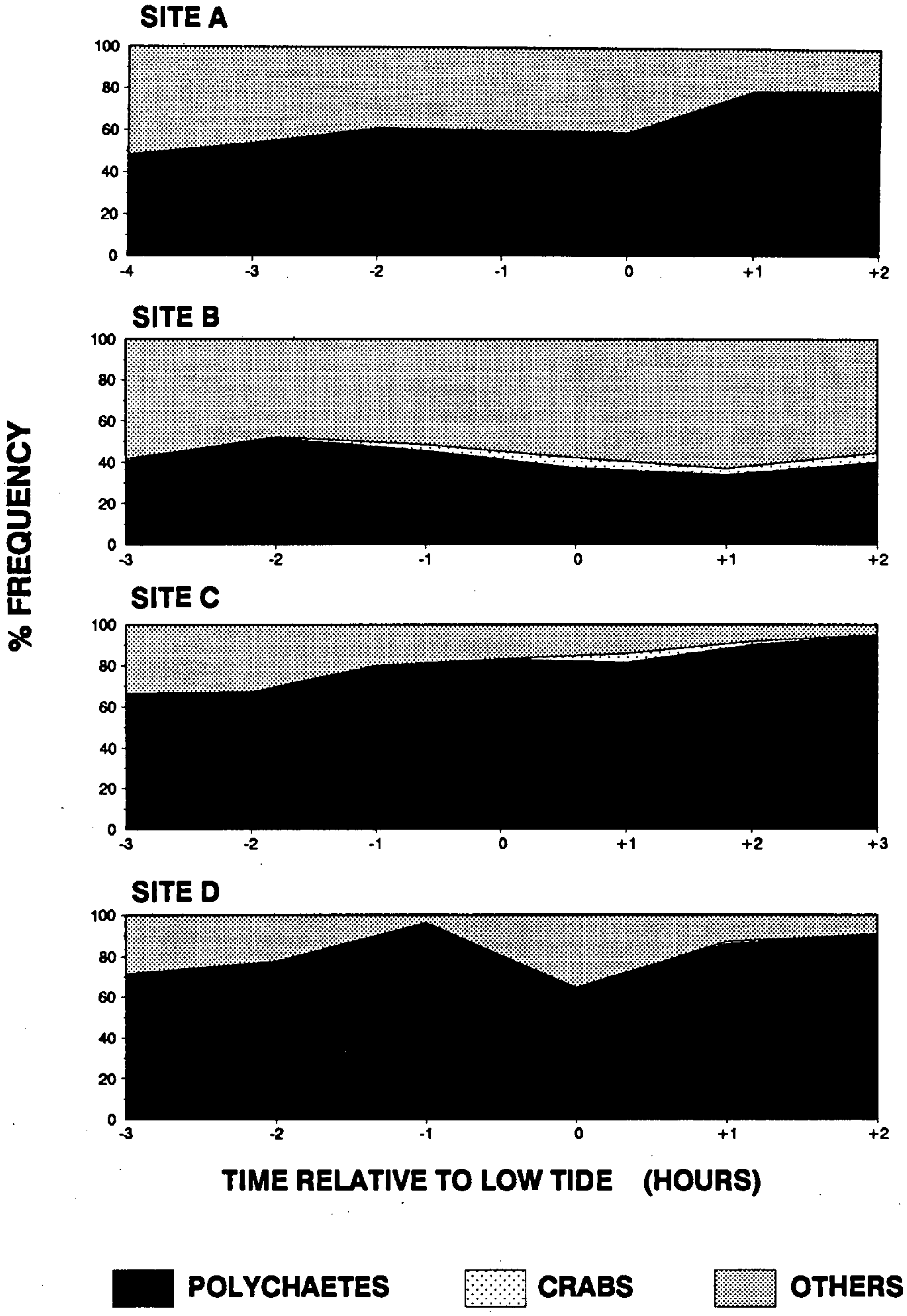


Figure 4.10. Changes in the proportion of different prey types taken by Curlew Sandpipers during the low tide period at the Berg River estuary.

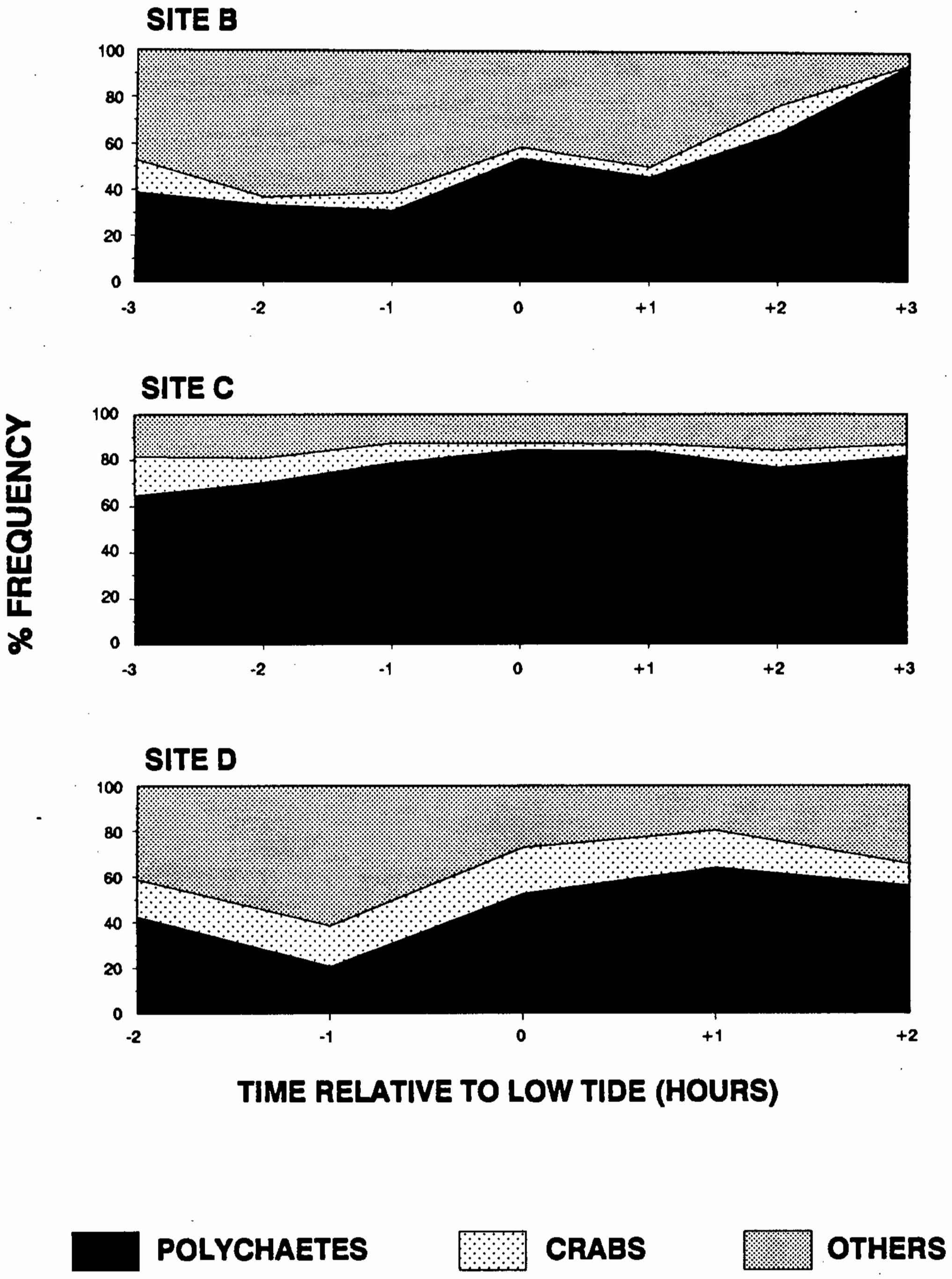


Figure 4.11. Changes in the proportion of different prey types taken by Grey Plovers during the low tide period at the Berg River estuary.

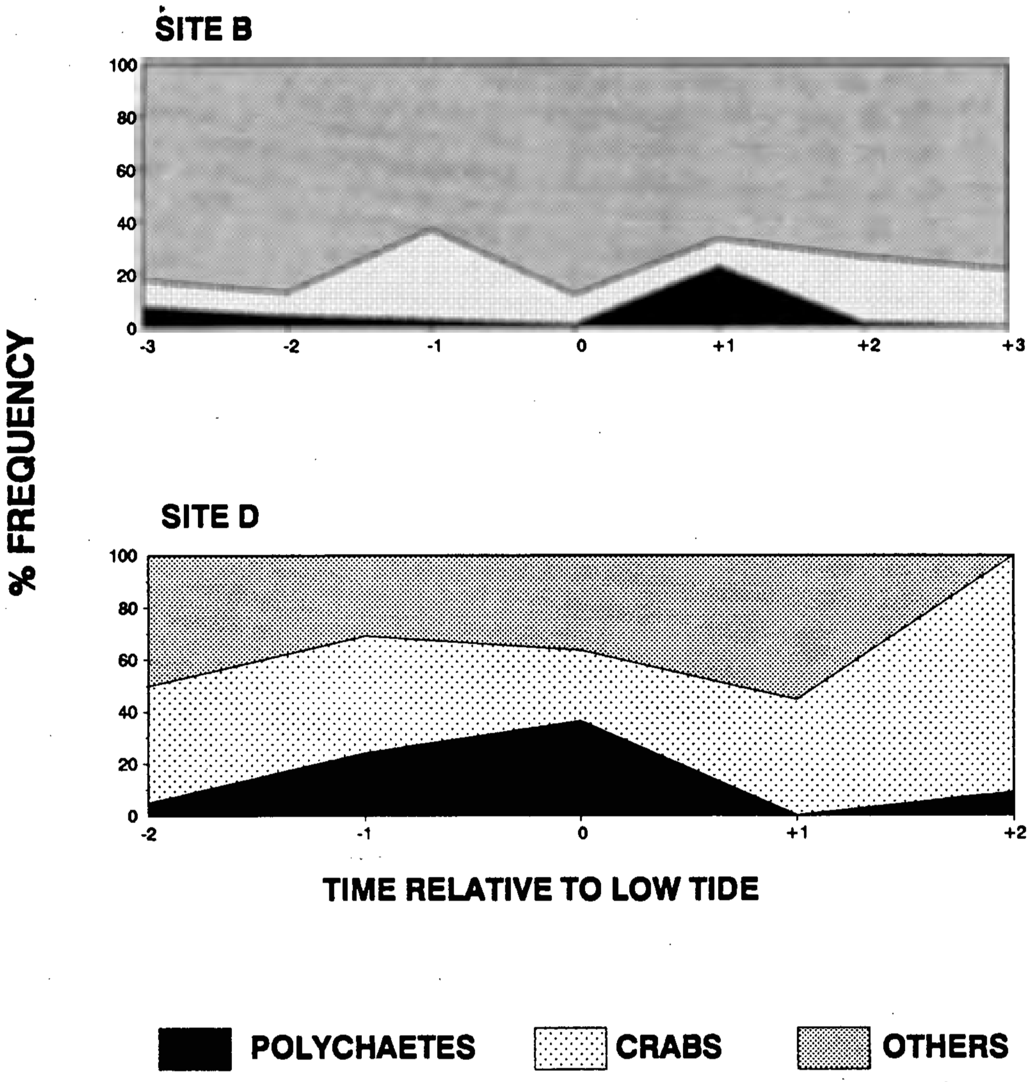


Figure 4.12. Changes in the proportion of different prey types taken by Greenshanks during the low tide period at the Berg River estuary.

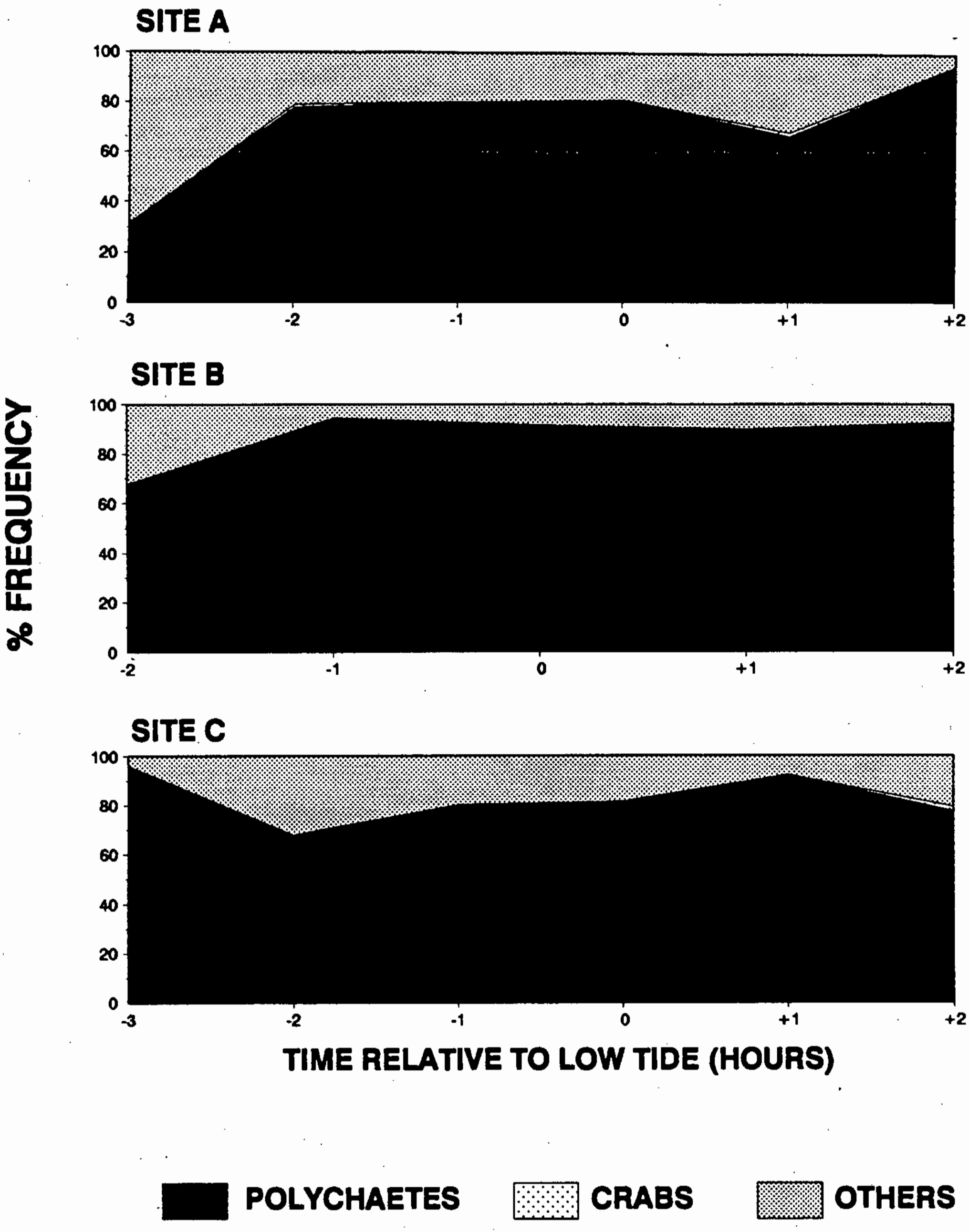


Figure 4.13. Changes in the proportion of different prey types taken by Kittlitz's Plovers during the low tide period at the Berg River estuary.

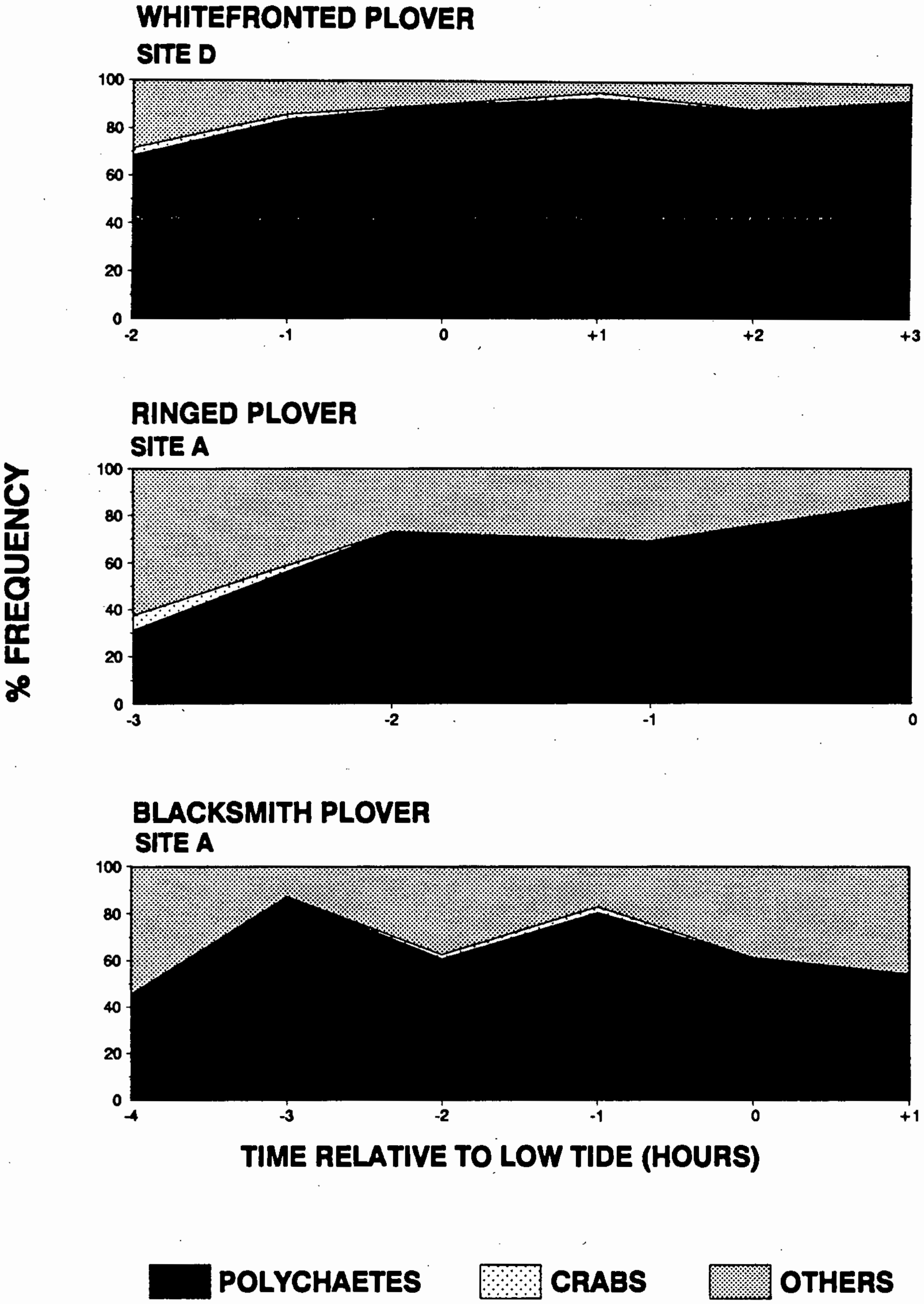


Figure 4.14. Changes in the proportion of different prey types taken by Whitefronted, Ringed and Blacksmith Plovers during the low tide period at the Berg River estaury.

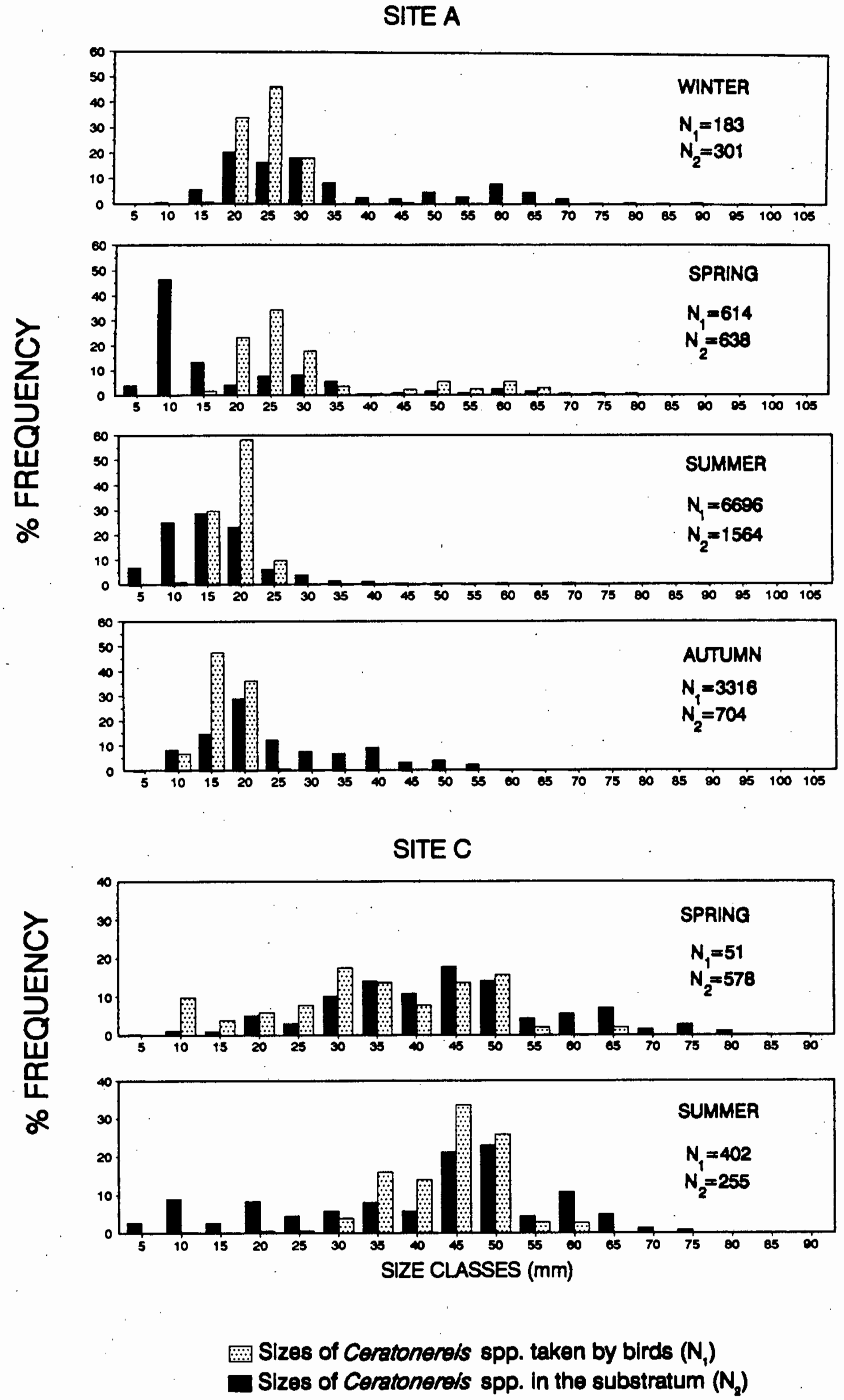


Figure 4.15. Sizes of nereids taken by Curlew Sandpipers (N_1) and present in the substratum (N_2) at the Berg River estuary.

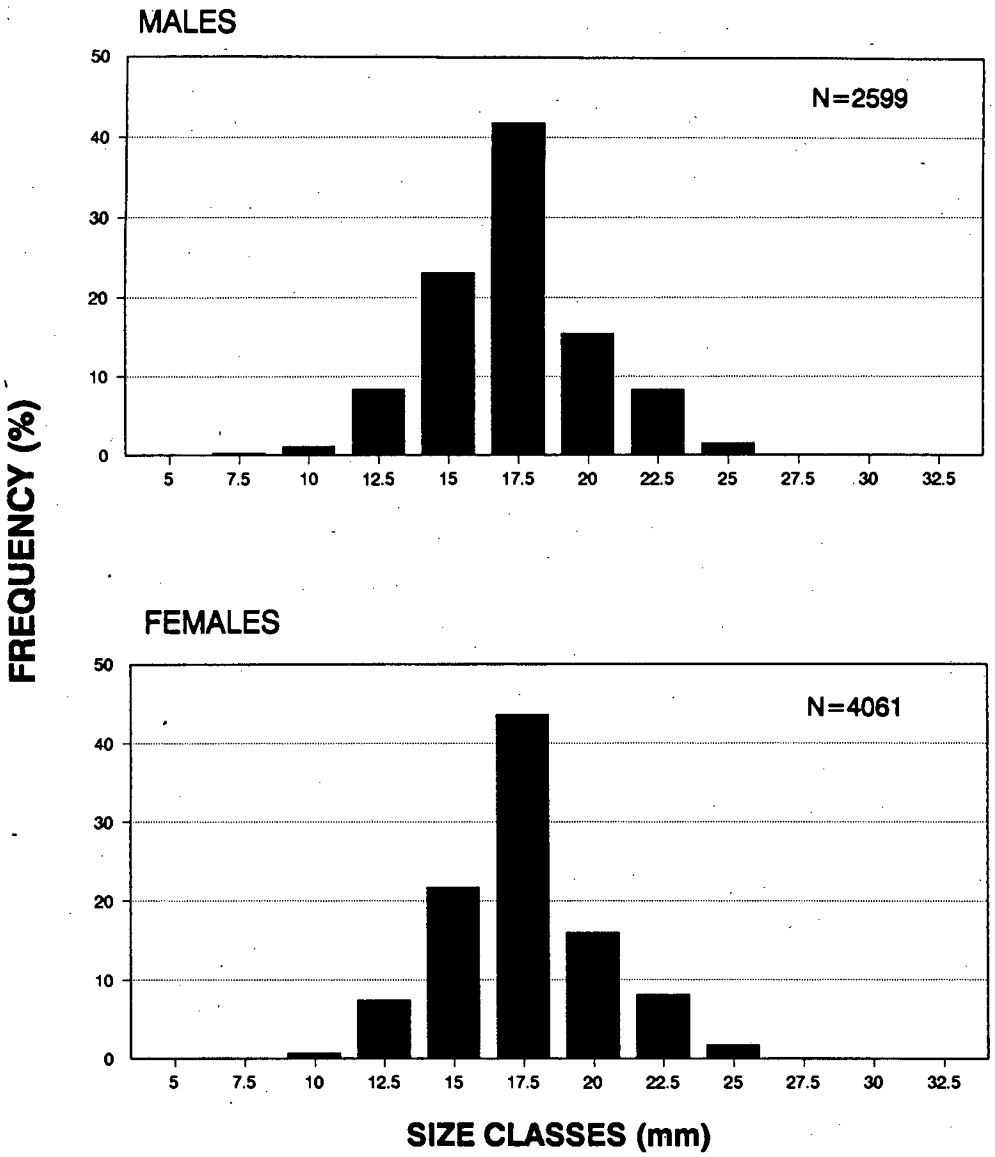


Figure 4.16. Sizes of nereids taken by male and female Curlew Sandpipers at the Berg River estuary.

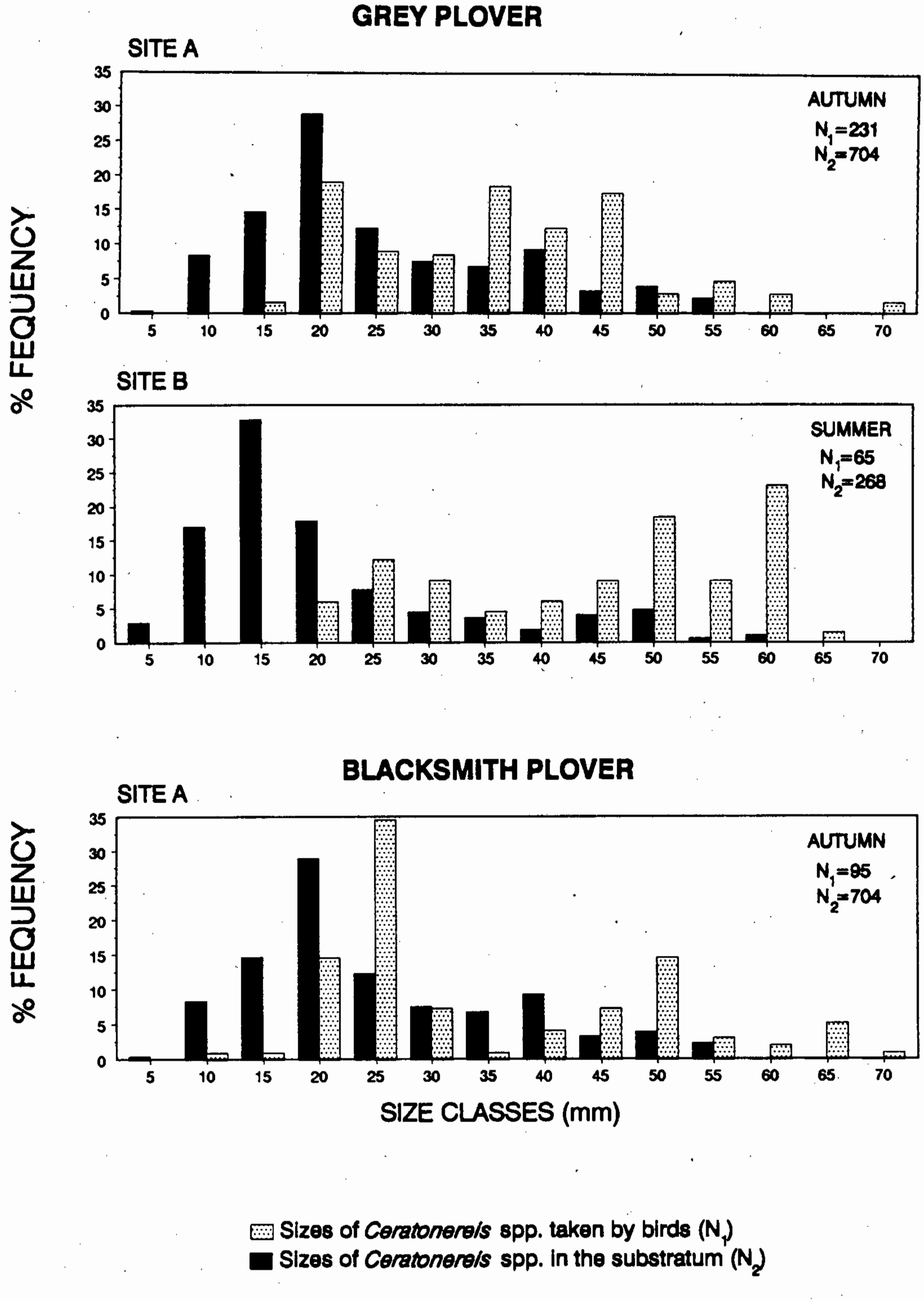


Figure 4.17. Sizes of nereids taken by Grey and Blacksmith Plovers (N_1) and present in the substratum (N_2) at the Berg River estuary.

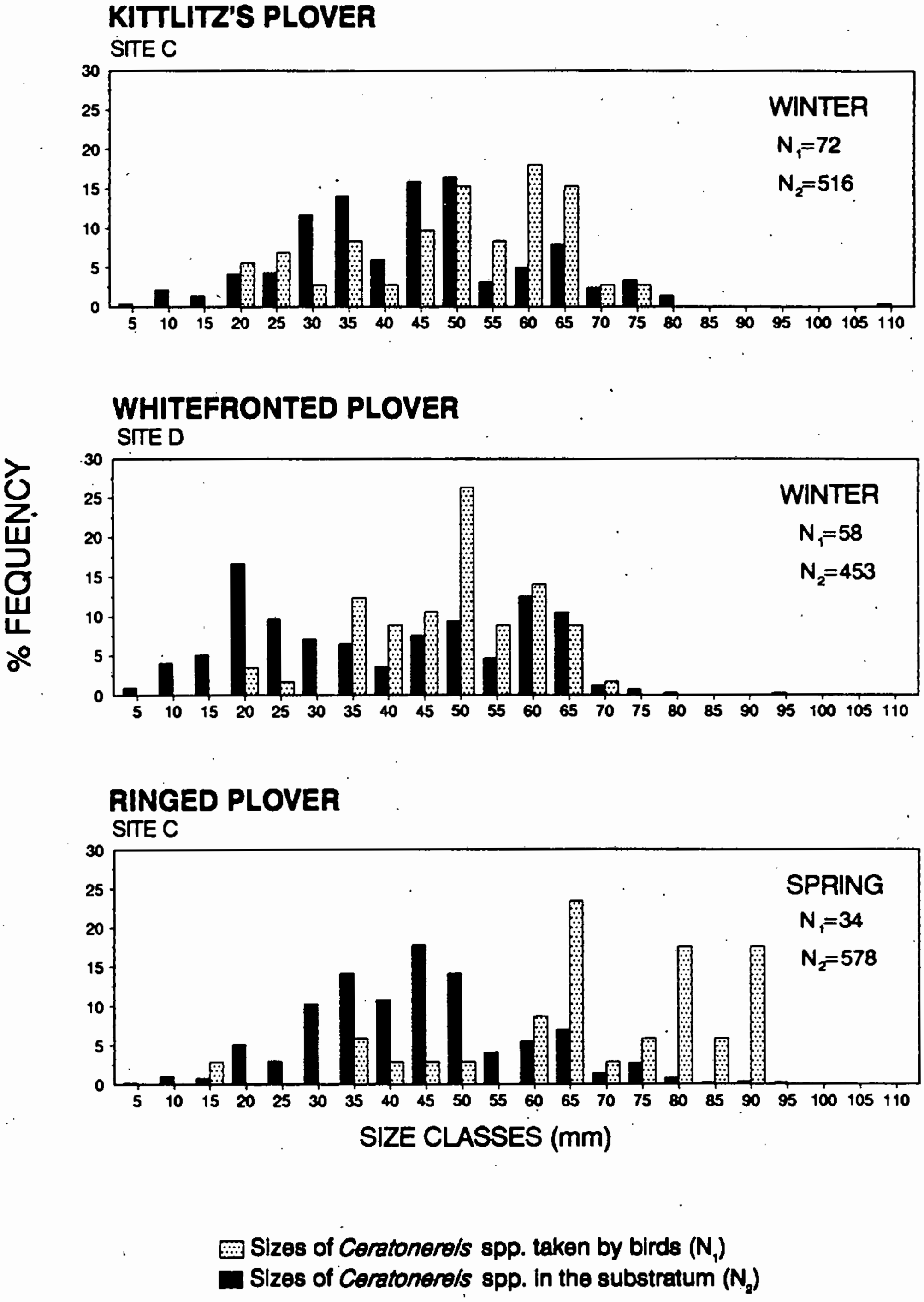


Figure 4.18. Size structure of nereids taken by Kittlitz's, Whitefronted and Ringed Plovers (N_1) and present in the substratum (N_2) at the Berg River estuary.

of worms in the substratum were most frequently taken by Curlew Sandpipers. In spring, the smallest and most abundant worms were ignored, and larger but less abundant individuals were taken. *Ceratonereis keiskama* was the only species taken by Curlew Sandpipers in winter and autumn. The proportion of *C. erythraeensis* consumed by Curlew Sandpipers increased to 0.5% in summer and, in spring, they made up 20% of the polychaetes taken.

In contrast to site A, a wider range of sizes of worms was available at site C and Curlew Sandpipers selected the most abundant size classes, tracking their seasonal availability (Fig 4.15). The preferred size classes of worms ranged between 30 and 50 mm in spring and between 45 and 50 mm in summer. There was no significant difference in the proportion of size classes of nereids taken by different sexes of Curlew Sandpiper (Kolmogorov-Smirnov Two-sample Test; $p > 0.05$) (Fig 4.16).

All plovers selected large polychaetes relative to those present in the substratum. Grey and Blacksmith Plovers preyed on nereids of comparable sizes (Fig 4.17), but they included different proportions of the two *Ceratonereis* species in their diets. *Ceratonereis erythraeensis* accounted for 68% of all *Ceratonereis* taken by Grey Plovers, as opposed to 40% taken by Blacksmith Plovers.

Resident Kittlitz's and Whitefronted Plovers at sites C and D, respectively, fed on a similar range of size classes of polychaetes (Fig 4.18). However, whereas polychaetes between 50 and 65 mm in length were taken most frequently by Kittliz's Plovers, polychaetes *ca* 50 mm in length were preferred by Whitefronted Plovers. The migrant Ringed Plovers selected larger nereids than those taken by any other species (Fig 4.18).

DISCUSSION

Diet of shorebirds

At the Berg River estuary, nereid worms were the principal food for the majority of both migrant and resident waders. In addition, crabs *Hymenosoma orbiculare*, gastropods *Hydrobia* sp., isopods *Exosphaeroma hyloecetes*, insects, both adults and larvae, and seeds were commonly taken by birds. Similar catholicism in the diets of waders has been reported elsewhere. At the Swartkops estuary, South Africa, mudprawns *Upogebia africana* dominate the invertebrate fauna and are the most important prey for the majority of waders (Martin, 1991). However, gastropods *Assiminea bifasciata*, insects, vegetation and small crabs are important components of Curlew Sandpipers' diet; polychaetes, gastropods and insects are frequently taken by Grey Plovers, and crabs and fish supplemented the diet of Greenshanks. In Tasmania, Thomas and Dartnall (1971) listed molluscs, seeds and insect larvae and pupae as the most important prey of Curlew Sandpipers. A similar range of prey items is taken by Curlew Sandpipers at Langebaan Lagoon to those at the Berg River (Puttick, 1978). The most important prey taken by Curlew Sandpipers at Langebaan Lagoon include nereid worms *Ceratonereis erythraeensis*, gastropods *Assiminea globulus*, amphipods *Urothoe grimaldii* and crabs *Cleistostoma edwardsii* and *Hymenosoma orbiculare*.

In Europe, Pienkowski (1982) listed the polychaetes *Arenicola*, *Notomastus* and *Scoloplos* as major prey of Grey and Ringed Plovers and added bivalves, gastropods and crustaceans as supplementary dietary components of these birds. Ragworms, *Nereis diversicolor* and crustaceans, *Corophium volutator* are the major dietary components of Grey Plovers at the Wash, U.K. (Durell & Kelly, 1990; Goss-Custard *et al.*, 1977), whereas barnacles and small polychaetes are preyed on at the Banc d'Arguin, Mauritania (NOME, 1982). Polychaetes *N. diversicolor* and nemertean worms *Cerebratulus lacteus* are major components of Grey Plover diet in the Bay of Fundy, Canada (Hicklin & Smith, 1979).

Feeding observations vs analysis of stomach contents, droppings and pellets

Various techniques have been used to describe diet of shorebirds: direct observations, analysis of stomach contents, regurgitated pellets and faecal droppings (Prater, 1972; Thomas & Dartnall, 1971; Durell & Kelly, 1990). Each of these methods has weak points and has been criticized. Goss-Custard (1973) proposed that "as much as possible should be described by the observations and any gaps should be filled by the analysis of pellets and droppings".

In the present study, feeding observations showed the importance of small prey in the diets of almost all species: however, these prey were too small to be identified in the field. In such situations, analysis of stomach contents, droppings and pellets is necessary. Because different prey have different resistances to digestion, the composition of stomach contents may not always reflect the real proportions of prey taken by birds. Prey least resistant to anaerobic conditions will be underestimated from the stomach analysis and those without indigestible parts may not be detected. Analysis of birds' stomachs at the Berg River estuary was only partly successful since soft-bodied animals, lacking indigestible parts, such as soft-bodied polychaetes, were absent from all the stomachs collected. Their presence was detected only in the oesophagi of Curlew Sandpipers, before digestion had occurred.

It is not known how long the indigestible parts of prey are kept in the stomachs. Some stomachs of birds collected during this study contained remnants of animals which did not occur in the area where birds were shot. A sound knowledge of the prey composition in the feeding area is therefore necessary to interpret the results correctly. Durell & Kelly (1990) pointed out that food ingested by Knots takes approximately 40 minutes to pass through the digestive tract. If this applies to all waders, droppings collected from a particular feeding area may not always reflect the prey composition of that area.

Worrall (1984) has shown that differences in the thickness and sizes of indigestible parts of different prey may lead to differential representation in pellets and droppings. Larger and more irregular shells of *Macoma balthica* are common in the pellets of Dunlin *Calidris alpina*, whereas finely ground shells of *Hydrobia ulvae* are better represented in the droppings.

Comparison between stomach contents and droppings of Whitefronted and Blacksmith Plovers (Tables 4.4 & 4.5) suggests that analysis of each on their own is not a good indicator of what is eaten by birds, and a combination of these two methods provides a better description of the birds' diet. Some prey species were absent from the stomachs of these birds but were well represented in droppings, and *vice versa*.

Prey selection

Bird diet is determined chiefly by the abundance and availability of the preferred invertebrate prey. The preference of birds for particular prey species might be explained by Optimal Foraging Theory, which assumes that birds should concentrate on taking the most profitable prey in terms of net energy intake (MacArthur & Pianka, 1966). Although *Hydrobia* sp. numerically dominated the invertebrate fauna at sites B and D (Chapter 2), these small gastropods have a high shell:flesh ratio, and soft-bodied nereids were the preferred prey for the majority of birds. Goss-Custard (1979) assumes that birds are able to assess the profitability associated with alternative food items. The preference of birds for a particular prey species may not always be related to the rate of energy gain alone, but may be associated with other components of food quality such as a scarce nutrient (Goss-Custard, 1981) or chemical composition (Pulliam, 1980). The preference may also be associated with digestibility (Zwarts & Blombert, 1990) or the behaviour of prey. Although *Upogebia africana* is the most important component of the creek fauna at the Swartkops estuary, Grey Plovers and Whimbrels select *Cleistostoma edwardsii* rather than *U. africana*. Both bird species probably develop a search image for *Cleistostoma* in the creeks because they are more frequently encountered by birds due to their habit of feeding on the surface (Martin, 1991).

Seasonal fluctuations in the availability of preferred prey are often reflected in seasonal changes in the birds' diet. Dunlin in the Severn Estuary, U.K., respond to reductions in the availability of their preferred prey, *Nereis diversicolor* and *Macoma balthica* in winter by selecting smaller, less rewarding, but more readily available *Hydrobia ulvae* (Worrall, 1984). Curlew Sandpipers in spring at Langebaan Lagoon increased the proportion of polychaetes and crustaceans in their diet when the availability and preferred sizes of snails *Assiminea* were reduced (Puttick, 1978).

Fluctuations in the diets of birds during the tidal cycle may reflect temporal changes in prey availability. The availability of nereid worms to birds may fall during the low tide period as worms move deeper into the substratum to avoid desiccation (Evans, 1976). *Hydrobia* has a peak in surface activity during the ebbing tide and then buries itself in the surface layer as the sediment begins to dry out (Newell, 1960 cited by Prater, 1972). The surface activity of crabs *Uca tangeri* and prawns *Upogebia africana* has also been related to the tidal cycle and moisture of the substratum (Zwarts, 1985; Martin, 1991).

A decrease in the density of preferred prey may lead to changes in the birds' diet (Martin, 1991). At the Berg River estuary, as the nereid population at site B decreased, Curlew Sandpipers switched their diet to small prey and Grey Plovers increased the spectrum of prey taken and included small prey, crabs and prawns in their diet. A similar switch in diet is reported for Redshanks at the Ythan estuary, U.K. (Goss-Custard *et al.*, 1977). *Corophium volutator* is preferentially taken by Redshanks when its density is high. When the density of *C. volutator* drops, *Nereis diversicolor* becomes the preferred prey item. Martin (1991) reported that Whimbrels *Numenius phaeopus* do not change their diet in response to a decrease in the availability of their preferred prey *Upogebia africana*, but switch feeding technique from predominantly visual in summer to tactile in winter when prey became scarce on the surface.

Size selection

According to Optimal Foraging Theory birds should select the most profitable sizes of prey; although the maximum size taken is limited by the ability of birds to handle them (MacArthur & Pianka, 1966). At the Berg River estuary, Grey Plovers were seen on several occasions to abandon large crabs which they had caught, possibly because they were not worth the energy expended in handling them. Alternatively, the chance of prey escaping or being lost due to kleptoparasitism increases with prey size, and birds therefore might abandon larger prey to escape these risks (Hockey, 1980; Thompson, 1983; Hockey & Steele, 1989; Martin, 1991). Martin (1991) notes that small prawns frequently were dropped by birds, presumably because of their high carapace to flesh ratio relative to larger individuals.

The profitability of *Nereis diversicolor* to foraging Curlews *Numenius arquata* increases with size (Zwarts, 1989). Despite this simple correlation, it might not be easy for Curlews to assess the profitability of nereids since only part of their body emerges from the burrow and the width of the burrow entrance on the surface is not well correlated with worm length (Zwarts, 1989). As in this study, smallest sizes of nereids are ignored by Curlews. Although Curlews handle small worms relatively rapidly, this was not fast enough to compensate for the small amount of flesh taken (Zwarts, 1989). Alternatively, small worms might not be included in the diet of birds because they are less detectable.

Despite a considerable overlap in prey species taken by the most abundant waders on the estuary, there were differences in the size classes of nereids taken by the birds. All plovers (Charadriidae) selected large nereids regardless of their abundance. In contrast, Curlew Sandpipers took the most abundant size classes of nereids, except in spring at site A (Fig 4.15). A possible explanation is that small recruits, which appeared in spring at site A, contained less energy than older and larger individuals, and the latter were selected despite their lower abundance. The availability of larger individuals might also have increased at this time of the year, as they move to the upper layer of the substratum for spawning. Results of the stomachs analyses in this particular case must be treated cautiously. Curlew Sandpipers fed exclusively on *C. keiskama* at site A in all seasons except spring. However, the sizes of *C. erythraeensis* found in stomachs at site A in spring, fell well within the range of those taken by Curlew Sandpipers in this particular season at site C. It is possible therefore that birds had fed on *C. erythraeensis* at site C before they were collected at site A.

Differences in feeding technique, size and bill morphology result in birds' selecting different sizes of the same prey; there is a pronounced tendency for larger birds to feed on larger prey (Hutchinson, 1959). Selection of different size classes of fiddler crabs *Uca tangeri* by different bird species was recorded on the intertidal mudflats of Guinea-Bissau (Zwarts, 1985). Martin (1991) also demonstrated selection of different size classes of *Upogebia africana* by different birds at the Swartkops estuary. In both studies, selection of different sizes of prey by birds was associated with the handling abilities of the birds. A clear correlation between body size and prey size is not apparent in this study. Ringed Plovers, one of the smallest species on the estuary, consumed larger polychaetes than any other species, and Curlew Sandpipers consumed polychaetes at site B which were within the range of those taken by the much larger Grey Plovers. However, only one Ringed Plover stomach was analyzed in this study and it is not known whether selection for larger polychaetes by this species is consistent.

In contrast to this study, Puttick (1978) found a marked difference in the sizes of prey selected by male and female Curlew Sandpipers, with the larger and longer-billed females taking larger prey than males. At site A at the Berg River estuary, where Curlew Sandpipers were collected, there is a very narrow range of size classes of worms available and therefore birds are very restricted in their choice.

Tactile vs visual foragers

Tactile foragers, represented at the Berg River by Curlew Sandpipers, use different cues to visual foragers, such as plovers, to detect their prey. The latter are probably more efficient in selecting profitable sizes of prey because the visual cues used to detect prey allow them to assess the value of prey before consuming it, and then respond accordingly. The possible cues used by these birds include burrow diameter of prawns, cast production or outflows of water from the holes of polychaetes, or swimming movements of amphipods and isopods (Pienkowski, 1983; Martin, 1991). In contrast, tactile foragers cannot assess the quality of the food until they touch it with their bill or capture it (Baker & Baker, 1973). It is more likely therefore, that tactile foragers will consume every food item they encounter. This difference in feeding technique between tactile and visual foragers may explain why, at the Berg River estuary, the most abundant size classes of polychaetes predominated in the diet of Curlew Sandpipers, whereas less abundant but larger polychaetes dominated the diet of plovers.

The present study has shown that despite the overlap in the diet of birds at the prey species level there is size-based segregation between bird species which feed on common prey types. Quantitative analysis of birds' diet is, however, not sufficient to establish the existence or otherwise of competitive interactions among the birds. An understanding of habitat segregation and aggression between different species is necessary to explain their coexistence. These aspects are investigated in Chapters 7 and 8.

REFERENCES

Baker, M. C. & Baker, A. E. M. 1973 Niche relationship among six species of shorebirds on their wintering and breeding ranges. *Ecological Monographs* **43**, 193-212.

Durell, S. E. A. le V. dit & Kelly, C. P. 1990 Diets of Dunlin *Calidris alpina* and Grey Plover *Pluvialis squatarola* on the Wash as determined by dropping analysis. *Bird Study* **37**, 44-47.

Evans, P. R. 1976 Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. *Ardea* **64**, 117-139.

Goss-Custard, J. D. 1973 Current problems in studying the feeding ecology of estuarine birds. *Coastal Ecology Research* Paper No **4**, 1-33.

Goss-Custard, J. D. 1979 The energetics of foraging Redshank, *Tringa totanus*. *Studies in Avian Biology* **2**, 247-257.

Goss-Custard, J. D. 1981 Feeding behavior of Redshank, *Tringa totanus*, and optimal foraging theory. In: *Foraging Behavior, Ecological, Ethological and Psychological Approaches* (Kamil, A. C. & Sargent, T. D., eds). Garland STPM Press, New York, pp 115-133.

Goss-Custard, J. D. Jones, R. E. & Newbery, P. E. 1977 The ecology of the Wash. 1. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology* **14**, 681-700.

Hicklin, P. W. & Smith, P. C. 1979 The diets of five species of migrant shorebirds in the Bay of Fundy. *Proceedings of the Nova Scotian Institute of Science* **29**, 483-488.

Hockey, P.A. R. 1980 Kleptoparasitism by Kelp Gulls *Larus dominicanus* of African Black Oystercatcher *Haematopus moquini*. *Cormorant* **8**, 97-98.

Hockey, P. A. R. & Steele, W. K. 1989 Intraspecific kleptoparasitism and foraging efficiency as constraints on food selection by Kelp Gulls *Larus dominicanus*. In:

Behavioural Mechanisms of Food Selection (Hughes, R. N., ed). NATO ASI Series **G20**, pp 679-705.

Holmes, R. T. 1966 Feeding ecology of the Red-backed Sandpiper (*Calidris alpina*) in arctic Alaska. *Ecology* **47**, 32-45.

Holmes, R. T. & Pitelka F. A. 1968 Food overlap among coexisting sandpipers on northern alaskan tundra. *Systematic Zoology* **17**, 305-318.

Hutchinson, G. E. 1959 Homage to Santa Rosalia, or why are there so many kinds of animals. *American Naturalist* **93**, 145-159.

MacArthur, R. H. & Pianka, E. R. 1966 On the optimal use of a patchy environment. *American Naturalist* **100**, 603-609.

Martin, A. P. 1991 Feeding ecology of birds on the Swartkops estuary, South Africa. Unpubl. PhD thesis. University of Port Elizabeth, Port Elizabeth, South Africa.

NOME, 1982 Foraging of Grey Plovers. In: *Wintering waders on the Banc d'Arguin.* Communication No. 6, Wadden Sea Working Group. The Netherlands, pp 150-152.

Pienkowski, M. W. 1982 Diet and energy intake of Grey and Ringed Plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. *Journal of Zoology of London* **197**, 511-549.

Pienkowski, M. W. 1983 Surface activity of some intertidal invertebrates in relation to temperature and the foraging behavior of their shorebird predators. *Marine Ecology-Progress Series* **11**, 141-150.

Prater, A. J. 1972 The ecology of Morecambe Bay. III. The food and feeding habits of Knots (*Calidris canutus* L.) in Morecambe Bay. *Journal of Applied Ecology* **9**, 179-194.

Pulliam, H. R. 1980 Do Chipping Sparrows forage optimally? *Ardea* **68**, 75-82.

Puttick, G. M. 1978 The diet of the Curlew Sandpiper at the Langebaan Lagoon, South Africa. *Ostrich* **49**, 158-167.

Recher, H. F. 1966 Some aspects of the ecology of migrant shorebirds. *Ecology* **47**, 393-407.

Thomas, D. G. & Dartnall, A. J. 1971 Ecological aspects of the feeding behaviour of two Calidritine sandpipers wintering in South-Eastern Tasmania. *Emu* **71**, 20-26.

Thompson, D. B. A. 1983 Prey assessment by plovers (Charadriidae); net rate of energy intake and vulnerability to kleptoparasitism. *Animal Behaviour* **31**, 1126-1236.

Worrall, D. H. 1984 Diet of the Dunlin *Calidris alpina* in the Severn Estuary. *Bird Study* **31**, 203-212.

Zwarts, L 1985 The winter exploitation of fiddler crabs *Uca tangeri* by waders in Guinea-Bissau. *Ardea* **73**, 3-12.

Zwarts, L. 1989 Versatility of male curlews *Numenius arquata* preying upon *Nereis divericolor*: deploying contrasting capture modes dependent on prey availability. *Marine-Ecology Progress Series* **56**, 255-269.

Zwarts, l. & Blombert, A. M. 1990 Selectivity of Whimbrel feeding on Fiddler Crabs explained by component specific digestibilities. *Ardea* **78**, 193-208.

APPENDIX 4.1

Sample sizes for Fig 4.5

SITE	SUMMER 1987/88	AUTUMN	WINTER	SPRING	SUMMER 1988/89	AUTUMN
A	79	124	13	250	326	145
B	106	20	-	173	100	-
C	194	139	-	274	155	93
D	-	-	-	35	68	67

Sample sizes for Fig 4.6

SITE	SUMMER 1987/88	WINTER	SPRING	SUMMER 1988/89	AUTUMN
A	-	11	16	19	43
B	48	137	76	173	67
C	81	64	104	124	70

Sample sizes for Fig 4.7

	SUMMER 1987/88	AUTUMN	WINTER	SPRING
Site B	33	18	130	61

Appendix 4.1 (cont.)

Sample sizes for Fig 4.8

	SUMMER 1987/88	AUTUMN	WINTER	SPRING
Site B	-	20	106	30
Site C	22	46	183	-

Sample sizes for Fig 4.9

	AUTUMN 1987/88	WINTER	SPRING	SUMMER 1988/89	AUTUMN
Site C	60	92	100	35	17

CHAPTER 5

ENERGY BUDGETS AND PREDATORY IMPACT OF WADERS AT THE BERG RIVER ESTUARY, SOUTH AFRICA

SUMMARY

The energy budgets of selected wader species foraging on the intertidal mudflats of the Berg River estuary, South Africa, were studied from December 1987 to April 1989. Migratory species increased the amount of time spent foraging both by day and at night during the pre-migration period. Visual foragers spent a higher proportion of the available time foraging at night than during the day, whereas the reverse was true for species with a greater tactile component to their foraging. Pecking rate, distance travelled to capture prey and frequency of searching by Grey Plovers were reduced at night. The daily energy intake of Curlew Sandpipers varied between 76 and 392 kJ d^{-1}, averaging 183 ± 35.7 kJ d^{-1}. The energy balance of Curlew Sandpipers was negative immediately after their arrival from the breeding grounds and positive during the remainder of the residence period. The daily energy intake of Grey Plovers varied between 140 and 597 kJ d^{-1}, averaging 315 ± 52.3 kJ d^{-1}. The energy balance of Grey Plovers was negative throughout most of the austral summer, but their energy deficit was less than that recorded elsewhere. On average, Curlew Sandpipers consumed 113 ± 34.6 kg ha^{-1} y^{-1} of invertebrate dry mass, representing 1-25% of the total annual production of invertebrates. Grey Plovers consumed between 1 and 4% of the annual production of invertebrates. Curlew Sandpipers consumed 3-61% and Grey Plovers 2-8% of the annual production of nereids. The highest predation pressure by shorebirds coincided with the period of highest production of the most important invertebrate prey. The rate of prey removal by shorebirds at the Berg River estuary is one of the highest recorded on the east Atlantic seaboard and is maintained by the high production of invertebrate prey.

INTRODUCTION

Most species of migratory waders (Aves: Charadrii) obtain the majority of their prey from intertidal habitats during the nonbreeding season (Goss-Custard, 1977; Bryant, 1979; Evans, 1979; Zwarts, 1988; Zwarts *et al.*, 1990a). Of all intertidal habitats, estuaries support the highest densities of waders. The impacts of these birds on estuarine invertebrate populations have been examined by several authors (Baird *et al.*, 1985).

In order to establish the impact of estuarine waders on their prey populations, two measures are required: the daily intake of prey by birds, and the biomass or production of invertebrate prey. One of the difficulties in establishing daily prey intake by birds is that little is known about the contribution that nocturnal feeding makes to the birds' total daily energy consumption. Various techniques have been used to try and quantify nocturnal feeding by waders, but these inevitably contain untested assumptions (Evans, 1976; Schramm, 1978; Dugan, 1981; Pienkowski, 1983a; Martin, 1991). Furthermore, the majority of these studies were carried out in the northern hemisphere and, more recently, in tropical localities (Robert & McNeil, 1989; Robert *et al.*, 1989; McNeil, 1990). No study to date has quantified the relative efficiency of diurnal and nocturnal feeding in waders south of the equator.

The impact of shorebirds on their prey populations is usually expressed as proportional removal of either the mean annual biomass of prey (Schramm, 1978; Puttick, 1980) or of the total annual production of prey (Wolff *et al.*, 1975; Baird & Milne, 1981; Martin, 1991). Since prey biomass is not necessarily a good indicator of what is available to birds, the rate of biomass production is a more valuable measure in such studies (Smit, 1981). Production of prey varies seasonally, as does the predation pressure by birds. It is therefore important to establish the relationship between predation and production on a seasonal basis to determine whether there are critical periods of the year when the numbers of birds are limited by food. There are no studies to date which have examined this relationship in the southern hemisphere.

The intertidal mudflats of the Berg River estuary (34°47'S, 18°10'E), South Africa, support up to 70 Holarctic-breeding waders per hectare during the austral summer. The majority of these birds are Curlew Sandpipers *Calidris ferruginea* and Grey Plovers *Pluvialis squatarola* (Chapter 1).

This study quantifies the energy budgets of selected wader species on the mudflats of the Berg River, with special reference to the numerically dominant species. Emphasis is placed on the nocturnal foraging component and its seasonal contribution to the total energy intake by birds. Finally, the seasonal relationship between predation and production, especially of nereid worms, is analyzed.

METHODS

Four study sites (A, B, C and D), each of 2 000 m^2 (25 x 80 m) were established on intertidal mudflats at decreasing distances from the Berg River mouth (Fig 2.1). Twice a month, at spring tides, the numbers of feeding and roosting birds within these study plots were recorded at 20 minute intervals throughout the period of daytime tidal exposure. Simultaneously, additional activity scans were made over the entire mudflat from November 1988 onwards. One minute focal animal observations were used to determine the frequency of prey capture by birds as well as prey species and size. More accurate determination of the sizes of nereid worms eaten was made from stomach content analysis (Chapter 4). Polychaete jaws are retained in the stomachs of waders and the size frequency of nereids in the diet was reconstructed using equations in Chapter 2. Energy contents of invertebrate species were determined using a Phillipson microbomb calorimeter.

Night foraging

Between March 1988 and March 1989 observations of birds foraging at night were made at the most accessible site (site C). Observations, using an image-intensifer with a variable-power infra-red source, were made twice a month, on moonlit and moonless nights, and usually on the night following daytime observations. The numbers and activities of birds were recorded as for daylight observations. For comparative purposes from November 1988 onwards, additional activity scans were made over the entire adjacent mudflat as during the daylight hours. On a few nights it was possible to quantify some aspects of the foraging behaviour of Grey Plovers. Parameters recorded were: pecking rate, the frequency of "stand-up" positions per minute and the number of steps between "stand-up" positions. The same parameters were recorded during daylight observations.

At night it was impossible to identify small *Charadrius* plovers (Ringed Plover *Charadrius hiaticula*, Whitefronted Plover *C. marginatus* and Kittlitz's Plover *C. pecuarius*) to species level and they were grouped together as *Charadrius* spp. In analyses the same classification was applied to daytime observations.

Daily and annual energy intake

Energy intake per hour, available foraging time and the percentage of available time spent foraging by Curlew Sandpipers and Grey Plovers were combined to calculate the average daylight energy intake for these birds. The energy intake at night was calculated from the percentage of time spent foraging at night by both species, assuming that the energy intake per hour at night was the same as during the day. The ratio of diurnal/nocturnal energy intake at site C was assumed to be representative of the ratio at the other three sites. Due to the low numbers of Curlew Sandpipers and Grey Plovers present during winter (May-July), calculations

Curlew Sandpipers and Grey Plovers present during winter (May-July), calculations of daily energy intake are presented only for the austral summer of 1988/89. These values are compared with theoretical daily energy requirements (in kJ) calculated from the equation for Field Metabolic Rate (FMR): $FMR = 10.9 \, w^{0.640}$, where w is the body weight in grams (Nagy, 1987). FMR was corrected to Daily Energy Intake (DEI) assuming an assimilation efficiency of 75% (Hockey, 1984).

In order to determine the annual energy consumption of these species, the average intake rate for the period August-April was used for the winter months. The number of foraging birds recorded during each activity scan at the study sites was multiplied by 20 (time interval in minutes between scans) and was summed over the whole observation period to give a total foraging time in bird-minutes per day. The total foraging time was then multiplied by energy intake rate and the number of days in each month to give a total energy consumption per month. Annual production of invertebrates at the Berg River estuary has been determined by averaging production in those months which were sampled in more than one year (December-April) (Chapter 2). The same averaging method was employed to calculate annual energy consumption by birds and its relation to prey production.

RESULTS

Diurnal and nocturnal activity of waders

During the winter months, and in the immediate post-arrival period (September-October), there was almost no nocturnal use of mudflats by birds (Fig 5.1). From December onwards, however, there was a gradual increase in nocturnal activity up to the time when migrant waders left on their northward migration (March-April). High numbers of birds foraging by day and at night in December was due to an unusually short period of mudflat exposure during the previous days which severely reduced available foraging time. At the same time, the area available for foraging

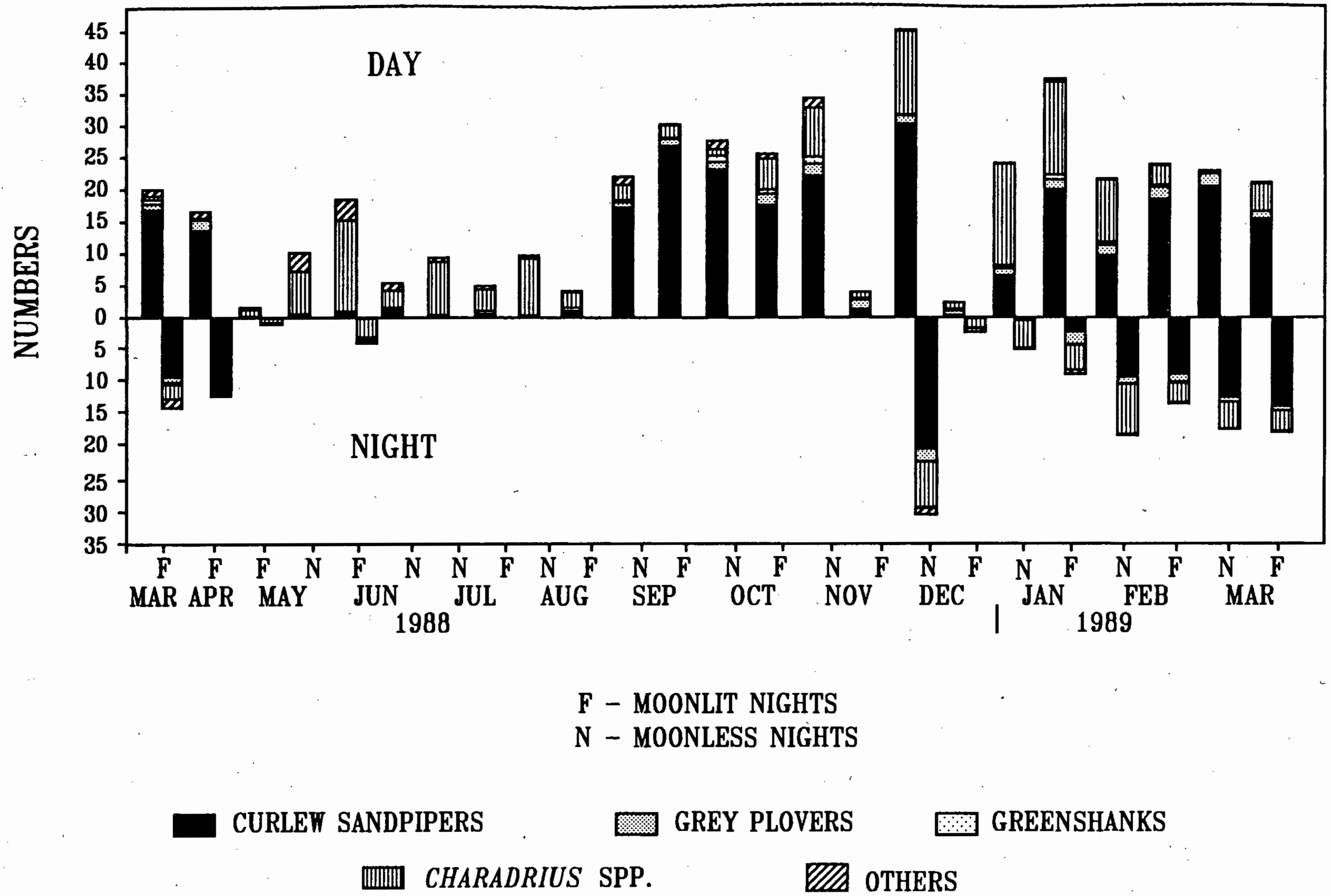


Figure 5.1. Average numbers of birds present at site C (2 000 m^2) during the day and at night from March 1988 to March 1989.

mudflats (Chapter 2). Although no birds were recorded in the study plot at night between May and November, scans of the surrounding mudflats indicated that there were small numbers of Curlew Sandpipers and *Charadrius* spp. present between August and November. Combining all nights of observation between December and March (N=10 nights), the mean (±SE) ratios of night to day foraging numbers were: Curlew Sandpiper 0.79 ± 0.16, Grey Plover 0.72 ± 0.15, Greenshank *Tringa nebularia* 0.13 ± 0.06 and *Charadrius* spp. 2.85 ± 1.40. The number of birds foraging at night was independent of moon phase. However, during the pre-migration period between January and March, there was a gradual increase in the amount of foraging by Curlew Sandpipers and Grey Plovers on moonless nights (Table 5.1). This pattern was not mirrored by Greenshanks, which satisfy their energy requirements relatively easily by day (see below), or by *Charadrius* spp., a group which includes both resident and migrant species. Diurnal and nocturnal foraging activity relative to the tidal cycle differed between months, both between and within species (Fig 5.2).

Diurnal and nocturnal foraging effort

The proportion of time spent foraging by each species throughout the low tide varied, but without a clear pattern within species or between months (Fig 5.3). There was a difference in the amount of time spent foraging during the day and at night between species (Fig 5.4). Grey Plovers, which forage entirely visually, spent significantly more time foraging at night than during the day ($T=-1$; $n=7$, $p<0.05$; Wilcoxon paired-sample test) (Fig 5.4). This pattern was not mirrored by Curlew Sandpipers or Greenshanks which have a greater tactile component to their foraging, or by *Charadrius* spp., a group which included both residents and migrants. If time spent foraging during the day and at night is combined, Curlew Sandpipers and Grey Plovers spent the longest time foraging on the mudflats (9.73 and 9.13 hours, respectively), whereas Greenshanks spent the least time foraging (4.76

Table 5.1. Relative foraging densities of waders on moonless and moonlit nights between January and March at the Berg River estuary.

	Ratio moonless/moonlit nights			
Month	Curlew Sandpipers	Grey Plovers	Greenshanks	*Charadrius* spp.
January	0.00	0.19	0.00	1.30
February	0.88	0.69	0.53	3.96
March	1.00	0.94	0.00	0.87

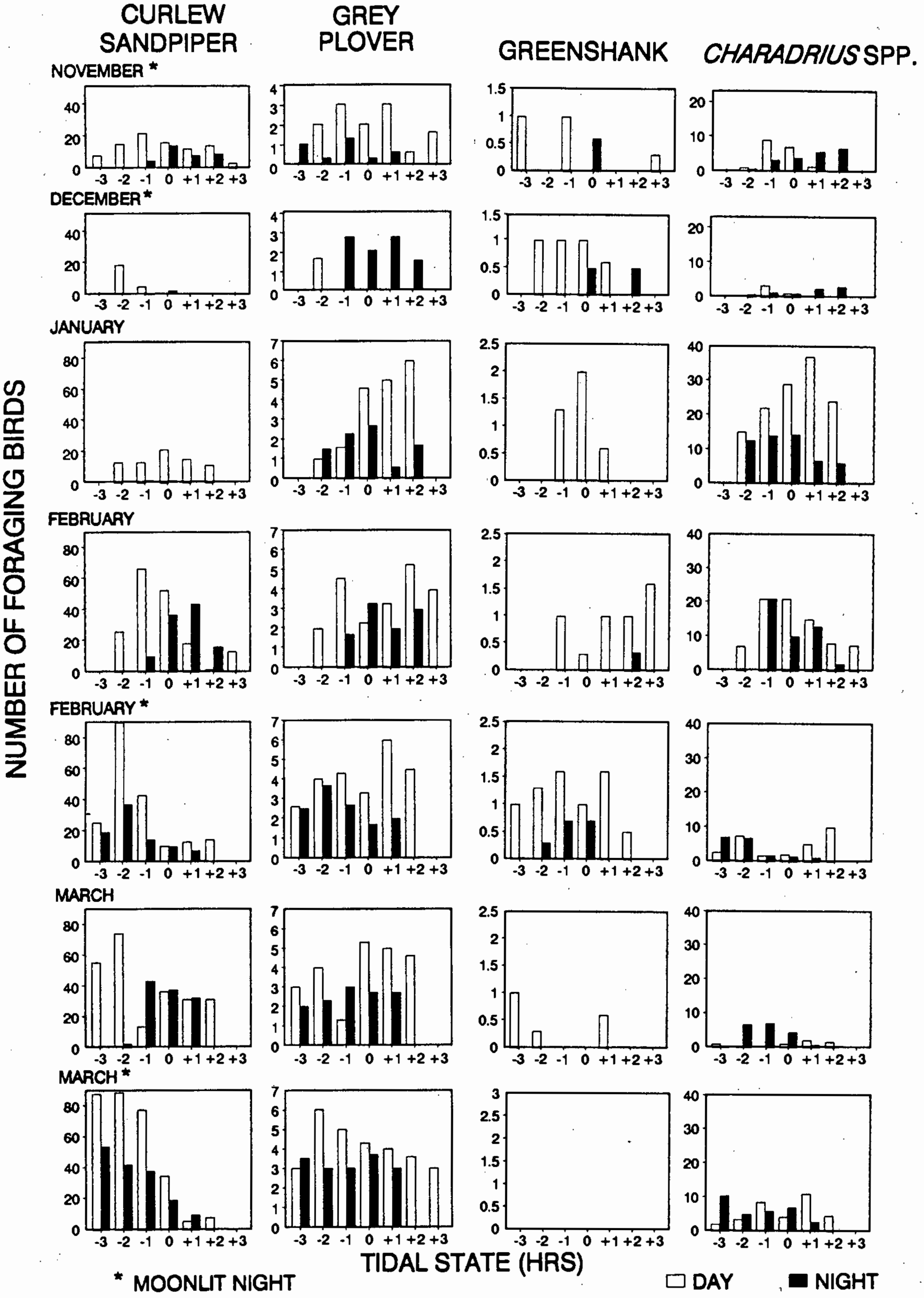


Figure 5.2. Diurnal and nocturnal foraging rhythms of common wader species throughout the low tide period at site C between November 1988 and March 1989.

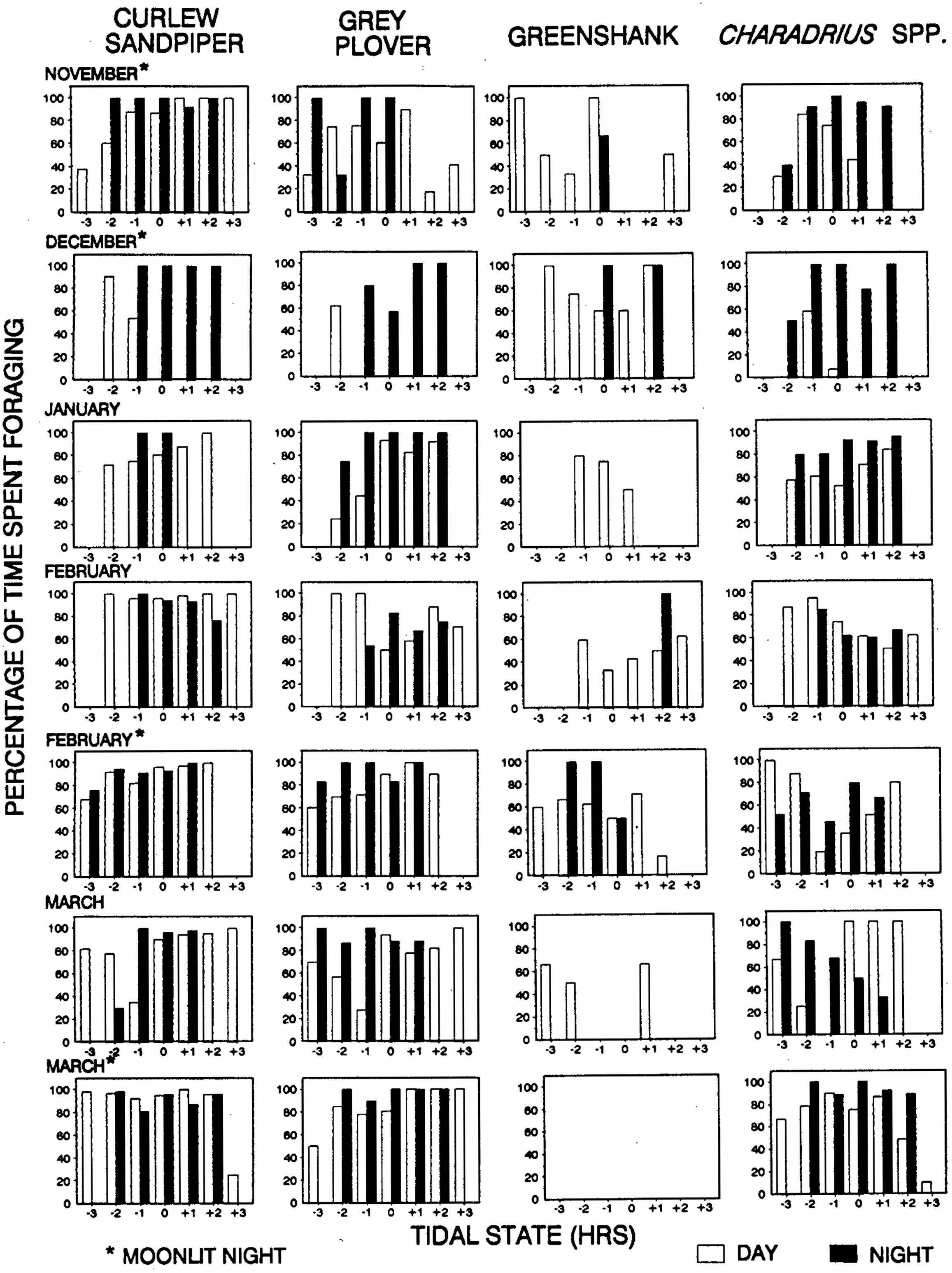
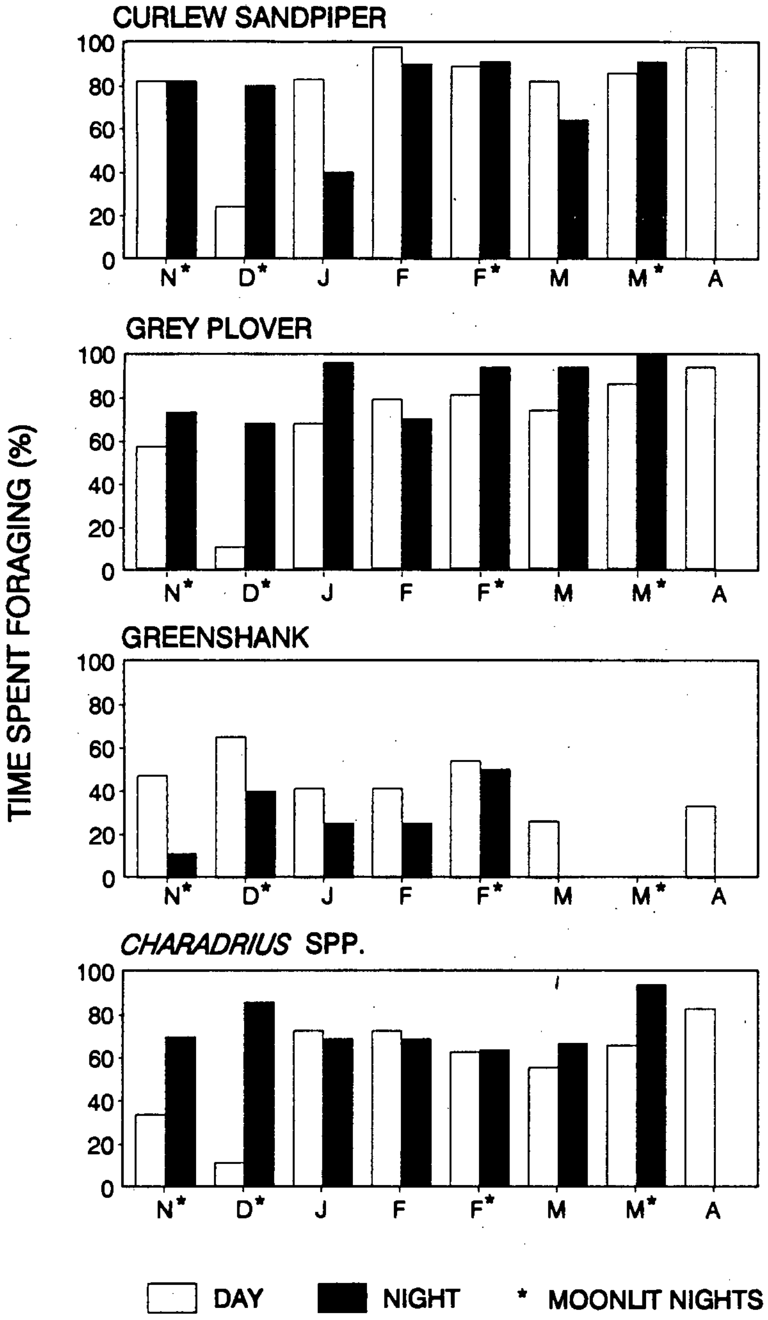


Figure 5.3. Proportion (%) of available time spent foraging throughout the low tide period during the day and at night by Curlew Sandpipers, Grey Plovers, Greenshanks and *Charadrius* spp. at site C from November 1988 to March 1989.



Curlew Sandpiper: Day X̄=80± 8.4 (4.9 ±0.7); Night X̄=77± 7.1 (4.8 ± 0.7)

Grey Plover: Day X̄=68± 9.1 (4.1 ± 0.6); Night X̄=84± 5.2 (5.1 ±0.5)

Greenshank: Day X̄=44± 4.9 (2.7 ± 0.5); Night X̄=31± 8.5 (2.1 ± 0.5)

Charadrius spp.: Day X̄=56± 8.1 (3.2 ± 0.4); Night X̄=74± 5.0 (4.6 ± 1.6)

Figure 5.4. Proportion (%) of available time spent foraging per month during the day and at night by Curlew Sandpipers, Grey Plovers, Greenshanks and *Charadrius* spp. at site C from November 1988 to April 1989. Mean percentage of the available time spent foraging for the whole study period and, in parenthesis, average time spent foraging in hours, are also given.

hours). There were differences in the time spent foraging by birds during the day on two different mudflats, A and C, with birds at site A foraging for longer then those at site C (Table 5.2, Fig 5.4). Generally, smaller birds fed for longer than larger ones, regardless of their foraging technique (Table 5.2). Curlew Sandpipers and Little Stints spent the highest proportion of the available time foraging during the day.

Grey Plovers foraged significantly more slowly at night than during the day, averaging only 4.7 ± 0.3 (SE) prey capture attempts per minute at night compared with 6.7 ± 0.3 by day ($F=24.14$, df=1, 215, $p<0.01$) (Table 5.3). The distance travelled (number of steps) to a potential prey item and frequency of "stand-up" positions were also significantly less at night (30.3 ± 1.9 and 4.2 ± 0.4 respectively) than by day (59.1 ± 1.2 and 9.3 ± 0.3 respectively) ($F=173.08$, df=1, 215, and $F=97.14$, df=1, 215, both $p<0.01$). There was no significant difference in the pecking rate, travelling distance between capture attempts or frequency of "stand-up" positions by Grey Plovers between moonlit and moonless nights ($F=0.01$, df=1, 25, $p<0.9$; $F=1.3$, df=1, 25, $p<0.3$; $F=0.7$, df=1, 25, $p<0.4$, respectively) (Table 5.4).

Daily energy intake

On average, Curlew Sandpipers consumed 305 ± 27.3 (SE) prey items per hour with a total dry mass of 1.8 ± 0.4 g and an energy content of 23.8 ± 3.8 kJ (Table 5.5). Grey Plovers consumed a greater invertebrate dry mass per hour than Curlew Sandpipers, and their average energy intake rate was consequently higher (Table 5.5). Nereids were consumed at an average rate of 187 ± 21.4 (SE) per hour (11.0 ± 1.9 kJ) by Curlew Sandpipers and at a rate of 267 ± 75.5 per hour (19.5 ± 4.3 kJ) by Grey Plovers. Although both species obtained the largest number of food items per hour at site A, their energy intake per unit foraging time was

Table 5.2. Time spent foraging during the day by waders at site A from September 1988 to January 1989 as a percentage of the available foraging time.

		Little Stint		Curlew Sandpiper		*Charadrius* spp.		Grey Plover		Greenshank		Bartailed Godwit		Whimbrel	
	Available foraging time (min)	Time spent foraging %	hrs	Time spent foraging %	hrs	Time spent foraging %	hrs	Time spent foraging %	hrs	Time spent foraging %	hrs	Time spent foraging %	hrs	Time spent foraging %	hrs
SEP	360	94	5.6	87	5.2	76	4.6	79	4.7	87	5.2	70	4.2	63	3.8
OCT	340	100	5.7	97	5.5	86	4.9	85	4.8	57	3.2	86	4.8	-	-
NOV	380	100	6.3	99	6.3	91	5.8	75	4.7	49	3.1	95	6.0	46	2.9
DEC	300	91	4.5	95	4.7	76	3.8	78	3.9	77	3.8	57	2.8	77	3.8
JAN	250	84	3.5	88	3.7	87	3.6	67	2.8	80	3.3	34	1.4	71	3.0
Mean	326	94	5.1	93	5.1	83	4.5	77	4.2	70	3.7	68	3.9	64	3.4
(SE)	(23.1)	(3.0)	(0.5)	(2.4)	(0.4)	(3.1)	(0.4)	(12.9)	(0.4)	(7.2)	(0.4)	(10.7)	(0.8)	(6.7)	0.2)

Table 5.3. Grey Plover: comparison of pecking rates, distance travelled and frequency of "stand-up" positions per minute (±SE) by night and day.

		Night				Day		
Month	N	Pecking rate	Number of "stand-ups"	Number of steps	N	Pecking rate	Number of "stand-ups"	Number of steps
May	14	5.70	2.70	21.07	7	14.14	10.14	51.43
		(0.59)	(0.40)	(0.02)		(1.10)	(0.99)	(3.23)
January	22	5.64	6.45	34.68	62	6.48	9.19	56.20
		(0.64)	(0.88)	(3.72)		(0.27)	0.36)	(2.11)
February	15	3.93	4.47	35.20	39	6.26	7.74	60.79
		(0.40)	(0.29)	(4.06)		(0.34)	(0.37)	(1.80)
March	12	3.50	3.58	26.92	46	6.48	10.73	64.06
		(0.47)	(0.44)	(3.40)		(0.32)	(0.58)	(2.07)

Table 5.4. Grey Plover: comparison of pecking rates, number of steps and number of "stand-up" positions (±SE) per minute on moonless and moolit nights.

		Moonless nights				Moonlit nights		
		Pecking rate	Number of steps	Number of "stand-ups"		Pecking rate	Number of steps	Number of "stand-ups"
February	N=9	37.5 (5.4)	3.8 (0.4)	4.2 (0.4)	N=6	31.6 (6.5)	4.0 (0.9)	4.8 (0.5)
March	N=5	29.2 (4.7)	3.4 (0.7)	3.2 (0.7)	N=7	25.2 (5.0)	3.5 (0.6)	3.8 (0.6)

Table 5.5. Total prey and nereid consumption (±SE) in term of numbers, dry mass (g) and energy (kJ) per hour by individual Curlew Sandpipers and Grey Plovers at the four study sites from December 1987 to April 1989. N = sample size = number of months and, in parenthesis, total number of one minute observations (see methods).

	Prey consumption per hour											
	site A			site B			site C			site D		
	Numbers	Dry mass (g)	Energy (kJ)	Numbers	Dry mass (g)	Energy (kJ)	Numbers	Dry mass (g)	Energy (kJ)	Numbers	Dry mass (g)	Energy (kJ)
Curlew Sandpiper	N = 12 (932)			N = 8 (415)			N = 13 (872)			N = 5 (171)		
all prey	383	1.20	17.66	305	1.90	23.96	261	1.22	19.37	274	2.88	34.41
(SE)	(31.74)	(0.06)	(0.72)	(26.62)	(0.29)	(2.64)	(10.65)	(0.15)	(1.55)	(29.72)	(1.53)	(12.69)
Nereids	228	0.44	7.83	127	0.44	7.75	200	0.81	14.38	195	0.86	15.20
(SE)	(28.80)	(0.06)	(1.04)	(13.63)	(0.09)	(1.54)	(12.99)	(0.05)	(0.86)	(20.74)	(0.09)	(1.66)
Grey Plover	N = 5 (89)			N = 13 (471)			N = 13 (436)			N = 1 (64)		
All prey	560	2.73	41.20	267	4.18	45.92	239	3.42	40.64	247	8.70	85.10
(SE)	(113.40)	(0.31)	(5.86)	(13.89)	(0.42)	(3.52)	(22.03)	(0.46)	(4.28)	-	-	-
Nereids	485	1.76	31.19	143	0.78	13.88	195	1.16	20.58	92	0.70	12.37
(SE)	(107.00)	(0.39)	(6.88)	(23.18)	(0.13)	(2.26)	(22.47)	(0.13)	(2.37)	-	-	-

greatest at sites B and D. Intake rates of Grey Plovers at site D refer only to one month (April) when they were feeding on fish, prey with a high individual biomass. There was a trend for the intake rates of both species to be consistently higher in the summer of 1987/88 than in the corresponding months at 1988/89 (Table 5.6) but this difference was significant only for Grey Plovers (Sign Test: $n=5$, $X^2=0$, $p<0.05$).

The daily energy intake of Curlew Sandpipers ranged between 76 and 392 kJ d^{-1}, averaging 183 ± 35.7 (SE) kJ d^{-1}. In general, if Curlew Sandpipers fed only on mudflats, they experienced a negative energy balance immediately after their arrival on the estuary (August to October) and a positive energy balance during the remainder of the residence period (Table 5.7).

The daily energy intake of Grey Plovers ranged between 140 and 597 kJ d^{-1}, with an average value of 315 ± 52.3 (SE) kJ d^{-1}. Grey Plovers were unable to meet their daily energy requirements by foraging on the mudflats alone throughout most of the austral summer (Table 5.8).

Limited data on the energy intake of Greenshanks and the resident Blacksmith, Kittlitz's and Whitefronted Plovers indicate that, of these, only Blacksmith Plovers may experience a real energy deficit at some times of year (Table 5.9).

Annual prey consumption and the impact of birds
on production of benthic invertebrates

Curlew Sandpipers consumed on average 113.4 ± 34.6 (SE) kg $ha^{-1} y^{-1}$ of invertebrate dry mass, equivalent to $3.61*10^6 \pm 2.24*10^3$ kJ $ha^{-1} y^{-1}$. Grey Plovers consumed on average 22.5 ± 9.7 kg $ha^{-1} y^{-1}$ of invertebrates, equivalent to $5.45*10^5 \pm 2.41*10^2$ kJ $ha^{-1} y^{-1}$ (Table 5.10). These values are calculated using

Table 5.6. Comparison of the energy intake rate (kJ h^{-1}) of Curlew Sandpipers and Grey Plovers in 1987/88 and 1988/89 at the Berg River estuary.

	Energy intake (kJ h^{-1})			
	Curlew Sandpiper		Grey Plover	
	1987/88	1988/89	1987/88	1988/89
Dec	28.76	21.51	67.67	37.54
Jan	18.56	15.45	49.80	28.52
Feb	21.06	17.69	54.11	41.50
Mar	20.59	20.09	37.14	35.37
Apr	19.73	20.86	45.75	41.34
Average	21.74	19.73	50.29	36.85
(SE)	(1.80)	(1.28)	(4.97)	(2.38)

Table 5.7. Estimated daily energy budget of Curlew Sandpipers at the Berg River estuary, South Africa.

Month	Energy intake per hour (kJ h^{-1})	Daytime[1] intake energy (kJ)	Nighttime[2] energy intake (kJ)	Daily energy intake (kJ d^{-1})	Energy[3] balance (kJ)
AUG	22.2	106	?	106	-85
SEP	15.0	67	8	76	-115
OCT	20.3	114	*	114	-77
NOV	21.1	150	124	274	83
DEC	21.5	112	95	207	16
JAN	15.4	75	34	109	-81
FEB	40.0	198	193	392	201
MAR	20.1	98	91	189	-2
APR	20.9	112	?	?	?

[1] Proportion of time spent foraging by birds from Fig 3 and Table 2.

[2] Proportion of time spent foraging by birds from Fig 3.

[3] Theoretical energy requirement is 191 kJ d^{-1} (Nagy, 1987) given an average body mass of 56 g (Summers, 1977) and an assimilation efficiency of 75% (Hockey, 1984).

* No birds present

Table 5.8. Estimated daily energy budget of Grey Plovers at the Berg River estuary, South Africa.

Month	Energy intake per hour (kJ h^{-1})	Daytime[1] intake energy (kJ)	Nighttime[2] energy intake (kJ)	Daily energy intake (kJ d^{-1})	Energy[3] balance (kJ)
SEP	30.1	123	17	140	-359
OCT	43.3	201	*	201	-298
NOV	65.1	261	336	598	98
DEC	37.5	161	138	299	-200
JAN	28.5	105	149	254	-245
FEB	41.5	175	179	354	-145
MAR	35.4	163	167	360	-139
APR	41.3	211	?	?	?

[1] Proportion of time spent foraging by birds from Fig 3 and Table 2.

[2] Proportion of time spent foraging by birds from Fig 3.

[3] Theoretical energy requirement is 499 kJ d^{-1} (Nagy, 1987) given an average body mass of 251 g (Maclean, 1985) and an assimilation efficiency of 75% (Hockey, 1984).

* No birds present.

Table 5.9. Comparison between theoretical and observed energy consumption ($\pm$SE) of Greenshanks, Blacksmith, Kittlitz's and Whitefronted Plovers at the Berg River estuary.

Species	Observed total prey consumption per hour Numbers	dry mass (g)	energy (kJ)	Theoretical* energy intake (TEI) (kJ d^{-1})	Time of continuous foraging needed to meet TEI (hours)
Greenshank	271 (49.7)	12.9 (2.3)	115.1[1] (17.8)	456 (225)	4.0
Blacksmith Plover	295 (30.0)	2.5 (0.2)	29.6[2] (0.5)	369 (157)	12.5
Kittlitz's Plover	228 (27.5)	1.5 (0.2)	26.0[3] (3.8)	161 (43)	6.2
Whitefronted Plover	327 (22.7)	1.9 (0.1)	31.1[4] (2.6)	176 (49)	5.7

[1] Average for the period January-November
[2] Average for two months May and June
[3] Average for the period May-September
[4] Average for the period January-November
* From Nagy, 1987 - in parenthesis, the body mass in grams used in calculation

Table 5.10. Relationship between invertebrate production and consumption by Curlew Sandpipers and Grey Plovers at four sites at the Berg River estuary. In parentheses, the percentage of total production removed by birds.

			Annual consumption kg ha^{-1} y^{-1}							
	Production kg ha^{-1} y^{-1}		Curlew Sandpipers				Grey Plovers			
			all prey		nereids		all prey		nereids	
Site	all prey	nereids	study site[1]	mudflat[2]	study site[1]	mudflat[2]	study site[1]	mudflat[2]	study site[1]	mudflat[2]
A	663	121	166.2 (25)	117.0 (18)	62.7 (51)	51.4 (42)	8.3 (1)	5.6 (1)	4.2 (3)	1.2 (1)
B	1469	203	137.9 (9)	102.3 (7)	23.7 (12)	16.1 (8)	39.8 (3)	27.7 (2)	4.2 (2)	4.6 (2)
C	864	161	137.8 (16)	50.9 (6)	99.9 (61)	39.5 (24)	44.7 (4)	10.0 (1)	15.6 (8)	4.8 (3)
D	1381	175	11.6 (1)	19.8 (1)	5.90 (3)	8.1 (5)	*	3.2 (<1)	*	1.9 (1)

[1] average density of birds at the study site throughout the tidal cycle was used to calculate the consumption.
[2] density of birds on the whole mudflat recorded once at low tide was used to calculate the consumption.
* Data available for one month only.

average densities of birds measured over the low tide period within the study sites. Densities recorded over the whole mudflat area during low tide surveys were lower (except at site D) and if these values are used in calculations, estimates of prey removal rates range between 26 and 63% of the values calculated from study site data alone (Table 5.10).

Curlew Sandpipers removed between 1 and 25% of the annual production of all invertebrates and between 3 and 61% of the annual nereid production at different sites. Grey Plovers removed between 1 and 4% of the annual production of all invertebrates and between 2 and 8% of the annual nereid production (Table 5.10).

Seasonal changes in energy consumption

The highest energy consumption by Curlew Sandpipers occurred shortly after their arrival, in November, and again just prior to northward migration between February and April (Fig 5.5). Lowest predation pressure by Curlew Sandpipers was at site D, despite the fact that this species experienced its highest energy intake per unit time at this site. Predation pressure by Grey Plovers was low and constant throughout the residence period at sites A and C, but varied considerably at site B. For both species the calculated energy consumption was less than the theoretical energy consumption (Nagy, 1987) (Fig 5.5). The pattern of seasonal consumption of all invertebrates by shorebirds reflects the seasonal variation in the consumption of nereids (Figs 5.6 & 5.7). Production of nereids has been calculated only at sites A and C (Chapter 3). Although the period of negative production by nereids coincides with high predation pressure by birds in the immediate post-arrival period, birds do not experience a food shortage because the high standing stock biomass of nereids compensates in the short term for low production (Fig 5.6).

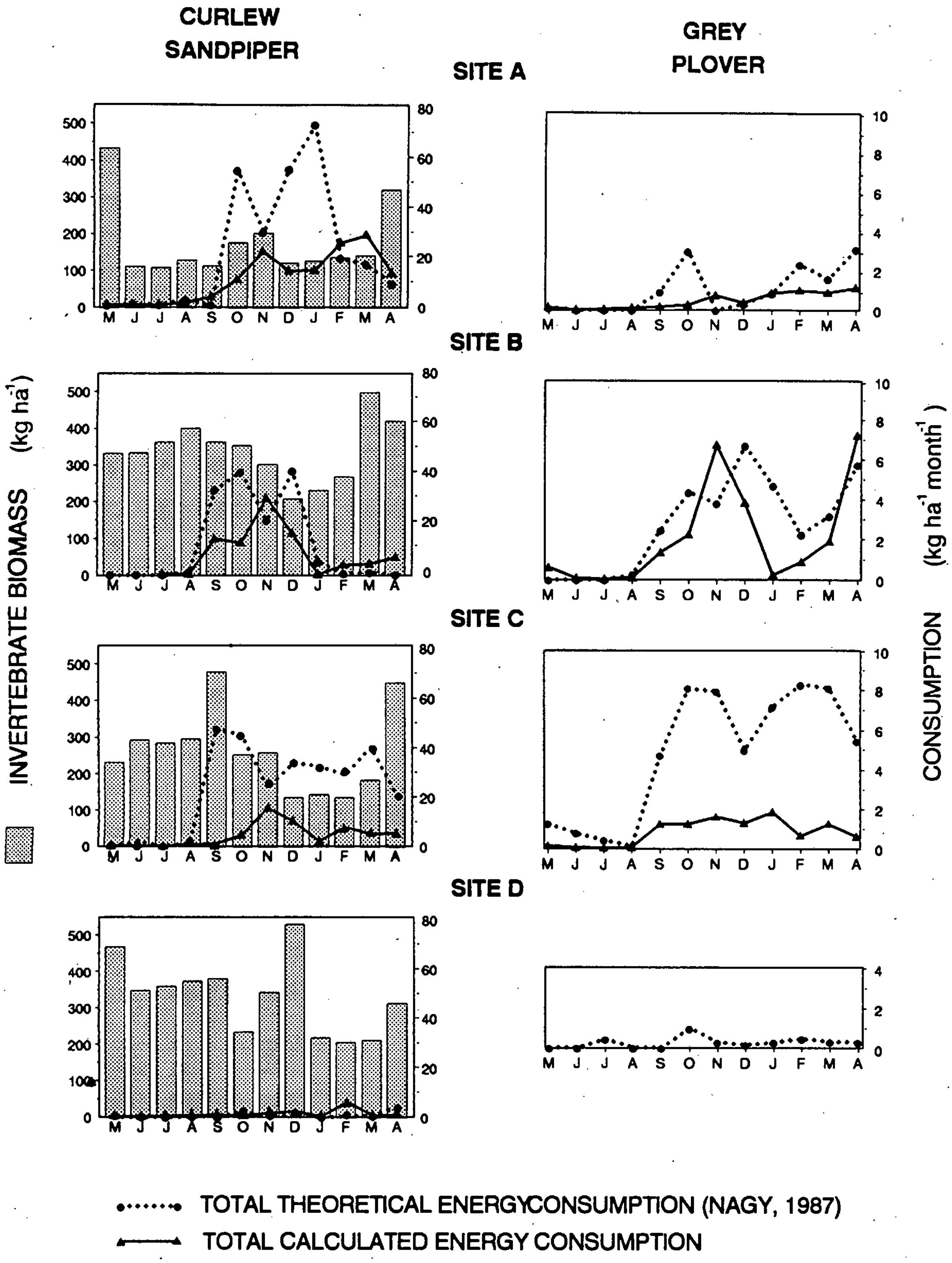


Figure 5.5. Total invertebrate biomass (kg ha^{-1}), total theoretical consumption (Nagy, 1987) and calculated total consumption by Curlew Sandpipers and Grey Plovers (kg ha^{-1} month^{-1}) from March 1988 to April 1989.

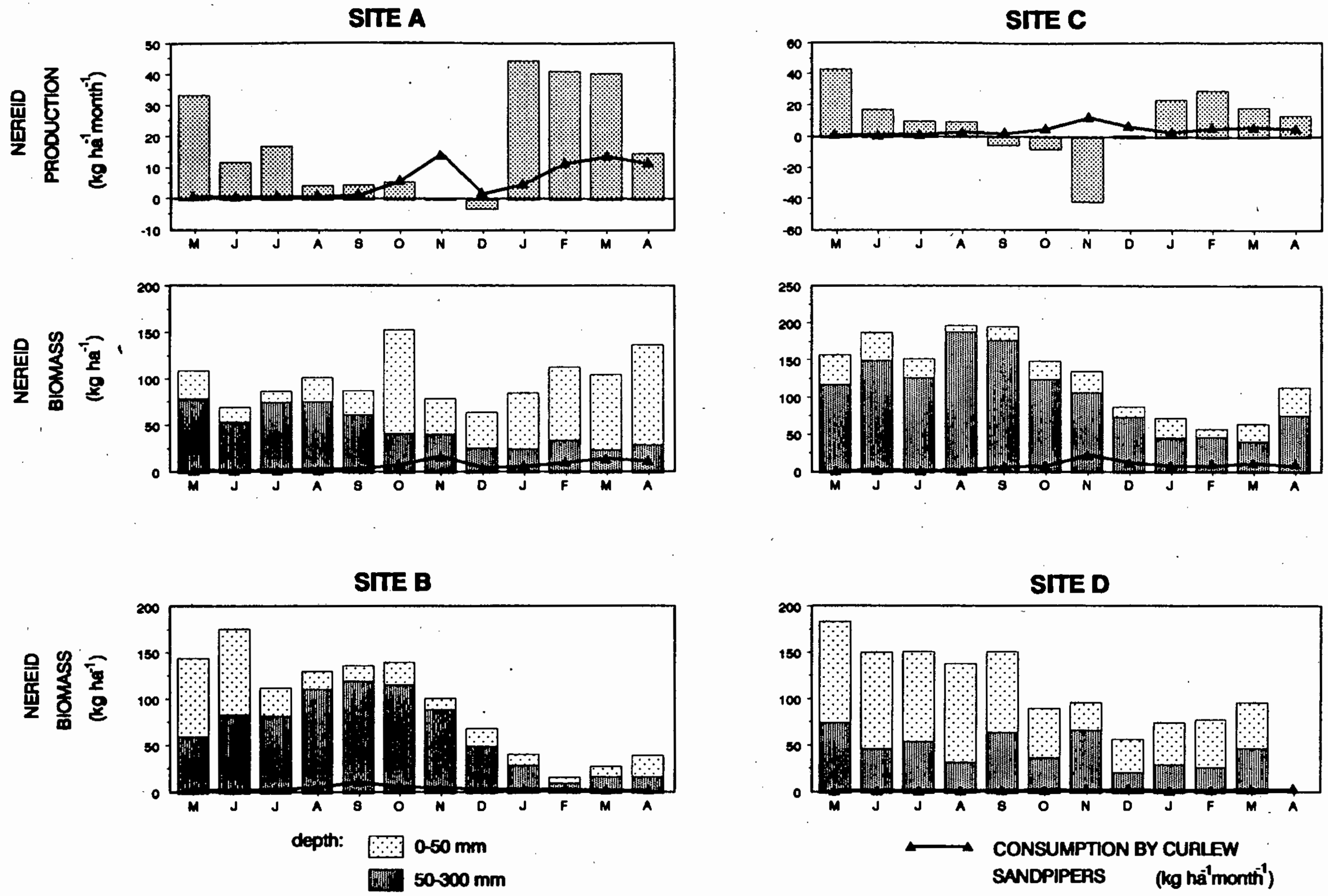


Figure 5.6. Production (kg ha^{-1} month^{-1}) and biomass (kg ha^{-1}) of nereid worms and their monthly consumption by Curlew Sandpipers (kg ha^{-1} month^{-1}) at four sites at the Berg River estuary.

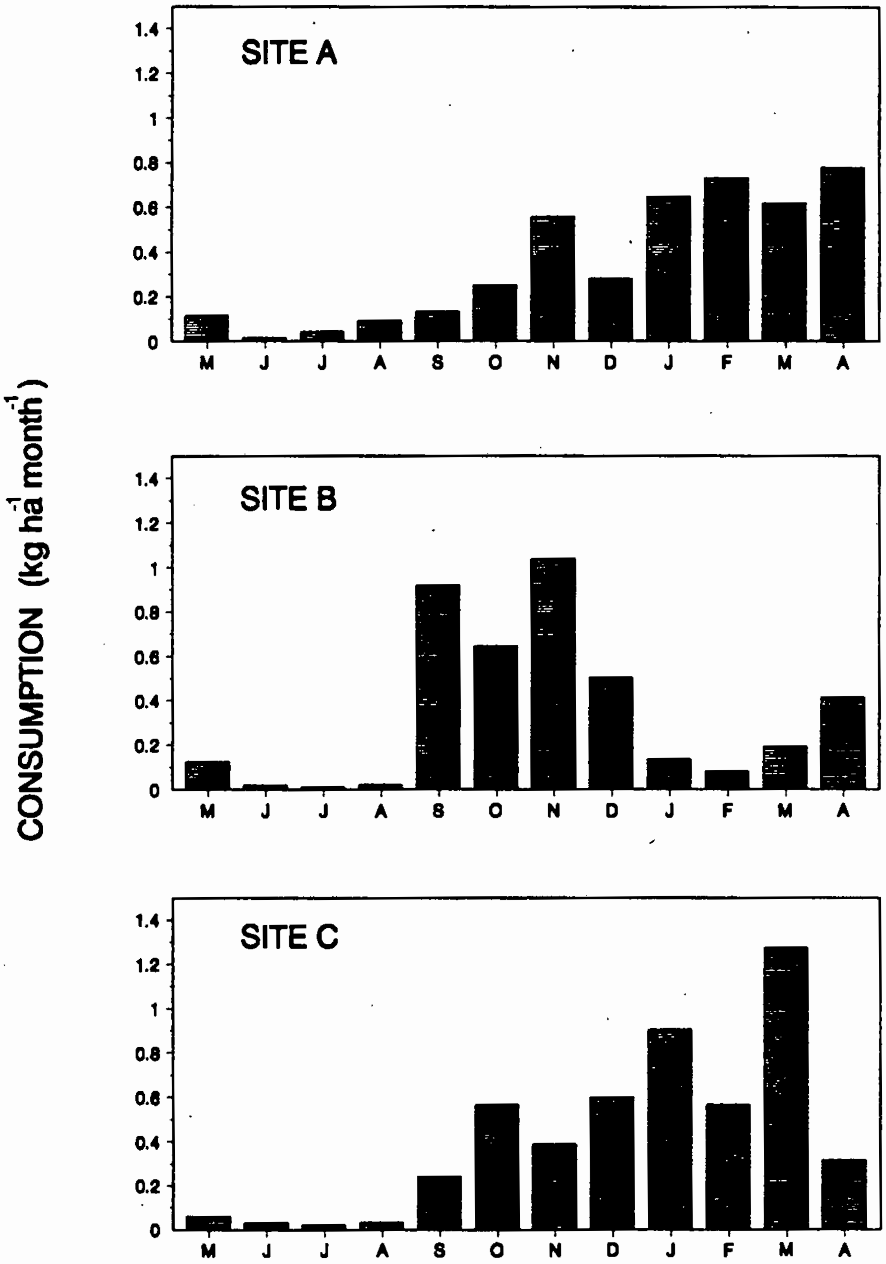


Figure 5.7. Energy intake per month (kg ha^{-1} month^{-1}) of Grey Plovers at three sites at the Berg River estuary.

Predation pressure by both Curlew Sandpipers and Grey Plovers at site B peaked earlier than at other sites (Figs 5.6 & 5.7), reflecting a seasonal redistribution of birds within the estuary (Chapter 7).

DISCUSSION

Foraging activities

The Berg River estuary lies very close to the southern limit of the Palearctic-Afrotropical flyway. The energetic cost of migration for birds which migrate this far is thus greater than for those which spend the nonbreeding season closer to their breeding grounds.

At the Berg River, the amount of nocturnal foraging by waders increases markedly during the pre-migration period when daylight foraging alone is apparently insufficient to meet the increased energy requirements for fat and protein deposition. A similar pre-migratory increase in the foraging activity of waders, both during the day and at night, is reported from the Banc d'Arguin, Mauritania (Zwarts *et al.*, 1990b). However, for small birds this increase was not readily detected in Mauritania because they foraged for nearly 100% of the available time throughout the nonbreeding season.

In post-migration time it is predictable that birds should also feed at night to recover from a long distance migration, but this did not happen at the Berg River estuary. The absolute values for night foraging activity used in this study must be interpreted cautiously since only one study site was monitored at night and the situation at other mudflats was assumed to be similar. Although some waders change foraging sites at night (Goss-Custard, 1969; Dugan, 1981), at the Berg River estuary there was no evidence to support this: Grey Plovers use the same foraging site both during the day and at night (pers. obs.).

On average, Curlew Sandpipers spent a high proportion of the available time foraging at the Berg River relative to other South African localities. Curlew Sandpipers spend only 68-84% of available daylight hours foraging at the Swartkops estuary (Martin, 1991), and at Langebaan Lagoon they forage for 55-65% of the available time during the summer (Puttick, 1979). Puttick (*op. cit.*) further showed that less efficient juvenile Curlew Sandpipers spend up to 80% of the available time foraging during the winter. Grey Plovers spent a similar amount of time foraging at the Berg River (75%) as at the Swartkops estuary (62-75%), whereas Greenshanks fed for less time at the Berg River (43-69%) than at the Swartkops estuary (71-84%) (Martin, 1991)

Differences in the amount of time spent foraging by any one species at different localities might be due to several factors influencing both the energy requirements of the birds at a particular time of the year or day and the rate at which these demands can be satisfied. The following environmental factors are likely to be important: duration of tidal exposure, prey type and availability, and weather conditions (Evans, 1976; Burger *et al*, 1977). Birds at site A at the Berg River estuary had to feed for longer than those at site C because their energy intake per unit time was lower (Table 5.5).

Although the duration of foraging by waders on tidal mudflats at the Berg River has been established in this study, theoretically the birds could forage for longer during the low tide period. There is a lag in the time of low water between the mouth of the river and mudflats farther upstream. Low tide at study site D is 2.5 hours earlier than at site A. Birds could move between the mudflats following the falling and rising tide and feed in the most profitable sites, profitability being determined to a large extent by the moisture content of the sediment. There are, however, no data at present with which to test this hypothesis.

Waders which spend the nonbreeding season in Europe spend most of the available daylight hours foraging (Goss-Custard, 1969; Baker, 1981; Pienkowski, 1982). Low winter temperatures result in high energy demands of birds at this time of the year (Evans, 1976). With shorter daylight hours in winter coupled with low prey availability, birds need to spend more time foraging than at other times of the year.

Night foraging efficiency

Although the seasonal pattern of nocturnal foraging activity is predictable, without knowing the intake rate of birds it is impossible to establish empirically the importance of nocturnal foraging. The intake rate of birds foraging at night on the Berg River is not known. Hulscher (1976) showed that food intake rates of European Oystercatchers *Haematopus ostralegus* were identical in daylight and in darkness. Evans (1976) and Pienkowski (1983a & b) found, as in this study, that pecking rates by Grey Plovers were lower at night than by day. They concluded that this implies a lower intake rate at night. On the other hand, Turpie & Hockey (in prep) found that although Grey Plovers at the Swartkops estuary took significantly fewer steps, and made fewer moves and pecks per minute at night than during the day, their net energy intake was similar at night and during the day.

There is evidence that the activity and hence availability of some invertebrate species may increase at night (Dugan, 1981; Pienkowski, 1983a; Hockey & Underhill, 1984; Evans, 1987). Additionally, the temperature at night is lower than during the day, reducing the rate at which mudflat sediments dry up when exposed. The movement of invertebrates, notably nereids, deeper into the substratum to avoid desiccation will presumably be correspondingly slow. Large nereids might thus be present closer to the surface for longer at night than during the day. In energetic terms, differences in the prey sizes available by night and day may offset differences in foraging rates. Dugan (1981) suggested that increased availability of nereids at night is sufficient to offset any decrease in intake rate due to poor visibility at night.

Some waders change their foraging behaviour from using predominantly visual cues during the day to predominantly tactile foraging at night (Evans, 1976; Sutherland, 1982; Robert & McNeil, 1989; McNeil, 1990). This might be a response to either increased availability or activity of prey at night, or to an inability of birds to detect prey visually at night. Alternatively, prey with luminescent properties may encourage birds to forage visually at night (Pienkowski, 1983a). At the Berg River, there was no evidence that either Grey Plovers or Curlew Sandpipers changed their foraging mode at night. Grey Plovers clearly used visual cues by day and night and Curlew Sandpipers foraged largely tactilely at all times. Curlew Sandpipers, however, changed their foraging microhabitats at night. Instead of dispersing uniformly over the exposed mudflat as during the day, they foraged exclusively at the water's edge on both falling and rising tides.

According to both Evans (1976) and Pienkowski (1982), predators hunting by sight are less efficient at night than during the day. If this is true, densities or pecking rate of visual foragers should be greater on moonlit than on moonless nights, with birds taking advantage of improved light conditions. At the Berg River estuary, foraging densities and foraging rates of Grey Plovers at night were independent of moon phase. Robert *et al* (1989) found that a higher proportion of time was spent foraging by small plovers on moonlit than moonless nights.

Energy balance

The apparently negative energy balance of some waders at the Berg River estuary throughout much of the austral summer suggests either that foraging efficiency is underestimated, or that birds are able to make up these deficits by foraging in other habitats during the periods when mudflats are inundated. It has been established that birds do use adjacent saltpans and saltmarshes as supplementary foraging grounds. High tide foraging is most pronounced in Curlew Sandpipers, Greenshanks, Little Stints and Ruffs (Velasquez & Hockey, in prep). Curlew Sandpipers may obtain up to 17% of their theoretical daily energy requirements from these supplementary feeding grounds (Velasquez & Hockey, in prep).

Large day-to-day variations in energy intake have been reported for Grey Plovers (Pienkowski, 1982) and European Oystercatchers (Hulscher, 1974) in Europe. In mid-winter, the daytime energy intake of Grey Plovers in Northumberland, U.K., falls to a minimum survival level even if the birds feed throughout the night (Pienkowski, 1982). The deficit in daylight energy intake by Grey Plovers during the winter months at the Tees estuary ranges between 37 and 93% of the theoretical energy requirements (Dugan, 1981; Nagy, 1987). The average daily energy consumption by Grey Plovers at the Swartkops estuary has been calculated as 125 kJ d^{-1} (Schramm, 1978) and 163 kJ d^{-1} (Martin, 1991), far below the expected value of 499 kJ d^{-1} (Nagy, 1987). Both studies estimated night feeding intake rate as 50% of daytime intake rate. However, subsequent work has found that nocturnal foraging of Grey Plovers on the same estuary is as efficient as daytime and birds do not experience a deficit in their daily energy intake (Turpie & Hockey, in prep). At the Berg River, Grey Plovers achieve an average daily intake of 315 kJ d^{-1} during the austral summer. Although this is still 37% below their theoretical energy requirement, it is well above the values reported from western Europe.

The daily energy intake of Curlew Sandpipers feeding on mudflats at the Berg River estuary (183 kJ d^{-1}) was close to values obtained at the Swartkops estuary (192 kJ d^{-1}) (Martin, 1991) and at Langebaan Lagoon (180 kJ d^{-1}) (Puttick, 1980). Puttick (*op. cit.*) reported similar seasonal fluctuations in the daily energy intake of Curlew Sandpipers to those found in this study. The estimated winter daily energy deficit at Langebaan Lagoon varied between 7 and 20%. This estimate includes energy derived from saltmarshes at high tide, which contributes up to 31% of the daily energy intake of these birds at Langebaan Lagoon. Puttick's (*op. cit.*) study assumed that Curlew Sandpipers did not forage at night. She concluded that although birds apparently had a negative energy balance in winter they did not spend all the available time foraging and therefore it is unlikely that they experienced a real energy deficit at this time. It is, however, likely that Curlew Sandpipers at Langebaan Lagoon experience digestive bottlenecks since prey with high inorganic matter to flesh ratio, such as gastropods and crabs, are a major portion of their diet (Puttick, 1978). Because the presence of inorganic matter may reduce a bird's digestive efficiency (Speakman, 1987; Zwarts & Blomert, 1990) Curlew Sandpipers may stop feeding for some time to allow the food to be processed.

Although the energy balance of shorebirds at the Berg River was negative during much of the austral summer, birds do better in terms of energy intake at the Berg River estuary than farther north. Additionally, the daily energy intake of birds might be underestimated since birds may take advantage of the 2.5 hour delay in the time of low tide between mudflats.

Both this and other studies have found, for several wader species, that daily energy intake, as derived from field observations of prey intake rates and foraging time regularly falls well below the predicted energy requirements of the birds. Kersten & Piersma (1987) have found that migratory waders have high basal metabolic rates. How these high BMRs relate to field metabolic rate is unknown. The negative energy budgets reported from field studies, however, suggest either that intake is consistently underestimated or that field metabolic rates are lower than predicted from standard equations. Regressions constructed to calculate daily energy requirements of birds (e.g. Nagy, 1987) do not take into account the fact that energy budgets vary on a seasonal basis in relation to factors such as temperature, breeding or migration.

Predation pressure by waders

It is impossible to produce a figure for total predation pressure by migratory waders at the Berg River estuary because not all species were studied in detail. The total theoretical consumption of invertebrates by migratory waders on the intertidal mudflats during the austral summer was calculated as 404 g ha^{-1} d^{-1} (5 851 kJ ha^{-1} d^{-1}), with a maximum consumption of 693 g ha^{-1} d^{-1} in February. These values are overestimates because, as has been shown, birds do not meet their daily energy requirements by feeding on the mudflats alone. Although the real figure is unknown, predation pressure by migratory waders at the Berg River is probably one of the highest on the East Atlantic Seaboard. Predation pressure by migratory waders in Europe varies between 8 g ha^{-1} d^{-1} in the Danish Wadden Sea and 81 g ha^{-1} d^{-1} in the Dutch Wadden Sea (Zwarts, 1988). The highest consumption reported previously on the East Atlantic coast, was 390 g ha^{-1} d^{-1} for intertidal mudflats at the Banc d'Arguin, Mauritania (Zwarts *et al.*, 1990b). Birds of body size 160-320 g (Greenshank, Grey Plover and Bartailed Godwit) contribute the most to the total predation by waders at the Banc d'Arguin. In Europe, on the other hand, larger waders, such as Oystercatchers and Curlews, are the most important consumers of the intertidal prey (Zwarts *et al.*, 1990b). This contrasts with the Berg River estuary where neither of the above groups makes a major contribution to the total predation pressure. Small waders of body size 40-80g, Curlew Sandpipers being the most important, accounted for up to 75% of the total predation. High predation pressure by the small-bodied waders at the Berg River estuary reflects the composition of the intertidal fauna on the mudflats, where small invertebrates, notably polychaetes and gastropods, are numerically dominant. High overall predation pressure at the Berg River estuary is paralleled by a high production of benthic invertebrates (87.59 g m^{-2} y^{-1}) (Chapter 2). Small-bodied, short-lived polychaetes and gastropods have a high turnover and account for 88% of the total production of invertebrates at the Berg River estuary (Chapter 2).

Although the amount of prey consumed by waders at the Berg River is large relative to other wetlands, it represents only 17% of the total production of invertebrate prey. The impact of migratory waders at the Berg River estuary falls within the range recorded at other South African localities, but is lower than those reported from some sites in western Europe (Table 5.11). The proportions of invertebrate production taken by Curlew Sandpipers and Grey Plovers are similar to those recorded at other South African sites (Tables 5.10 & 5.11).

Why do shorebirds migrate so far?

Energy budgets of breeding Semipalmated Sandpipers *Calidris pusilla* in Alaska were negative for the whole breeding season implying that birds rely heavily upon the food resources available on the nonbreeding grounds and at stop-over points during northward migration (Ashkenazie & Safriel, 1979). The predictability and abundance of food resources to the south of the breeding grounds may therefore play a key rôle in determining the choice of nonbreeding grounds and migration routes. One of the advantages of migration to the southern limits of Africa is the high production of benthic invertebrates. Three of the most important wintering grounds for migratory waders at the southern tip of Africa, Langebaan Lagoon (33°05'S,18°00'E), the Swartkops estuary (33°52'S 25°38'E) and the Berg River estuary have an exceptionally high production of benthic invertebrates (Fig 2.5 - Chapter 2). Additionally, maximal reproductive output of invertebrates coincides with the peak energy demand of birds just prior to migration. This contrasts with north temperate estuaries where benthic invertebrates do not reproduce until spring, when most migrant birds have departed. At high latitudes, scarce food resources during the winter may be further limited by accessibility. Several invertebrate species retreat deeper into the substratum when temperatures are low or winds are strong (Pienkowski, 1983a; Evans, 1979), and certain prey species contain less energy in winter than in summer (Beukema & de Bruin, 1977). Severe

Table 5.11. Impact of shorebirds on the standing stock or annual production of their prey populations at different localities.

Locality	Latitude	Predator	Prey	Impact	Period	Source
Ythan estuary, Scotland	57°N	shorebirds	intertidal invertebrates	36% of annual production	12 months	Baird *et al.*, 1985
Tees Estuary, England	54°N	shorebirds	small invertebrates	44% of annual production	6 months	Baird *et al.*, 1985
Lindisfarne, England	54°N	plovers	small invertebrates	13-22% of annual production	6 months	Baird *et al.*, 1985
The Wash, England	54°N	shorebirds	polychaetes	21% of annual production	6 months	Baird *et al.*, 1985
Wadden Sea, Netherlands	53°N	waders, gulls, Shelduck *Tadorna cana*	intertidal invertebrates	11% of annual production	12 months	Smit, 1981
Grevelingen estuary, Netherlands	52°N	shorebirds	intertidal invertebrates	6% of annual production	12 months	Baird *et al.*, 1985
Langebaan Lagoon, South Africa	33°S	Curlew Sandpiper *Calidris ferruginea*	invertebrates	20% of annual production	12 months	Puttick, 1980
Swartkops estuary, South Africa	34°S	shorebirds	mainly mud prawn *Upogebia africana*	14% of annual production	12 months	Martin, 1991
Swartkops estuary South Africa	34°S	Grey Plover *Pluvialis squatarola*	mainly mud prawn *Upogebia africana*	0.3% of annual production	12 months	Schramm, 1978
Berg River estuary South Africa	34°S	shorebirds	intertidal invertebrates	17% of annual production	12 months	This study

weather conditions also directly affect survivorship of overwintering birds (Pilcher, 1964; Davidson & Evans, 1982).

The benefits of less extreme weather conditions, more predictable food resources and a high production of intertidal prey in the southern hemisphere might counterbalance the high energetic costs and risks associated with long distance migration.

REFERENCES

Ashkenzie, S. & Safriel, U. N. 1979 Time-energy budget of the Semipalmated Sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology* **60** (4), 783-799.

Baker, J. M. 1981 Winter feeding rates of Redshank *Tringa totanus* and Turnstone *Arenaria interpres* on a rocky shore. *Ibis* **123**, 85-87.

Baird, D & Milne, H. 1981 Energy flow in the Ythan estuary, Aberdeenshire, Scotland. *Estuarine, Coastal and Shelf Science* **13**, 455-472.

Baird, D., Evans, P. R., Milne, H. & Pienkowski, M. W. 1985 Utilization by shorebirds of benthic invertebrate production in intertidal areas. *Oceanography and Marine Biology Annual Review* **23**, 573-597.

Beukema, J. J & de Bruin, W. 1977 Seasonal changes in dry weight and chemical composition of soft parts of the tellinid bivalve *Macoma balthica* in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* **11**, 42-55.

Burger, J., Howe, H. A., Hahn, D. C. & Chase, J. 1977 Effects of tide cycles on habitat partitioning by migrant shorebirds. *Auk* **94**, 743-758.

Bryant, D. M. 1979 Effect of prey density and site character on estuary usage by overwintering waders. *Estuarine and Coastal Marine Science* **9**, 369-384.

Davidson, N. C. & Evans, P. R. 1982 Mortality of Redshanks and Oystercatchers from starvation during severe weather. *Bird Study* **29**, 183-188.

Dugan, P. J. 1981 The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. In: *Feeding and Survival Strategies of Estuarine Organisms* (Jones, N. V. & Wolff, W. J., eds). Plenum Press, New York, pp 275-290.

Evans, P. R. 1976 Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. *Ardea* **64**, 117-139.

Evans, P. R. 1979 Adaptations shown by foraging shorebirds to cyclical variations in the activity or availability of their invertebrate prey. In: *Cyclic Phenomena in*

Marine Plants and Animals (Naylor, E. & Hartnoll, R. G., eds). Pergamon Press, Oxford, pp 357-366.

Evans, A. 1987 Relative availability of the prey of wading birds by day and night. *Marine Ecology - Progress Series* **37**,103-107.

Goss-Custard, J. D. 1969 The winter feeding ecology of the Redshank (*Tringa totanus*). *Ibis* **111**, 338-356.

Goss-Custard, J. D. 1977 The density of migratory and overwintering Redshank *Tringa totanus* and Curlew *Numenius arquata* in relation to the density of their prey in south-east England. *Estuarine and Coastal Marine Science* **5**, 497-510.

Hockey, P. A. R. 1984 Growth and energetics of the African Black Oystercatcher *Haematopus moquini*. *Ardea* **72**, 111-117.

Hockey, P. A. R. & Underhill, L. G. 1984 Diet of the African Black Oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related variation. *South African Journal of Zoology* **19**, 1-11.

Hulscher J. B. 1974 An experimental study of food intake of the Oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. *Ardea* **64**, 292-310.

Hulscher, J. B. 1976 Localization of cockles (*Cardium edule* L.) by the Oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. *Ardea* **64**, 292-309.

Kersten, M. & Piersma, T. 1987 High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea* **75**: 175-187.

Maclean, G. L. 1985 *Roberts' Birds of Southern Africa*. The Trustees of the John Voelcker Bird Book Fund, Cape Town.

Martin, A. P. 1991 Feeding ecology of birds on the Swartkops estuary, South Africa. Unpubl. PhD thesis. University of Port Elizabeth, Port Elizabeth, South Africa.

McNeil, R. 1990 Nocturnality in shorebirds. *Abstracts, Proceedings of XX International Ornithological Congress*, New Zealand.

Nagy, K. E. 1987 Field metabolic rate and food scaling in mammals and birds. *Ecological Monographs* **57**, 111-128.

Pienkowski, M. W. 1982 Diet and energy intake of Grey and Ringed Plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. *Journal of Zoology, London* **197**, 511-549.

Pienkowski, M. W. 1983a Changes in the foraging pattern of plovers in relation to environmental factors. *Animal Behaviour* **31**, 244-264.

Pienkowski, M. W. 1983b Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. *Marine Ecology - Progress Series* **11**, 141-150.

Pilcher, R. E. M. 1964 Effect of the cold weather of 1962-63 on birds of the north coast of the Wash. *Wildfowl* **15**, 23-26.

Puttick, G. M. 1978 The diet of the Curlew Sandpiper at Langebaan Lagoon, South Africa. *Ostrich* **49**, 158-167.

Puttick, G. M. 1979 Foraging behaviour and activity budgets of Curlew Sandpipers. *Ardea* **67**, 111-122.

Puttick, G. M. 1980 Energy budgets of Curlew Sandpipers at Langebaan Lagoon, South Africa. *Estuarine and Coastal Marine Science* **11**, 207-215.

Robert, M. & McNeil, R. 1989 Comparative day and night feeding strategies of shorebird species in a tropical environment. *Ibis* **131**, 69-79.

Robert, M., McNeil, R. & Leduc, A. 1989 Nocturnal feeding of shorebirds and other water birds in a tropical lagoon. *The Auk* **106**, 94-101.

Schramm, M. 1978 The feeding ecology of Grey Plover on the Swartkops estuary. Unpubl. B.Sc. Hons project. University of Port Elizabeth, Port Elizabeth, South Africa.

Smit, C. J. 1981 Production of biomass by invertebrates and consumption by birds in the Dutch Wadden Sea area. In: *Birds of the Wadden Sea* (Smit, C. J. & Wolff, W. J., eds). A. A. Balkema, Rotterdam, pp 290-297.

Speakman, J. R. 1987 Apparent absorption efficiencies for Redshank (*Tringa* *totanus* L.) and Oystercatcher (*Haematopus ostralegus* L.): implications of optimal foraging models. *American Naturalist* **130**, 677-691.

Summers, R. W. 1977 Distribution, abundance and energy relationships of waders (Aves: Charadrii) at Langebaan Lagoon. *Transactions of the Royal Society of South Africa* **42**, 483-495.

Sutherland, W. J. 1982 Do Oystercatchers select the most profitable cockles? *Animal Behaviour* **30**, 857-861.

Wolff, W. J., Gueye, A., Meijboom, A., Piersma, T. & Sall, M. A. 1975 Distribution, biomass, recruitment and productivity of *Anadara senilis* (L.) Mollusca: Bivalvia on the Banc d'Arguin, Mauritania. *Netherlands Journal of Sea Research* **21**, 243-254.

Zwarts, L. 1988 Numbers and distribution of coastal waders in Guinea-Bissau *Ardea* **76**, 42-55.

Zwarts, L. & Blomert, A. M. 1990 Selectivity of Whimbrels feeding on fiddler crabs explained by component specific digestibilities. *Ardea* **78**, 193-208.

Zwarts, L., Blomert, A., Ens, B. J., Hupkes, R. & van Spanje, T. M. 1990a Why do waders reach high feeding densities on the intertidal flats of the Banc D'Arguin, Mauritania? *Ardea* **78**, 39-52.

Zwarts, L., Blomert, A. & Hupkes, R. 1990b Increase of feeding time in waders preparing for spring migration from the Banc d'Arguin, Mauritania. *Ardea* **78**, 237-256.

CHAPTER 6

THE IMPACT OF PREDATION BY WADERS ON NEREID POPULATIONS - AN EXPERIMENTAL TEST

SUMMARY

Four bird exclosure cages and four adjacent controls were established on intertidal mudflats at the Berg River estuary to determine the impact of predation by waders on populations of the nereid worms *Ceratonereis keiskama* and *C. erythraeensis*, the most important prey for the majority of waders. The experiment ran from January to April 1989. The use of exclosure cages was validated by direct observations of predation intensity.

An analysis of the stomach contents of southern mullet *Liza richardsonii* excluded them as potential predators of nereids. Direct observations on the use of control areas by birds showed that Curlew Sandpipers *Calidris ferruginea* were the most important avian predators and consumed, on average, 36% of *C. keiskama* numbers per month. This contrasts with the removal of 14% of *C. keiskama* numbers per month when the feeding intensity of birds was integrated over a larger area. The latter estimate was close to the rate of nereid depletion in the substratum.

The exclusion experiment revealed that the numbers and biomass of both *Ceratonereis* spp. in paired controls and exclosures tracked each other and did not diverge as predicted. The lack of such divergence was attributed to biological interactions inside the cages which masked the depletion caused by predators in the control areas.

INTRODUCTION

Shorebirds are important secondary consumers in many estuaries, and several studies have attempted to assess the impact that these birds have on invertebrate prey populations. Such impact can be assessed by direct observation of prey removal (Baird *et al.*, 1985; Chapter 5), calculations of removal based on the density and energy demands of the birds (Chapter 1) or through the use of cages to exclude birds from feeding areas (Quammen, 1984; Marsh, 1986; Raffaelli & Milne, 1987). Although the latter technique is perhaps the most empirical, interpreting the results of caging experiments requires caution (Virnstein, 1978) and results obtained from experiments to date are inconsistent. Using cages, Kent & Day (1983) in Australia and Raffaelli & Milne (1987) in England concluded that predation by waders did not affect the population density of invertebrates. In contrast, Bengtson (1976), Boates & Smith (1979), Evans *et al.*, (1979), Schneider & Harrington (1981) and Quammen (1984) showed that a considerable reduction in prey density was caused by shorebirds. In all these studies, differences between invertebrate populations inside and outside cages were assumed to reflect predation by shorebirds.

Predation intensity (prey biomass removed per unit area per unit time) by shorebirds at the Berg River estuary is among the highest on the East Atlantic Seaboard. Although birds at the Berg River estuary consume a considerable proportion of the annual invertebrate production, their numbers are apparently not limited by food resources (Chapter 5).

The aim of this study was to quantify the impact of predation by waders on populations of nereid polychaetes, the most important prey for the majority of waders on the estuary. Extrapolation from direct observations of predation intensity is validated empirically by the use of exclosure cages.

METHODS

An exclosure experiment was initiated in August 1988. However, due to exceptionally heavy deposition of the filamentous alga, *Cladophora* sp., on the estuary in the following months, this experiment was abandoned and restarted in January 1989 when most algae had been flushed from the estaury.

Design of the exclosure experiment

The experiment was established in an area which satisfied the following criteria: high bird and prey densities, low vegetation cover, low water movement and low human disturbance.

Four exclosure cages (A, B, C and D), each 3 m away from an adjacent control area of equal size, were established at mudflat A (Fig 1.1). The exclosure cages were designed to exclude both birds and fish. They were made from a galvanized steel frame, covered with stretched 10 mm aperture fishing mesh. Each measured 3 x 3 x 0.2 m. The tops of the cages could be opened for sampling the invertebrates inside. Control areas were marked with four stakes only. Exclosures were regularly cleaned of algae and floating debris.

Four randomly-placed core samples 60 mm in diameter and 300 mm deep were taken from each exclosure and control monthly. In order to avoid edge effects, no cores were taken within 0.35 m of the edge of any exclosure cage.

One way analysis of variance was used to compare difference in invertebrate density between and within treatments. To minimize the effect of within-treatment variability, each of the replicates was analyzed separately.

Direct observations of predation intensity

An area of 2 000 m^2 (80 x 25 m), which included the control areas, was established and birds foraging within this area were observed through a 22 x telescope during the period of tidal exposure. Birds were observed from a hide placed 15 m away from the edge of the study site. Observations were made during one full tidal cycle in January and two each in February and March. The number of birds foraging within the controls and on the entire study site was recorded at 20 minute intervals. Feeding activities of birds were recorded during 60 second observation periods. The number of prey taken per minute (success rate) was recorded for the most abundant migrant waders on the study site: Curlew Sandpipers, Grey Plovers and Ringed Plovers.

The nereid polychaetes, *Ceratonereis keiskama and C. erythraeensis* are the most important prey for the majority of waders (Chapter 4). It was therefore assumed that the impact of bird predation will be most apparent in these two nereids. Although Little Stints were common on the study area, they rarely eat nereids (Chapter 4) and were excluded from analyses.

The number of foraging birds in each control during activity scans was multiplied by 20 and summed over the whole observation period to give the total foraging time per control in bird-minutes per day. This value was then multiplied by the average intake rate of birds and the number of days in each month to give a total numerical prey intake per month. No data were collected on the intake rate of Kittlitz's Plovers, and their foraging performance was considered equal to that of Ringed Plovers.

Predation by fish was quantified by examining their diet. A total of 68 southern mullets were collected in October, December and March 1989/90. Their digestive tracts were immediately removed and preserved in 10% formalin for subsequent analysis.

RESULTS

Predation by waders

The density of waders in the study area was high (Table 6.1). Curlew Sandpipers are the most abundant wader on the estuary as a whole, and potentially are the major consumers of invertebrates. Their density on the study site ranged between 134 birds per hectare in January and 76 birds per hectare in February. Despite this high density on the study site, the numbers of birds foraging in the control areas were low (Table 6.2). The maximum number of Curlew Sandpipers visiting a single control area throughout the whole low tide period was eight birds, and the maximum time they spent foraging inside the control was 21% of the available foraging time.

Overall, all birds removed 5 702 ± 475 (SE) nereids per m^2 between January and March (Table 6.3). This is equivalent to 11.74 ± 1.79 g (dry weight) per m^2. The heaviest predation by birds occurred in control A, where more than 7 000 nereids, equivalent to 16.75 g (dry weight) per m^2 were removed during the study period. The heaviest predation by birds in all controls occurred in January when Curlew Sandpipers alone removed an average of 1 756 ± 239 (SE) nereids, equivalent to 2.17 ± 0.29 g (dry weight), per m^2.

Predation by fish

There was no obvious seasonal variation in the diet of mullets. Of the 68 fish sampled, only one contained a jaw of *C. erythraeensis*, four contained isopods *Paridotea ungulata* and fourteen contained plant material. The remaining stomachs were either empty or were filled with sand and well digested plant tissue.

Table 6.1. Average foraging density and duration of migrant and resident waders at the 2 000 m^2 study site in January, February and March.

	January		February*		March*	
	Numbers ha^{-1}	Bird foraging minutes	Numbers ha^{-1}	Bird foraging minutes	Numbers ha^{-1}	Bird foraging minutes
Migrant waders						
Curlew Sandpiper	134.2	9660	75.9	5310	131.5	8150
Little Stint	22.5	1620	42.6	2980	79.0	4900
Ringed Plover	40.0	2880	46.9	3280	13.1	810
Grey Plover	7.5	540	0.6	20	5.6	350
Greenshank	0.0	0	7.5	240	0.0	0
Knot	0.0	0	0.0	0.0	7.5	240
Sand Plover	0.0	0	3.8	120	1.0	30
Mongolian Plover	0.0	0	1.3	40	0.0	0
Bartailed Godwit	0.0	0	0.6	20	0.0	0
Terek Sandpiper	0.0	0	0.0	0	0.3	30
Resident waders						
Kittlitz's Plover	25.3	1820	25.7	1800	1.9	60
Whitefronted Plover	1.4	100	0.0	0	0.3	10
Chestnutbanded Plover	0.0	0	0.9	30	0.0	0

* Average for the month

Table 6.2. Average number (N) of Curlew Sandpipers, Little Stints, Grey, Kittlitz's and Ringed Plovers and bird foraging minutes per month (F) in controls A, B, C and D (each of 9 m^2) in January, February and March.

		JANUARY				FEBRUARY*				MARCH*			
CONTROLS		A	B	C	D	A	B	C	D	A	B	C	D
Curlew Sandpiper	N	0.33	0.28	0.22	0.33	0.10	0.06	0.39	0.29	0.23	0.43	0.10	0.18
	F	120	160	80	120	30	20	100	100	60	120	30	70
Little Stint	N	0.11	0.28	0.17	-	0.33	-	0.07	0.20	0.03	0.26	0.04	0.08
	F	40	100	60	120	100		10	60	20	80	10	20
Grey Plover	N	-	-	-	-	0.03	0.05	-	-	-	-	0.03	-
	F					10	10					10	
Ringed Plover	N	0.28	-	0.01	-	0.12	0.08	0.18	0.12	-	-	-	-
	F	100		20		60	30	80	50				
Kittlitz's Plover	N	-	0.01	-	-	0.08	-	0.03	0.03	-	-	-	-
	F		20			20		10	20				

* Average for the month

Table 6.3. Numbers (m^{-2}) and biomass ($g\ m^{-2}$) of *Ceratonereis keiskama* and *C. erythraeensis* consumed by Curlew Sandpipers, Grey Plovers and *Charadrius* spp. in four controls (A, B, C and D), each of 9 m^2, in January, February and March.

Controls	A		B		C		D	
	Numbers m^{-2}	Biomass $g\ m^{-2}$	Numbers m^{-2}	Biomass $g\ m^{-2}$	Numbers m^{-2}	Biomass $g\ m^{-2}$	Numbers m^{-2}	Biomass $g\ m^{-2}$
JANUARY								
Curlew Sandpiper	1 757	2.17	2 342	2.89	1 171	1.45	1 757	2.17
Grey Plover	*		*		*		*	
Charadrius spp.	2 800	8.38	463	1.68	463	1.68	*	
FEBRUARY								
Curlew Sandpiper	494	0.61	329	0.41	1 649	2.04	1 649	2.04
Grey Plover	251	0.91	251	0.91	*		*	
Charadrius spp.	920	3.33	460	1.67	1 227	4.44	767	2.78
MARCH								
Curlew Sandpiper	859	1.55	1 719	3.10	430	0.78	1 003	1.81
Grey Plover	*		*		45	0.16	*	
Charadrius spp.	*		*		*		*	

* no birds present

Changes in nereid density

Seventeen invertebrate species were recorded in either cages or control areas during the course of the experiment (Table 6.4).

Considerable changes in the density of both *C. keiskama* and *C. erythraeesis* took place in all treatments (Fig 6.1). Although the density of *C. keiskama* decreased with time in all treatments except exclosure C, this decrease was significant only in exclosures A and D (Fig 6.1 & Table 6.5). There was a significant difference in the initial density of *C. keiskama* in cage and control D ($F=15.83$, $p<0.007$). There was also a significant difference in the density of this species between cage and control B in February and March ($F=8.74$, $p<0.03$; $F=26.23$, $p<0.03$, respectively), but not in April. At the end of the experiment there were significant differences in the density of *C. keiskama* in cages and controls A and C ($F=7.94$, $p<0.003$; $F=6.05$, $p<0.05$, respectively).

There was an increase in the density of *C. erythraeensis* in all treatments due to reproduction (Fig 6.1, Chapter 3). This increase was significant in all treatments except control D (Table 6.5). Generally, the pattern of increase was consistent within and between the treatments. A significant difference in the density of *C. erythraeensis* was recorded in January, February and April between cage and control A ($F=6.00$, $p<0.05$; $F=5.67$, $p<0.05$; $F=6.19$, $p<0.05$, respectively), and in March between cage and control D ($F=7.74$, $p<0.03$).

Although the density of *C. keiskama* decreased simultaneously with the increase in abundance of *C. erythraeensis*, particularly in the cages, there was no significant correlation between the densities of these two species ($r=-0.04$, $p>0.05$).

Table 6.4. Invertebrates recorded during the experiment on the intertidal mudflats at the Berg River estuary.

ANNELIDA	**ARTHROPODA**		**MOLLUSCA**
Ceratonereis keiskama	**Isopoda**	**Amphipoda**	*Hydrobia* sp.
C. erythraeensis	*Exosphaeroma hyloecetes*	*Melita zeylanica*	
Boccardia sp.	*Paridotea ungulata*	*Orchestia* sp.	
Capitella capitata	*Leptanthura* sp.		
Prionospio sexoculata		**Brachyura**	
Desdemona ornata	**Anomura**	*Hymenosoma orbiculare*	
	Callianassa kraussi	*Thaumastoplax spiralis*	
	Upogebia capensis		
		Insecta	
		Circulionidae	

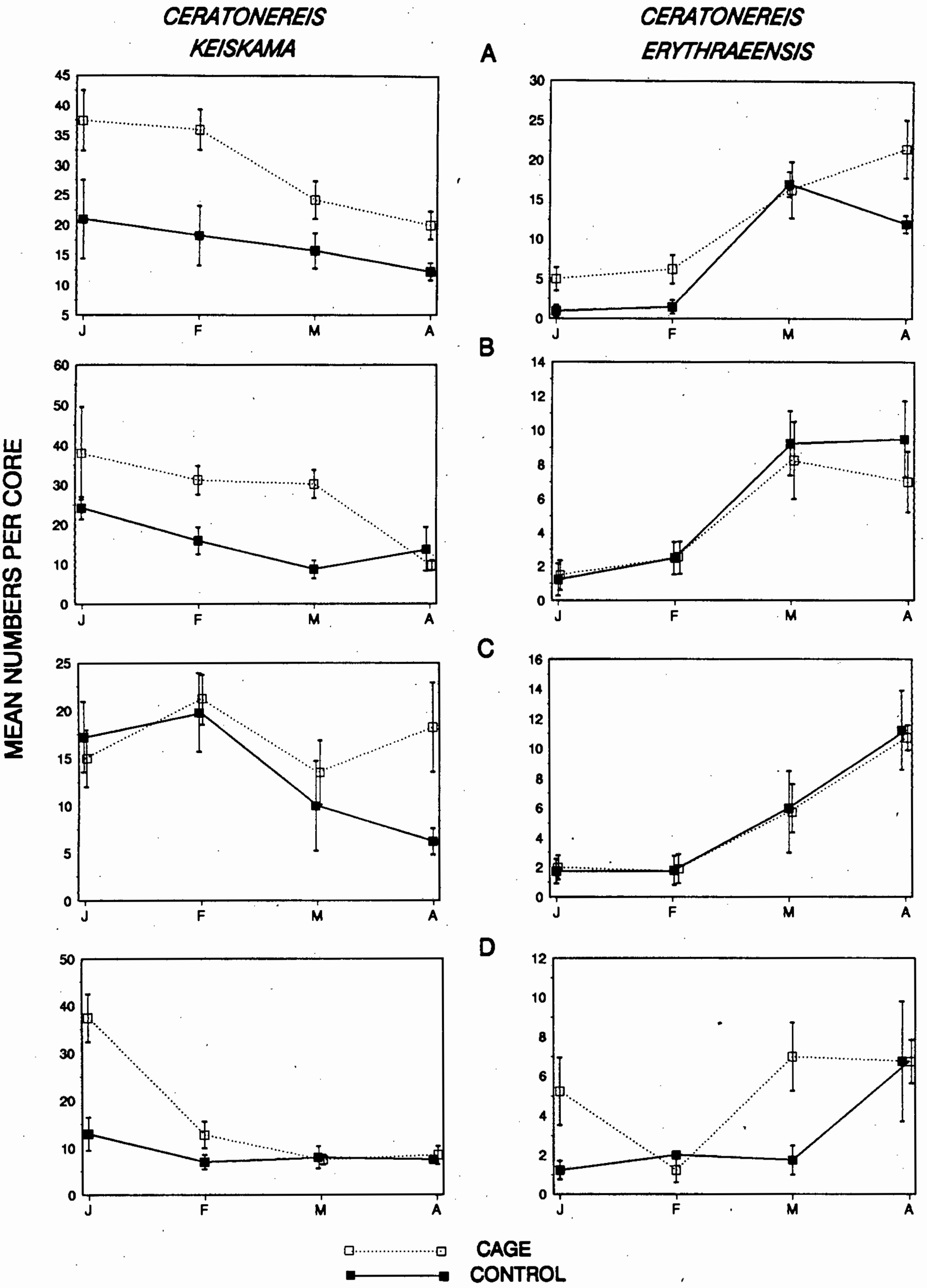


Figure 6.1. Mean numbers of *Ceratonereis keiskama* and *C. erythraeensis* per core (37.39 cm^2) in cages and controls A, B, C and D from January to April.

Table 6.5. Significance levels of differences in the density of *Ceratonereis keiskama* and *C. erythraeensis* within treatments A, B, C and D between January, February, March and April. In all cases df=3, 12.

	CAGES				CONTROLS			
	A	B	C	D	A	B	C	D
Ceratonereis keiskama								
	$F=5.71$ $p<0.01$	n.s.	n.s.	$F=21.07$ $p<0.001$	n.s.	n.s.	n.s.	n.s.
Ceratonereis erythraeensis								
	$F=8.08$ $p<0.003$	$F<4.44$ $p<0.03$	$F=7.32$ $p<0.005$	$F=3.75$ $p<0.04$	$F=51.03$ $p<0.001$	$F=7.27$ $p<0.005$	$F=7.28$ $p<0.005$	n.s.

Changes in the population structure of nereids

There were changes in the population structure of both *Ceratonereis* species with time but these were not consistent within or between the treatments (Fig 6.2 - 6.5). A higher proportion of small *C. keiskama* occurred in controls A and B than in the adjacent cages at the end of experiment (April) and the reverse was true for treatments C. Recruitment of *C. erythraeensis* in cages A and D occurred earlier (February and March, respectively) than in the adjacent controls.

Changes in nereid biomass

There were marked monthly changes in the biomasses of both nereid species within and between the treatments but without a consistent pattern (Fig 6.6). There was a gradual increase in the total biomass of *C. keiskama* in cages A and B within the first three months of the experiment, which coincided with a decrease in their abundance. This might reflect a rapid growth of younger individuals and little mortality of older animals inside the cages in contrast to adjacent controls, where predation resulted in decreases in nereid abundance and biomass. At the end of the experiment, the biomass of *C. keiskama* in cages A and C had increased by 34% and 64% of the initial biomass, respectively. This contrasts with a decrease in biomass in the adjacent controls by 9% and 23%, respectively. This discrepancy reflects differences in the size structure of nereids between the treatments.

There was a substantial increase in the biomass of *C. erythraeensis* in April in all treatments, reflecting an increase in abundance of recruits (Chapter 3). The greatest increase in the biomass of this species occurred in cage and control B (350% and 552% of the initial biomass, respectively). There was a decrease in the total biomass in cage and control D in the end of the experiment by 37% and 35%, respectively.

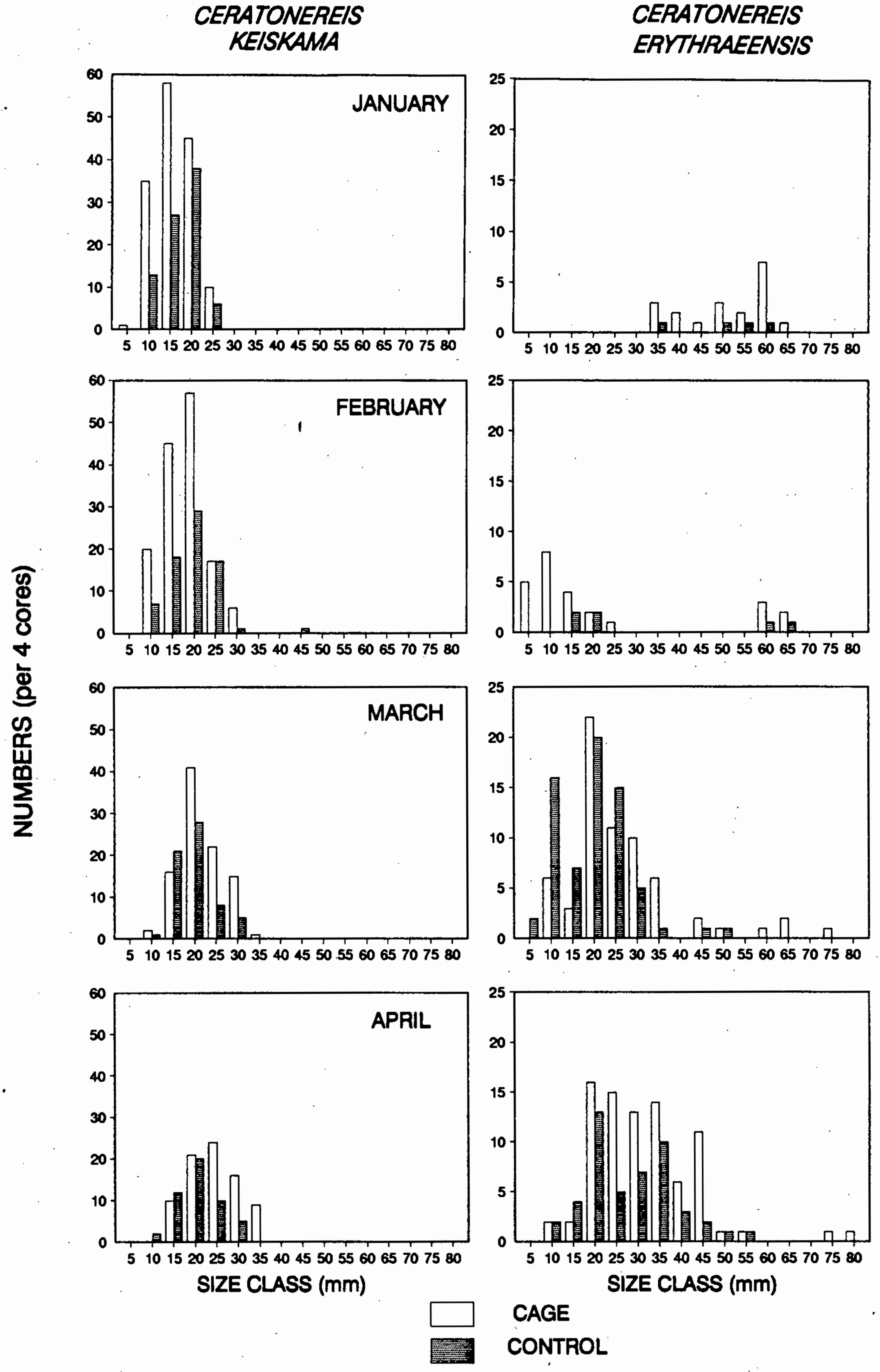


Figure 6.2. Size distribution of *Ceratonereis keiskama* and *C. erythraeensis* in cage and control A from January to April.

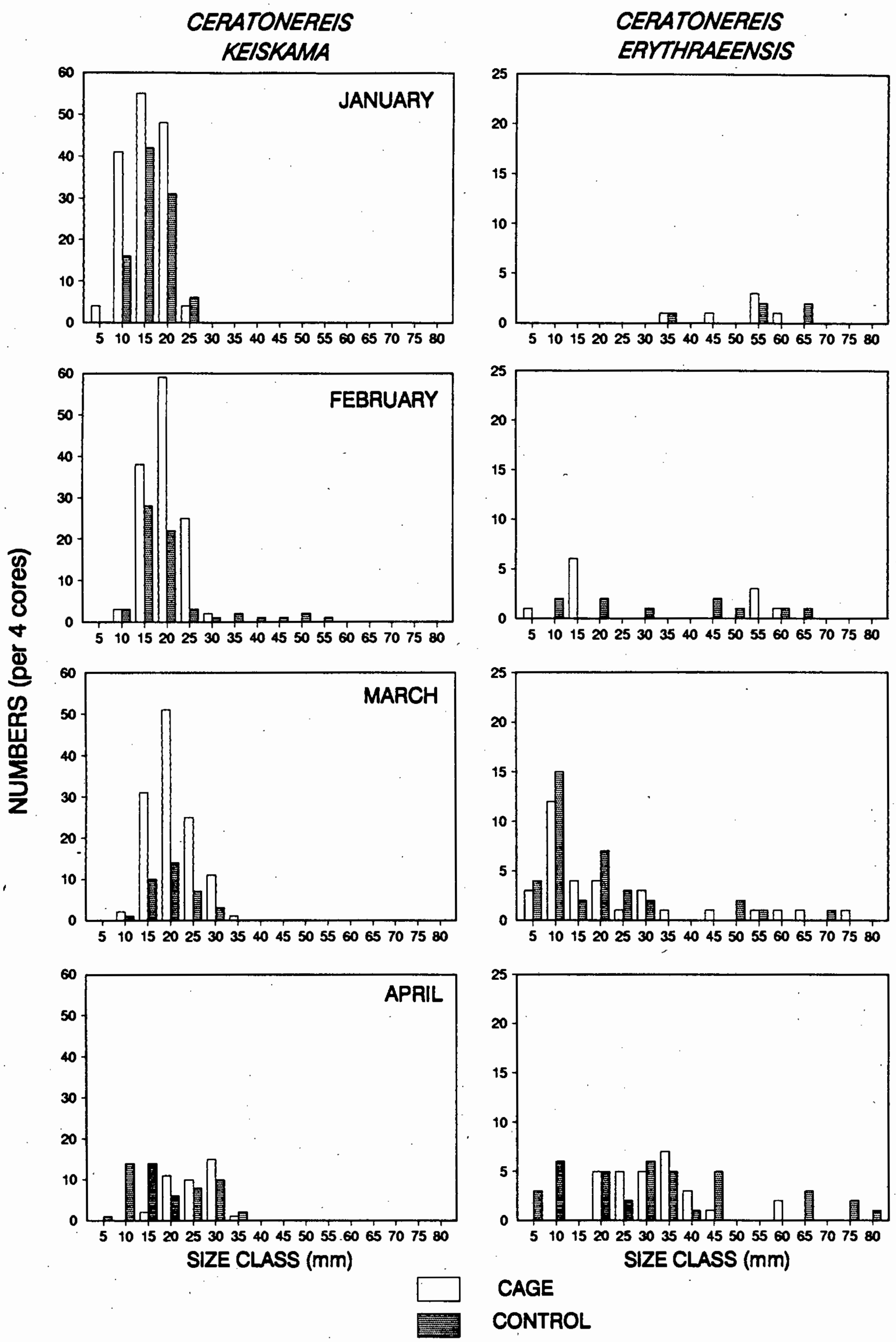


Figure 6.3. Size distribution of *Ceratonereis keiskama* and *C. erythraeensis* in cage and control B from January to April.

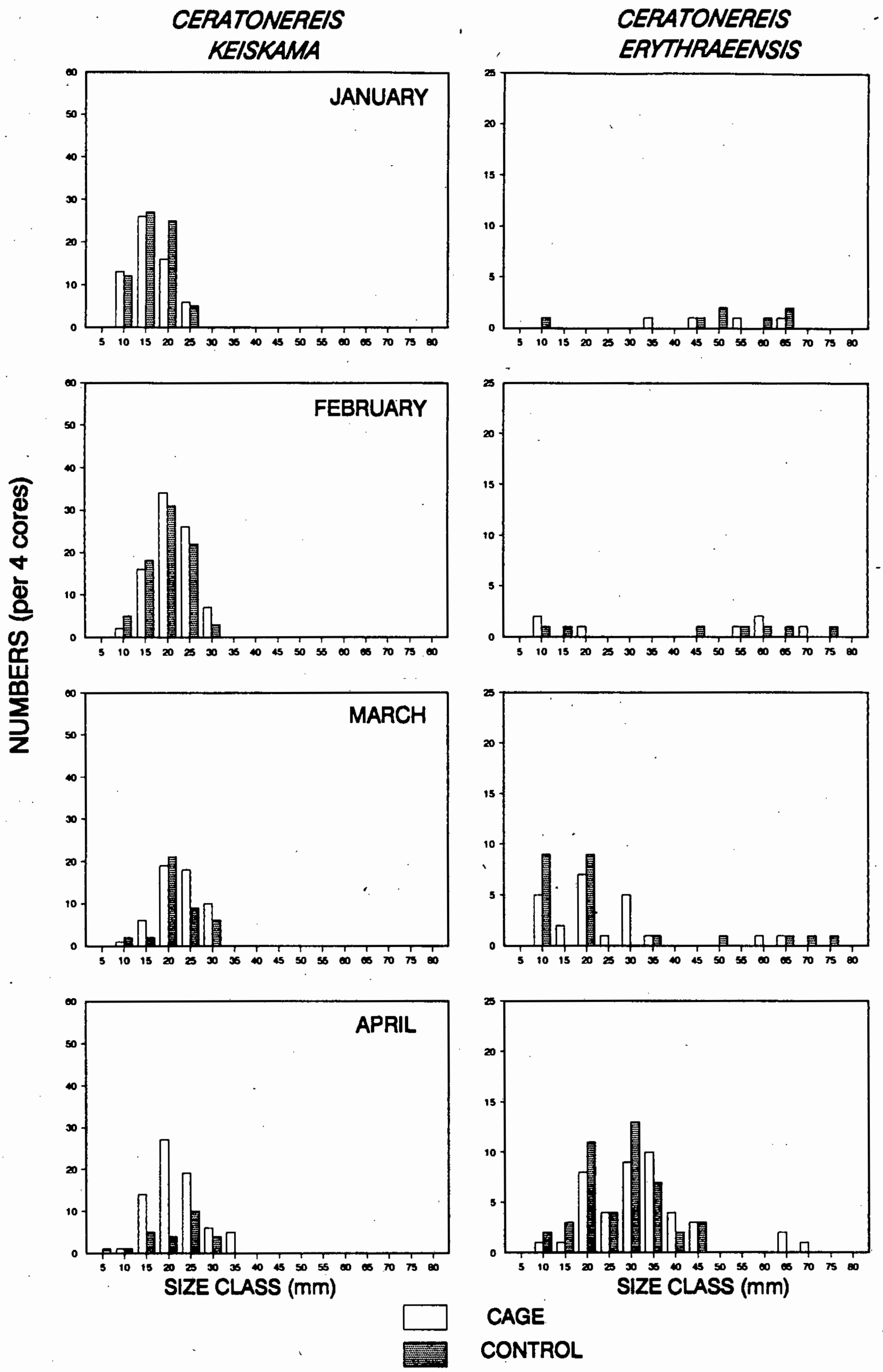


Figure 6.4. Size distribution of *Ceratonereis keiskama* and *C. erythraeensis* in cage and control C from January to April.

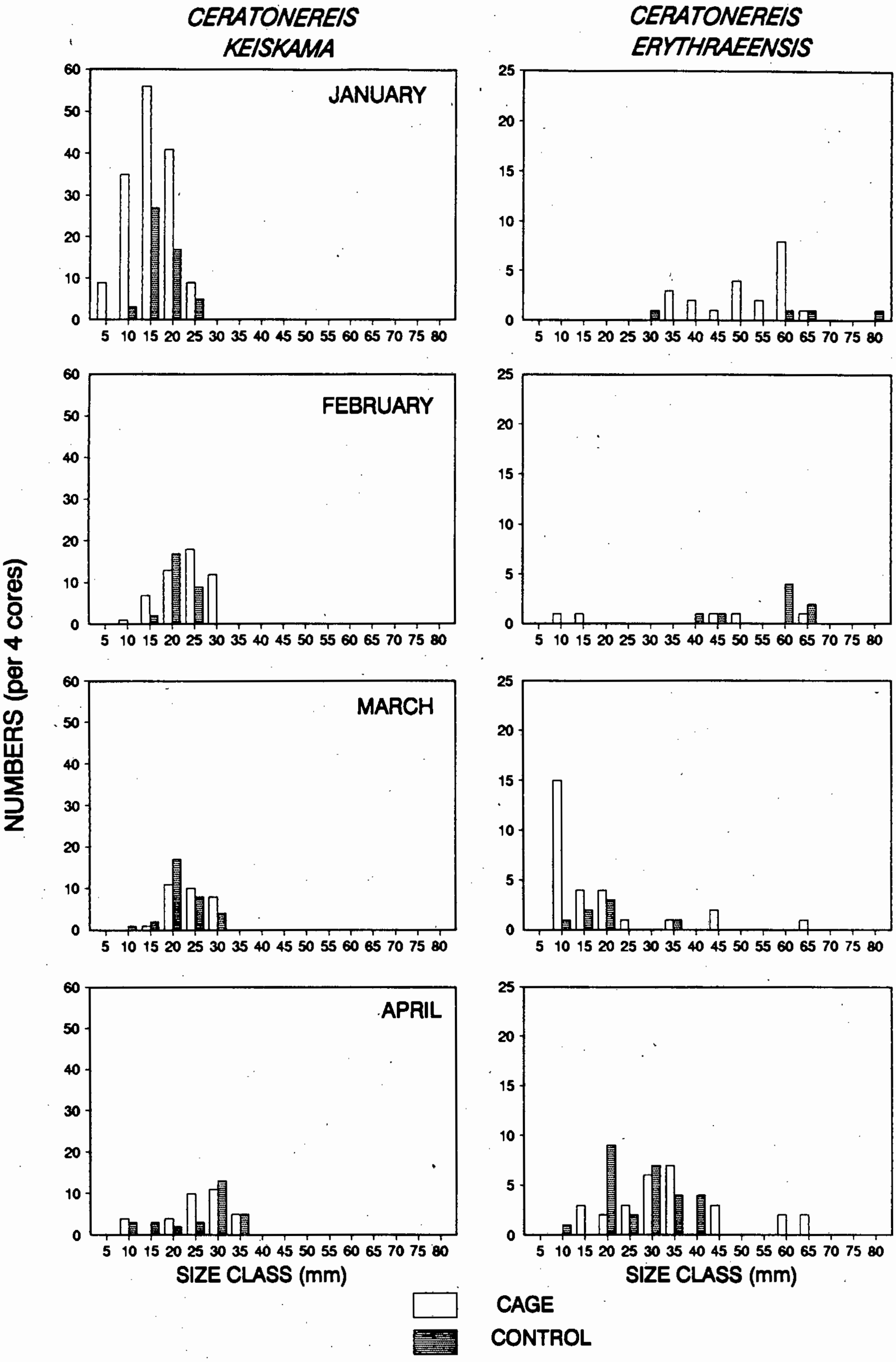


Figure 6.5. Size distribution of *Ceratonereis keiskama* and *C. erythraeensis* in cage and control D from January to April.

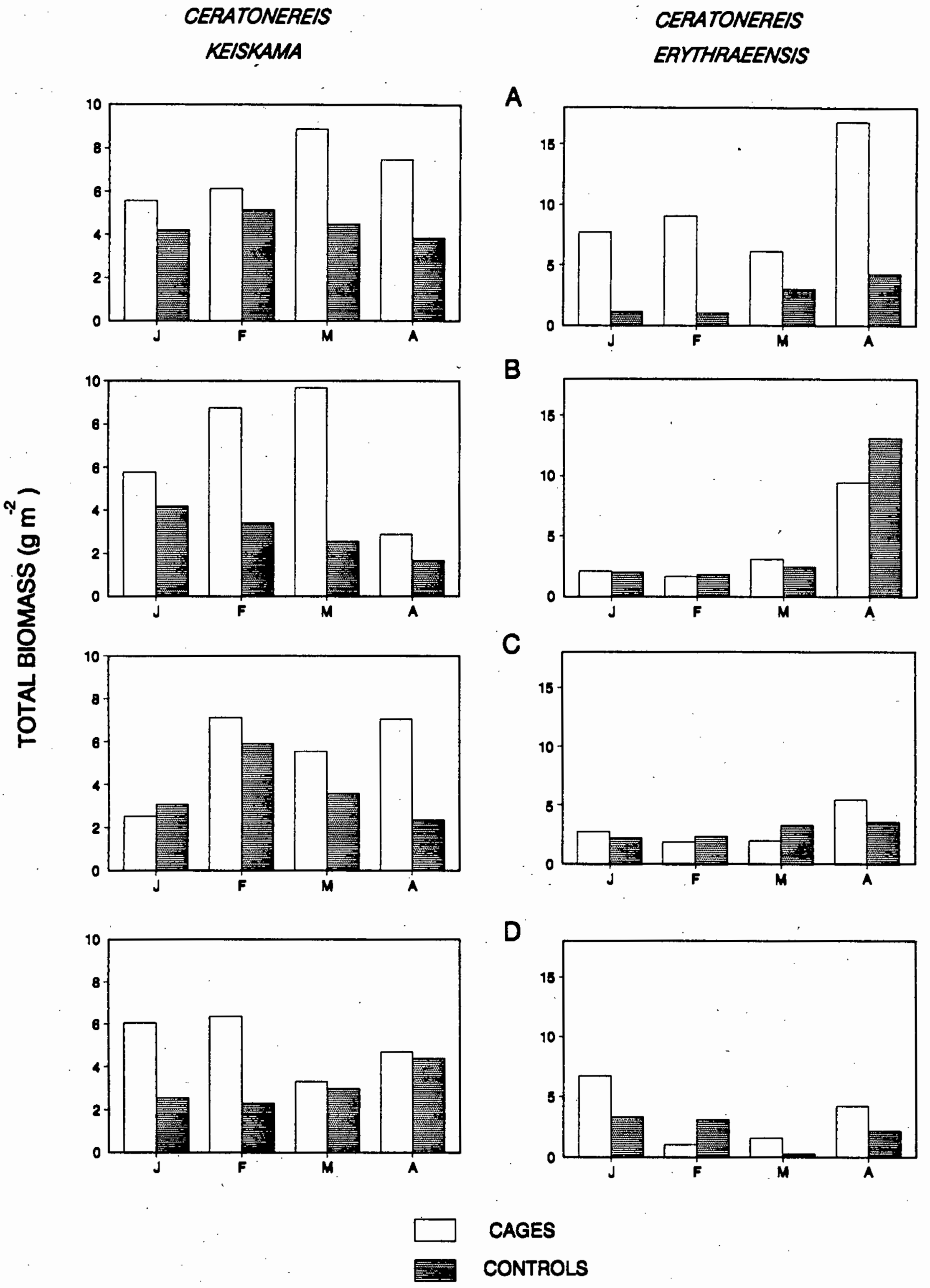


Figure 6.6. Total biomass (g m^{-2}) of *Ceratonereis keiskama* and *C. erythraeensis* in all cages and controls from January to April.

Proportion of nereid numbers and biomass removed by birds

Although the direct observations allow calculation of the total numerical consumption of nereids by all bird species, accurate determination of the proportion of nereid numbers and biomass removed by birds could only be made for Curlew Sandpipers. All plovers feed on both *Ceratonereis* spp. and take them in differing proportions which, in the experimental area, are unknown. By contrast, Curlew Sandpipers feed almost exclusively on *C. keiskama* and therefore the removal of nereids by this species could be related to changes in the abundance and biomass of *C. keiskama* in the substratum.

Curlew Sandpipers removed an average of 36 ± 7.1% (SE) of the numerical standing stock of *C. keiskama* per month, equivalent to 53 ± 9.5% (SE) of their biomass (Table 6.6). The highest proportion of *C. keiskama* numbers and biomass was removed monthly by Curlew Sandpipers at control D - 61.8 ± 13.2% (SE) of *C. keiskama* numbers and 77.5 ± 8.8% of biomass.

DISCUSSION

The experiment at the Berg River estuary was carried out during the pre-migration period when the energy demands of birds are maximal (Chapter 5). Waders occur at their highest density on the estuary at this time of the year (Chapter 1) and their foraging rate is high due to their increased energy requirements prior to migration. Despite this, however, the expected level of prey depletion due to predation was not detected in the caging experiment. The patterns of numbers of both *Ceratonereis* spp. in paired controls and cages tracked each other, and there was a general tendency for *C. keiskama* to decrease in numbers and *C. erythraeensis* to increase in numbers in all treatments. This pattern can be explained in terms of the life-history

Table 6.6. Mean numbers (N) (m^{-2}) and biomass (B) ($g\ m^{-2}$) of *Ceratonereis keiskama* and the percentage removed by Curlew Sandpipers in controls A, B, C and D in January, February and March.

	JANUARY				FEBRUARY				MARCH			
	Ceratonereis keiskama		Curlew Sandpiper		*Ceratonereis keiskama*		Curlew Sandpiper		*Ceratonereis keiskama*		Curlew Sandpiper	
Control	N m^{-2}	B $g\ m^{-2}$	N % removed	B	N m^{-2}	B $g\ m^{-2}$	N % removed	B	N m^{-2}	B $g\ m^{-2}$	N % removed	B
A	5616	4.23	31.3	51.3	4880	5.15	10.1	11.8	4212	4.50	20.4	34.4
B	6351	4.19	36.1	68.0	4279	3.41	7.7	12.0	2340	2.56	73.5	117.0
C	4613	3.10	25.4	46.8	5282	5.93	31.2	34.4	2674	3.62	16.1	21.6
D	3476	2.58	50.5	84.1	1872	2.31	88.1	88.3	2139	3.01	46.9	60.1

patterns of these nereids. In addition, two independent estimates of avian predation on nereid populations, one obtained through direct observation and the other from invertebrate samples, were inconsistent. From direct observation, the proportion of *C. keiskama* removed by Curlew Sandpipers over the three months of the experiment was almost twice as high (80.5 ± 15.9%, SE, of the initial numbers - Table 6.6) as the measured reduction in density (42.0 ± 7.9% - Fig 6.1). Direct observations also indicated that the numbers of nereids removed by Curlew Sandpipers in control D, exceeded the initial standing crop by 17%. The impact of predation calculated from direct observations is therefore likely to be an overestimate. The source of this error is probably the assumptions made in estimating bird foraging time from counts made in a small area of 9 m^2 at 20 minute intervals. As a comparison with this method, nereid consumption by birds was calculated using counts of the foraging density of birds in the larger study area of 2 000 m^2 (Table 6.1). Using this method, over the three month period, birds were estimated to remove a total of 2 521 nereids per m^2 (Table 6.7). This is 44% of the predation intensity calculated using birds foraging only in the control areas. Curlew Sandpipers alone removed 13.6 ± 2.58% (SE) of the initial *C. keiskama* numbers, equivalent to 20.5 ± 4.73% of their biomass per month. Over the whole study period, using corrected bird densities, Curlew Sandpipers were estimated to remove 31% of the initial numbers of *C. keiskama*. This is much closer to the observed decrease in prey density of 42%. The 11% difference between these two figures may be due to predation by other bird species. Nocturnal foraging is not considered in the estimates, although it is known that birds feed at night (Chapter 5).

This study has shown that although direct observations are a valuable tool in assessing the impact of bird predation, caution must be taken in planning, conducting and interpreting the results of such estimates. Bengtson (1976) in a similar cross-validation of the two methods, found little difference between the consumption by Golden Plovers *Pluvialis apricaria* calculated from direct

Table 6.7. Numbers (m^{-2}) and biomass ($g\ m^{-2}$) of *Ceratonereis* spp. consumed by Curlew Sandpipers, Grey Plovers and *Charadrius* spp. in the study site of 2 000 m^2 in January, February and March.

	Curlew Sandpiper		Grey Plover		*Charadrius* spp.	
	Numbers m^{-2}	Biomass $g\ m^{-2}$	Numbers m^{-2}	Biomass $g\ m^{-2}$	Numbers m^{-2}	Biomass $g\ m^{-2}$
JANUARY	636.0	0.786	49.2	0.178	489.6	1.773
FEBRUARY	394.0	0.487	2.3	0.008	350.6	1.270
MARCH	526.0	0.948	7.1	0.026	66.5	0.241

observations and depletion of lumbricids *Allolobophora caliginosa* and *Lumbricus rubellus* estimated from invertebrate sampling. In a study plot of 1 200 m^2 he counted Golden Plovers every 15 minutes over a 24-hour period. The reduction in lumbricid density and biomass over the three weeks was estimated at *ca* 50% by both techniques.

The initial densities of *C. keiskama* in three of the four cages were higher than in the adjacent controls, but subsequently decreased to the level of those in the controls (Fig 6.1). Initial numbers of the same species in cage C were almost twice as low as in the other cages. In this cage, nereid numbers increased towards the end of the experiment and, at the end of the experiment were significantly higher than the numbers in the adjacent control. These contrasting patterns clearly indicate that factors other than predation by birds influence the abundance of nereids.

In the absence of predation, increasing densities of invertebrates inside cages may result in competition for food or space: competition is recognized as being important in determining infaunal species abundance patterns and distribution in soft-sediment habitats (Dayton, 1971; Woodin, 1974; Virnstein, 1977). In crowded communities, cannibalism or migration away from areas of high density are likely to occur (Peterson, 1977; Underwood, 1990). However, if such effects were operating in the cages in this experiment, one would expect densities of invertebrates inside the cages to increase and subsequently reach a plateau maintained by density-dependent interactions. There was no evidence of this occurring (Fig 6.1): densities of nereids in some cages decreased from the start of the experiment.

Such decreases in nereid numbers inside cages may reflect mortality caused by predators other than birds. However, analysis of the stomach contents of the most abundant fish in the estuary showed that they do not eat polychaetes, or eat them very rarely. Crabs *Hymenosoma orbiculare* and *Thaumatoplax spiralis* are common inhabitants of intertidal mudflats and it is possible that they enter the cages either to seek refuge or to feed on the unnaturally high density of prey (Young *et al*., 1976). Since crabs are highly mobile animals, and core sampling is not a suitable technique for assessing their abundance, comparing crab densities inside and outside cages may not be valid. An increase in the carapace width of crabs was, however, more apparent in the exclosures than controls (Table 6.8). There was a significant difference in the carapace width of these crabs between cages and controls in March (Mann-Whitney Test: $U=1.0$, $n=7, 8$, $p<0.0001$). *Hymenosoma orbiculare* is an omnivore and amphipods are included in its diet (G. M. Branch, per. comm.). Although it is unknown if these crabs eat polychaetes, disturbance caused by their burrowing activity may affect the benthic fauna (Virnstein, 1977; Gee *et al*., 1985).

An increase in total prey abundance may not be the only effect of predator removal: species composition, size-class structure and distribution, growth and reproductive rates can all be affected (Virnstein, 1978).

At the Berg River estuary, reproduction of *C. erythraeensis* occurred earlier in cages than in the adjacent controls (Figs 6.2 & 6.5). Alterations in the population size structure were also detected for *C. keiskama*. Variations in the reproductive output might be caused by the higher numbers of spawning adults (exclosures A and D) and thus more larvae being available for settlement, or increased survival of larvae (Woodin, 1974), which might be a result of lowered predation levels. Kent & Day (1983) in Australia and Raffaelli & Milne (1987) in England, as in this study, found that although predation by waders and fish had little measurable impact on invertebrate density, it altered the population size structure of their prey *Ceratonereis pseudoerythraeensis* and *Corophium volutator*, respectively. Kent & Day (1983) further concluded that reduced recruitment of juveniles in cages was a result of high adult density which reduced the reproductive output of recruits in a density-dependent manner.

Table 6.8. Total number (N) and mean carapace width (mm) (±SD) of crabs *Hymenosoma orbiculare* and *Thaumatoplax spiralis* in the cages and controls in January, February, March and April.

	JANUARY		FEBRUARY		MARCH		APRIL	
TREATMENT	N	Carapace width (mm)	N	Carapace width (mm)	N	Carapace width (mm)	N	Carapace width (mm)
Cages (SD)	1	2.50 (0.00)	14	3.16 (1.81)	7	6.17 (2.68)	7	5.90 (3.45)
Controls (SD)	2	2.50 (1.15)	9	1.97 (0.70)	8	2.16 (0.19)	4	6.20 (3.80)

It has to be stressed that the site effect of the cages was not investigated in the present experiment. Studies elsewhere indicate that effects of cage structure, which may include sedimentation, shading or changes in water current inside the cages have little influence on the infaunal community (Quammen, 1981; Kent & Day, 1983). The cages used in this study were larger than those used elsewhere: large size should minimize disturbance effects away from the cage edge. A disadvantage of the large size, however, is that the cages attract gulls and terns which occasionally use them for roosting.

Taken together, the estimates of nereid consumption by waders calculated from direct observations are close to those calculated from invertebrate sampling when foraging densities of birds are considered over the entire study area and not only in the control areas. During the three months when predation by birds is the most intense, nereid numbers were depleted by up to 42%. Despite this, the predicted divergence in nereid density inside and outside cages was not detectable. The reasons for this are unknown as the cages were effective in excluding birds. It seems possible that the close tracking of nereid density in cages and their adjacent controls was due to local dispersal, from high to low density patches, which had the effect of equalizing density. Whilst caging experiments may be of great value in assessing predatory impact on truly sessile organisms, their value in studies where the prey are mobile requires more careful evaluation. If, as suggested here, prey disperse into nodes of low density, results are difficult to interpret empirically without an understanding of the extent of such movement.

REFERENCES

Baird, D., Evans, P. R., Milne, H. & Pienkowski, M. W. 1985 Utilization by shorebirds of benthic invertebrate production in intertidal area. *Oceanography and Marine Biology Annual Review* **23**, 573-597.

Bengtson, S. A. 1976 Effect of bird predation on lumbricid populations. *Oikos* **27**, 9-12.

Boates, J. S. & Smith, P. C. 1979 Length-weight relationships, energy content and the effects of predation on *Corophium volutator* (Pallas) (Crustacea: Amphipoda). *Proceedings of the Nova Scotia Institute of Science* **29**, 489-499.

Dayton, P. K. 1971 Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**, 351-389.

Evans, P. R., Herdson, D. M., Knights, P. J. & Pienkowski, M. W. 1979 Short-term effects of reclamation of part of Seal Sand, Teesmouth, on wintering waders and shelduck I. Shorebird diet, invertebrate density and the impact of predation on the invertebrates. *Oecologia* **41**, 183-206.

Gee, J. M., Warwick, R. M., Darvey, J. T. & George, C. L. 1985 Field experiments on the role of epibenthic predators in determining prey densities in an estuarine mudflat. *Estuarine, Coastal and Shelf Science* **21**, 429-448.

Kent, A. C. & Day, R. W. 1983 Population dynamics of an infaunal polychaete: the effect of predators and adult-recruit interaction. *Journal of Experimental Marine Biology and Ecology* **73**, 185-203.

Marsh, C. P. 1986 Rocky intertidal community organization: the impact of avian predators on mussel recruitment. *Ecology* **67**, 771-786.

Peterson, C. H. 1977 Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. *Marine Biology* **43**, 343-359.

Quammen, M. L. 1981 Use of exclosures in studies of predation by shorebirds on intertidal mudflats. *Auk* **98**, 812-817.

Quammen, M. L. 1984 Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: an experimental test. *Ecology* **65**, 529-537.

Raffaelli, D. & Mile, H. 1987. An experimental investigation of the effects of shorebirds and flatfish predation on estuarine invertebrates. *Estuarine, Coastal and Shelf Science* **24**, 1-13.

Schneider, D. & Harrington, B. 1981 Timing of shorebird migration in relation to prey depletion. *Auk* **98**, 801-811.

Woodin, S. A. 1974 Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. *Ecological Monographs* **44**, 171-187.

Underwood, A. J. 1990 Design and analysis of field experiments on competitive interactions affecting behaviour of intertidal animals. In: Behavioural Adaptation in Intertidal Life (Chelazzi, G. & Vannini, M., eds) NATO ASI Series, Series 10, *Life Sciences* **151**, 333-358.

Virnstein, R. W. 1977 The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* **58**, 1199-1217.

Virnstein, R. W. 1978 Predator caging experiments in soft sediments: caution advised. In: *An Estuarine Interaction* (Willey, M. L., ed). Academic Press, New York, pp 261-173.

Young, D. K., Buzas, M. A. & Young, M. W. 1976 Species densities of macrobenthos associated with seagrass: a field experimental study of predation. *Journal of Marine Research* **34**, 577-592.

CHAPTER 7

DISPERSION OF WADERS WITHIN THE BERG RIVER ESTUARY IN RELATION TO PREY DISTRIBUTION AND FORAGING TECHNIQUES

SUMMARY

The distribution of migrant and resident waders at the Berg River estuary was monitored from December 1987 to April 1989. Migrant waders occupied intertidal mudflats sequentially: the most profitable mudflats were occupied first, and the less profitable ones were occupied later in the season when the numbers of birds on the estuary increased. Resident waders occupied mudflats least preferred by the migrants when the latter were most abundant on the estuary and moved to more profitable sites in winter when migrant waders departed.

Site preference by migrant waders with different foraging techniques, Curlew Sandpiper (tactile forager) and Grey Plover (visual forager), were studied in detail. Curlew Sandpiper density was significantly and positively correlated with the combined density of their preferred prey *Ceratonereis keiskama* and *C. erythraeensis*. Curlew Sandpipers' preference for muddy substrata with minimal vegetation cover was interpreted as a means of reducing the energetic costs of tactile foraging.

Grey Plover density was positively correlated with the biomass of *C. erythraeensis*. Their ingestion rate increased as the biomass of both *Ceratonereis* spp. increased. The distribution of Grey Plovers on the estuary was independent of sediment type but was closely linked to vegetation cover.

The success rate of Curlew Sandpipers was positively correlated with their own density. Foraging and success rates of Grey Plovers were highest when the density of conspecifics was lowest. A positive linear correlation existed between foraging rate of Grey Plovers and the total density of migrant waders.

INTRODUCTION

Several studies have shown that the distribution of waders within and between estuaries is determined by the distribution and abundance of their preferred prey (Wolff, 1969; Goss-Custard, 1977a; Goss-Custard *et al.*, 1977; Bryant, 1979; Rands & Barkham, 1981). More recent studies have emphasized the importance of physical properties of the habitat in influencing the foraging efficiency of birds and hence their choice of foraging sites (Myers *et al.*, 1980; Quammen, 1982; Gerritsen & van Heezik, 1985).

The Berg River estuary contains many discrete mudflats which differ with respect to both the density and biomass of invertebrate prey and physical properties such as vegetation cover and sediment type (Chapter 2). Migrant waders which use different foraging techniques and have different food requirements may therefore respond to this habitat variability by occupying those mudflats where they can feed most profitably. In addition, the high density of migrant waders on the mudflats during the austral summer may have a considerable impact on the habitat choice of resident waders which utilize mudflats throughout the year.

In this Chapter, the distribution of both migrant and resident waders between intertidal mudflats is examined. A detailed investigation is made of the site preferences of two migrant waders representing different foraging guilds, Curlew Sandpiper (tactile forager) and Grey Plover (visual forager).

STUDY SITE AND METHODS

Twenty one intertidal mudflats at the Berg River estuary were grouped into five sections. There were four major mudflats, A, B, C and D, and six small and scattered mudflats which were grouped as 6-11. Four study sites, A, B, C and D, each of 2 000 m^2 (25 x 80 m), were established within the corresponding mudflats (Fig 7.1). Invertebrate samples were taken once a month from the four study sites. A detailed description of the methods used in sampling invertebrates and in determining their biomass and production are given in Chapter 2. Physical characteristics of the habitat such as vegetation cover and substratum particle size were also recorded and are described in detail in Chapter 2. Mudflats A, B, C and D differed with respect to both biotic and abiotic factors (Table 7.1). Mudflat A was the largest of all mudflats, with the lowest average vegetation cover, fine sediments and the lowest total invertebrate density, biomass and production. However, the highest density of nereid worms occurred at this mudflat. Mudflat B had the highest average vegetation cover, the finest sediments and the highest density, biomass and production of invertebrates. Mudflat D was similar to Mudflat B with respect to vegetation cover, prey density, biomass and production, but had the coarsest sediment of all the mudflats. Vegetation cover and sediment type were not recorded, and invertebrate samples were not collected at mudflats 6-11 (5.5 ha). The density of *Ceratonereis keiskama*, but not of *C. erythraeensis*, was positively correlated with its biomass on the estuary as whole ($r=0.53$, $N=22$, $p<0.01$; $r=-0.18$, $N=43$, $p>0.05$, respectively). This indicates that there were areas of high biomass and high density as well as areas of low biomass and low density of *C. keiskama* but not of *C. erythraeensis*.

All waders were counted on all mudflats twice a month at spring tides during the low tide period. Additional counts were made at the study sites: twice a month all foraging birds were counted at 20 minutes intervals throughout the spring low tide periods. The average of the two monthly counts at the study sites were used in regression analyses. Since migrant waders were most abundant at the Berg River estuary during the austral summer, data from the period September to March, when migration is either advanced or completed, were used in the regression analyses. Twice a month at each site, during spring tides, birds were observed through a 22 x

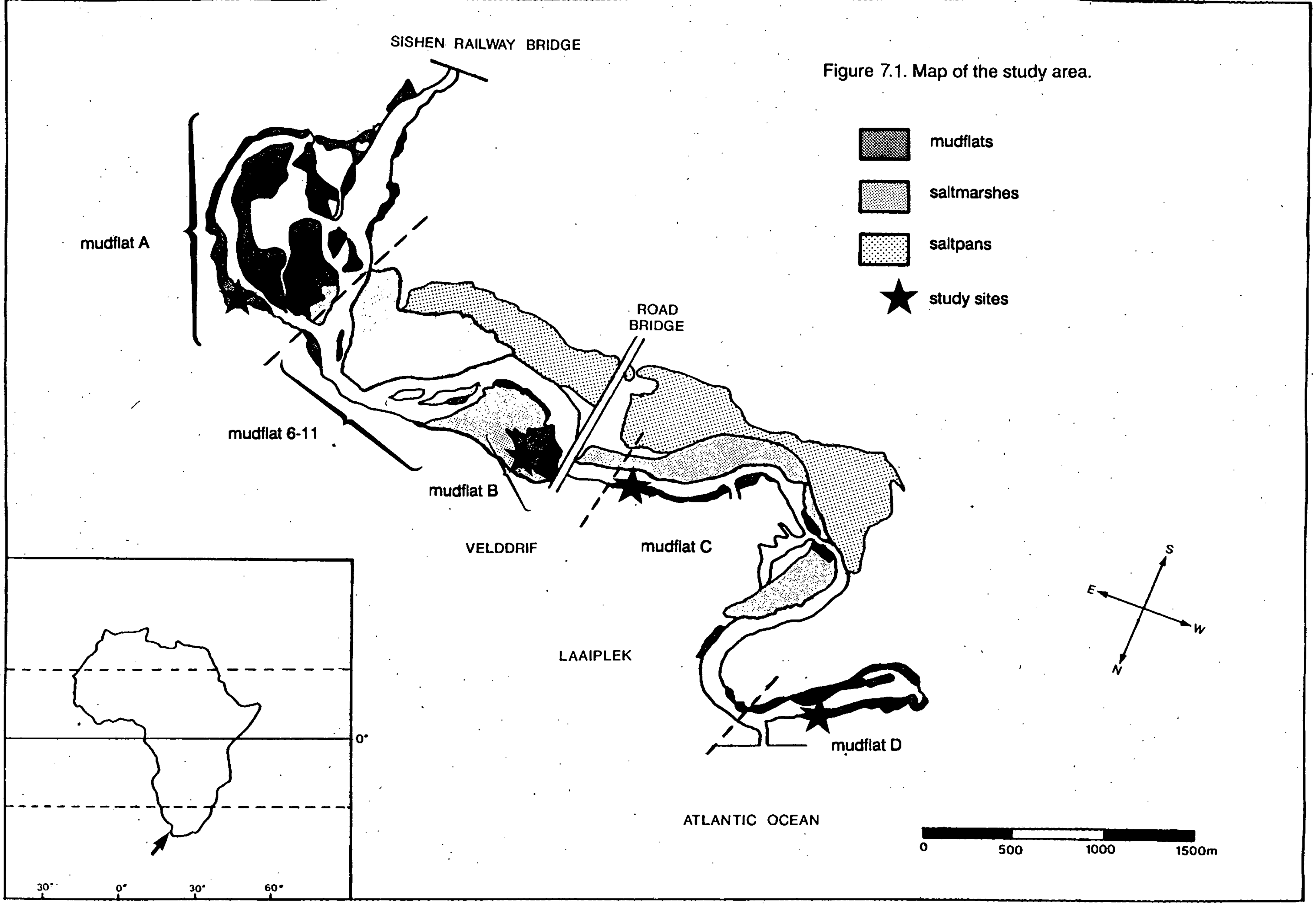


Figure 7.1. Map of the study area.

Table 7.1. Description of the mudflats (A, B, C and D) in terms of area, average vegetation cover, sediment type and the average density, biomass and production of nereids and of all invertebrates.

		Vegetation cover			All invertebrates			Nereids		
	Area ha^{-1}	Percentage %	Dry weight ($g\ m^{-2}$)	Sediment type (Mdϕ)	Numbers m^{-2}	Biomass $g\ m^{-2}$	Production $g\ m^{-2}\ y^{-1}$	Numbers m^{-2}	Biomass $g\ m^{-2}$	Production $g\ m^{-2}\ y^{-1}$
A	90.6	65.3	45.5	Very fine sand with high silt and medium sand fractions (2.37)	17 322	16.2	66.7	7 198	10.1	20.9
B	17.6	93.6	184.0	Predominantly silt to very fine sand (2.80)	89 416	32.6	146.9	3 749	11.2	22.2
C	12.3	77.7	72.2	intermediate texture between B and D (2.80)	30 346	26.0	86.3	3 736	13.2	16.1
D	17.7	87.8	124.1	coarse sand (0.66)	53 990	31.5	138.2	3 582	11.8	21.4

telescope and their foraging activities were recorded during 60 second observation periods. The total number of pecks (foraging rate) and number of successful pecks (success rate) were recorded for Grey Plovers and Curlew Sandpipers.

Studies of the diets of waders (Chapter 4) showed that nereid worms, notably *Ceratonereis keiskama* and *C. erythraeensis*, are the preferred prey of both Curlew Sandpipers and Grey Plovers. These two invertebrate species were therefore used exclusively in regression analyses involving bird and prey density/biomass.

Habitat overlap between the pairs of the most common species was calculated using Euclidean distance (Ricklefs & Lau, 1980):

$$D_{ij}=[(p_{ik}-p_{jk})^2]/\sqrt{2}$$

$$E_{ij}=1-D_{ij}$$

where:

p_{ik}=proportion of species i in habitat k

p_{jk}=proportion of species j in habitat k

The index is scaled from 0 (no overlap in the habitat use) to 1 (identical distribution).

Analyses of differences in substratum preferences by birds were made using median particle diameter of the sediment (Mdø) (Table 7.1; also see methods in Chapter 2 and Table 2.2).

RESULTS

Sequential occupancy of mudflats by birds

Migrant waders first arrived at the Berg River estuary in August (Chapter 1). The early arrivals occupied mudflats A, B and D whereas mudflats 6-11 and C were progressively filled later in the season as the number of birds on the estuary increased (November) (Fig 7.2A). This pattern was repeated in both study years. Different species, however, tended to concentrate on different mudflats. Curlew Sandpipers favoured mudflat A and their densities decreased gradually towards the mouth of the river (Fig 7.3). By contrast, Greenshanks were least abundant at mudflat A, and most abundant at mudflat D. Grey Plovers maintained their highest density on mudflat B, and Ringed Plovers on mudflat C.

Resident waders, during the period when migrants were most abundant on the estuary (September-April), tended to occupy mudflats which were least preferred by migrant waders (6-11 and C) (Fig 7.2B). During the winter months however, when migrant waders departed from the estuary, the density of resident waders increased considerably at mudflats A, B and D. This apparent seasonal change in the preference for certain mudflats by resident waders is best illustrated by Kittlitz's Plover, the most abundant resident wader on the estuary (Chapter 1). Mudflat C was favoured by this species during the austral summer. During the winter months, Kittlitz's Plovers moved to mudflats A and B, the favoured foraging sites of migrants (Fig 7.4).

Both, migrant and resident waders abandoned mudflat B in December 1987 due to a heavy deposition of algae *Cladophora* sp. which probably affected their foraging efficiency.

Habitat overlap

The index of spatial overlap was calculated for thirty six pairs of the most common waders in five sections of the estuary between September and December 1987 and 1988 (Fig 7.5). In general, the spatial overlap was higher in the immediate post-arrival time in 1988, when more birds were present on the estuary, than in 1987. In most cases there was a close agreement between the spatial overlap in both years.

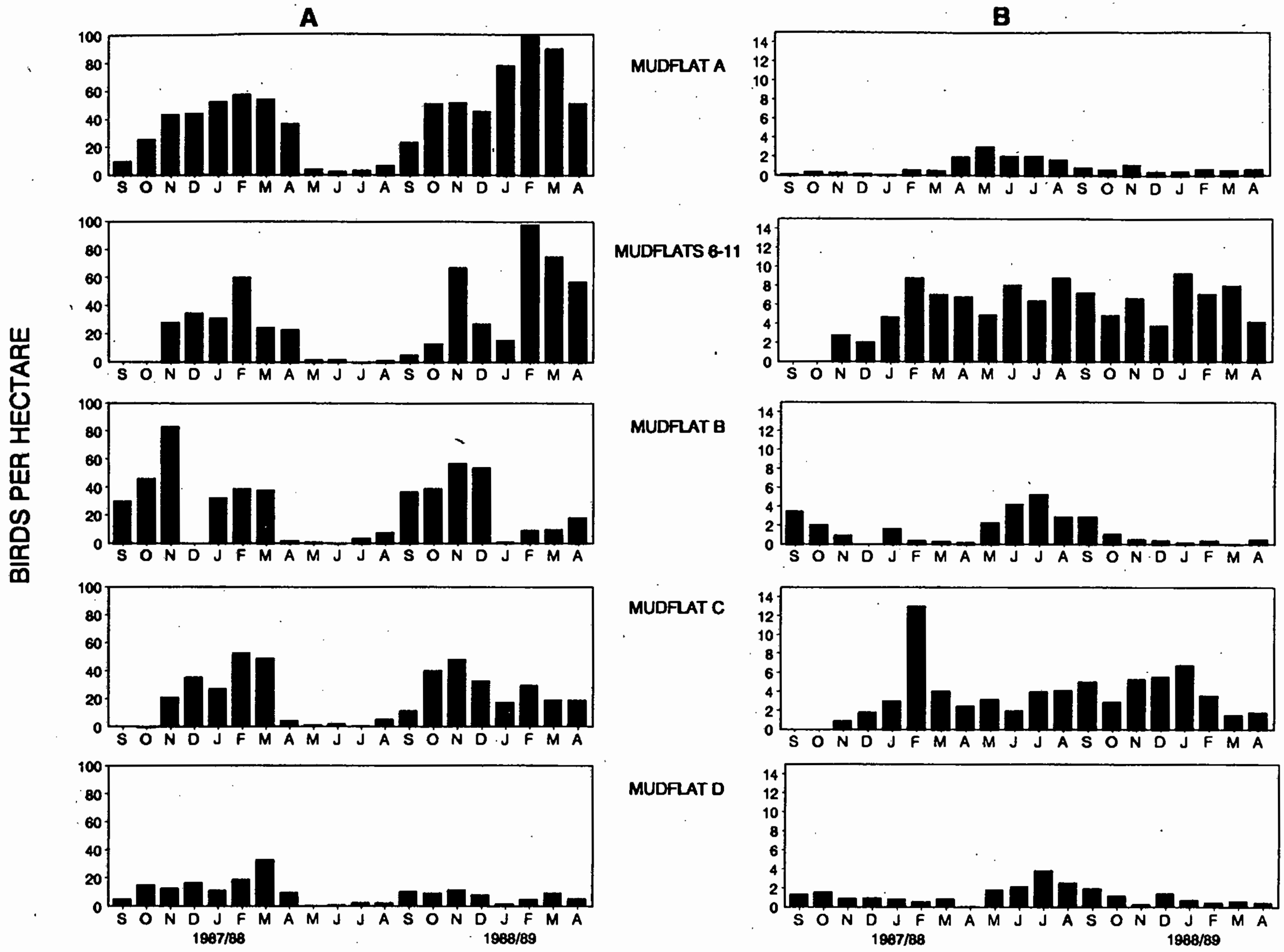


Figure 7.2. Densities (birds ha^{-1}) of migrant (A) and resident (B) waders on the intertidal mudflats of the Berg River estuary.

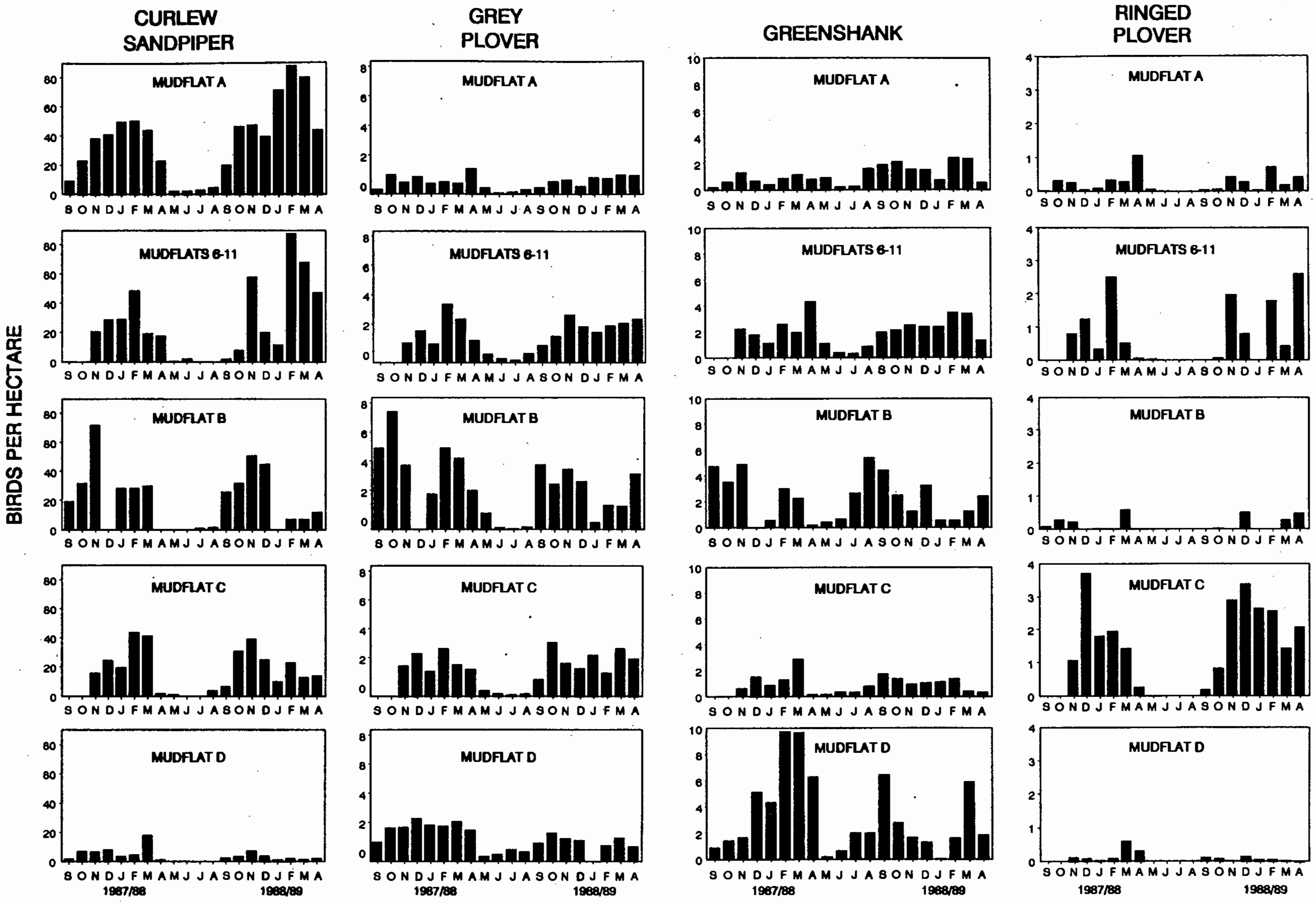


Figure 7.3. Densities (birds ha^{-1}) of Curlew Sandpiper, Grey Plover, Greenshank and Ringed Plover on the intertidal mudflats at the Berg River estuary.

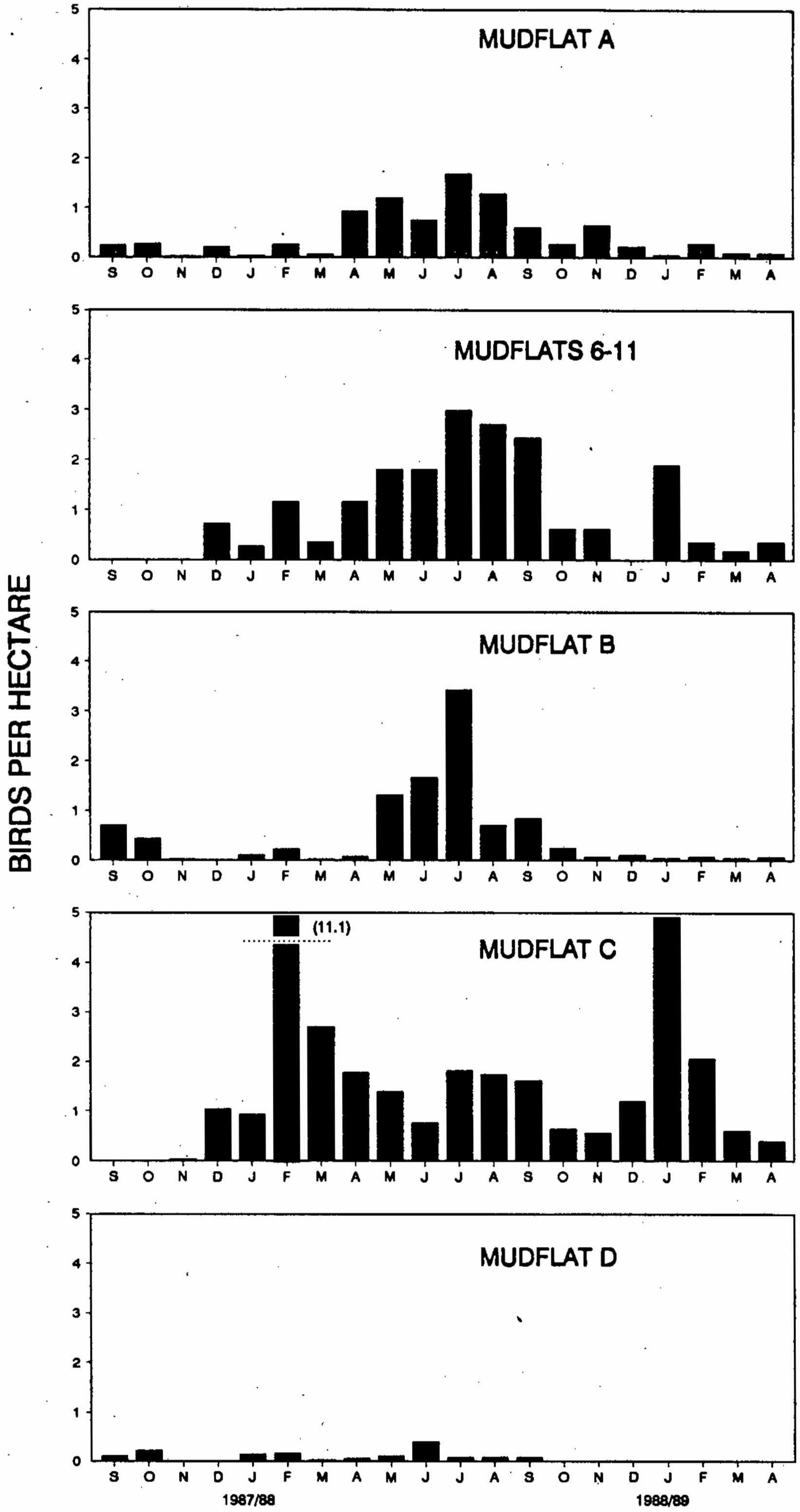


Figure 7.4. Densities (birds ha^{-1}) of Kittlitz's Plover on the intertidal mudflats at the Berg River estuary.

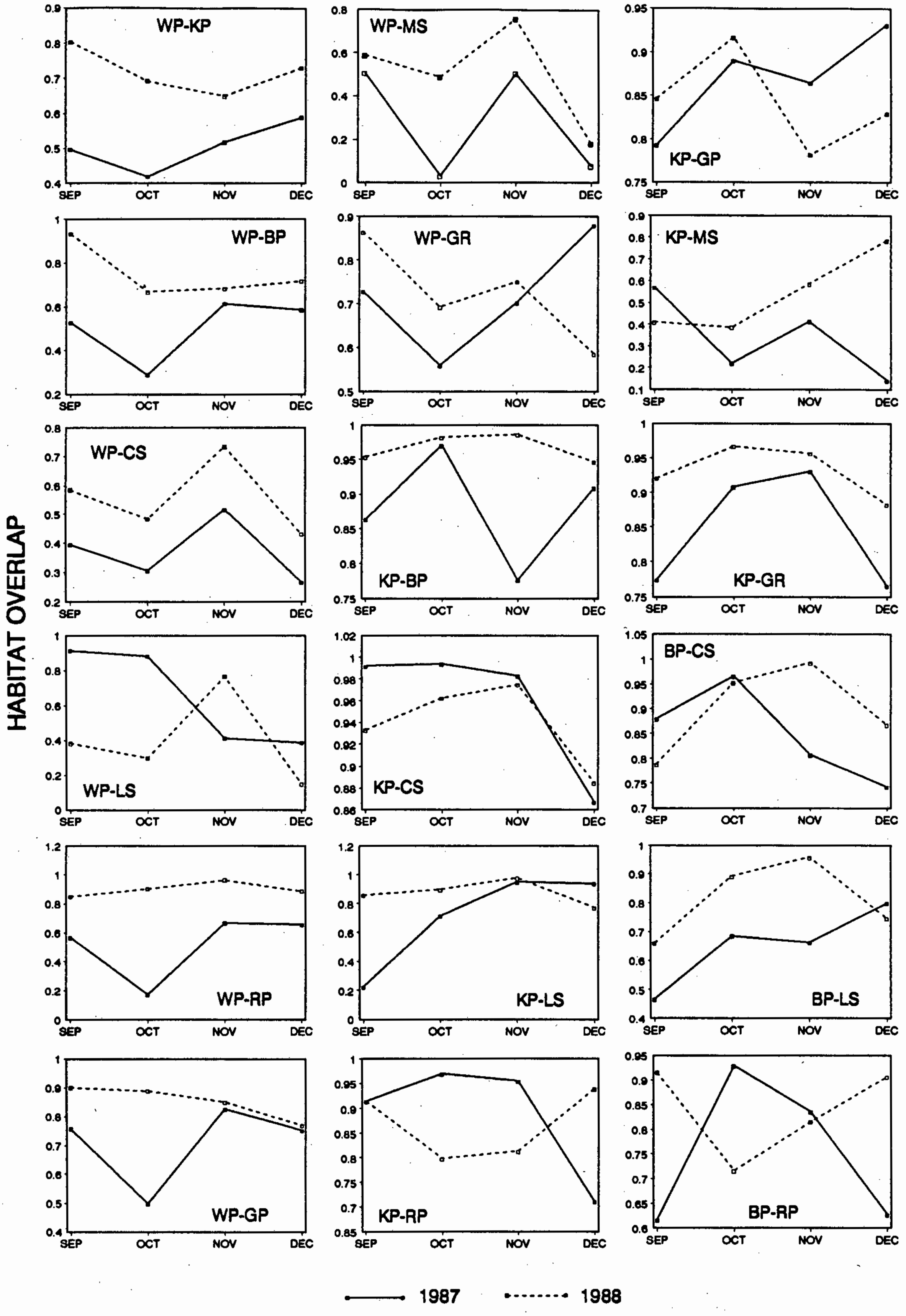
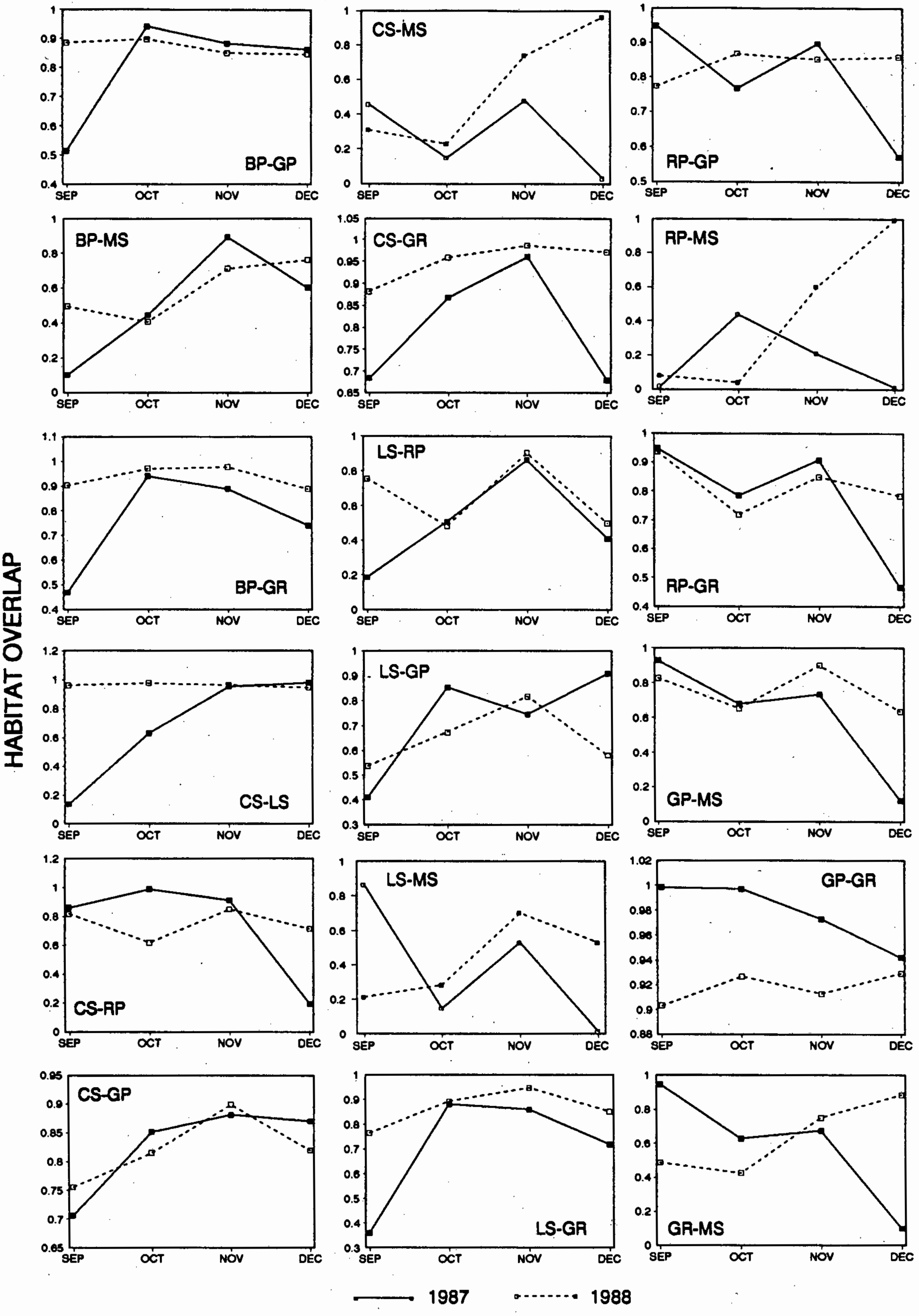


Figure 7.5. Habitat overlap indices (Euclidean distance - see methods) between 36 pairs of the commonest wader species in five sections of the Berg River estuary between September and December 1987 and 1988. The two-letter code indicates the bird species listed in Appendix 7.1.

Fig 7.5 (Cont.)


HABITAT OVERLAP
BP-GP
CS-MS
RP-GP
BP-MS
CS-GR
RP-MS
BP-GR
LS-RP
RP-GR
CS-LS
LS-GP
GP-MS
CS-RP
LS-MS
GP-GR
CS-GP
LS-GR
GR-MS
SEP
OCT
NOV
DEC
1987
1988

There was also no clear decrease in habitat overlap in species pairs as bird numbers gradually increased during the first four months after their arrival from the breeding grounds.

Bird density in relation to prey density, biomass and production

There was a positive linear correlation between the density of Curlew Sandpipers and the density, biomass and production of their preferred prey, *Ceratonereis keiskama*, in the area where this species occurs ($r=0.50$, $N=20$, $p<0.03$; $r=0.55$, $N=20$, $p<0.01$; $r=0.55$, $N=20$, $p<0.01$, respectively). Stepwise variable selection, however, retained only biomass of *C. keiskama* in the model (Fig 7.6A). The density of Curlew Sandpipers was also positively correlated with the density of *C. erythraeensis* ($r=0.57$, $N=40$, $p<0.0001$) and negatively with the density of gastropods ($r=-0.44$, $N=40$, $p<0.004$). The best correlation, however, existed between Curlew Sandpiper density and the combined density of *Ceratonereis* spp. ($r=0.65$, $N=40$, $p<0.00001$ - Fig 6.6B).

In contrast to Curlew Sandpipers, the density of Grey Plovers was negatively correlated with the biomass of *C. keiskama* ($r=-0.73$, $N=20$, $p<0.0003$ - Fig 7.7A) and with its density ($r=-0.51$, $N=20$, $p<0.02$). Grey Plover density was not correlated with the density of *C. erythraeensis*, but was positively correlated with its biomass ($r=0.55$, $N=39$, $p<0.0003$) (Fig 7.7B). Unlike Curlew Sandpipers, however, Grey Plovers are selective in the sizes of nereids they prey upon (Chapter 4). When those sizes of worms least preferred by Grey Plovers (<20 mm in length) were excluded, Grey Plover density was positively correlated with the biomass of both *C. keiskama* and *C. erythraeensis* ($r=0.50$, $N=20$ $p<0.03$; $r=0.55$, $N=39$, $p<0.0003$ - Fig 7.7 C & D). Stepwise variable selection analysis indicated that the total biomass of *C. erythraeensis* was the primary correlate of Grey Plover density ($r=0.50$, $N=39$,

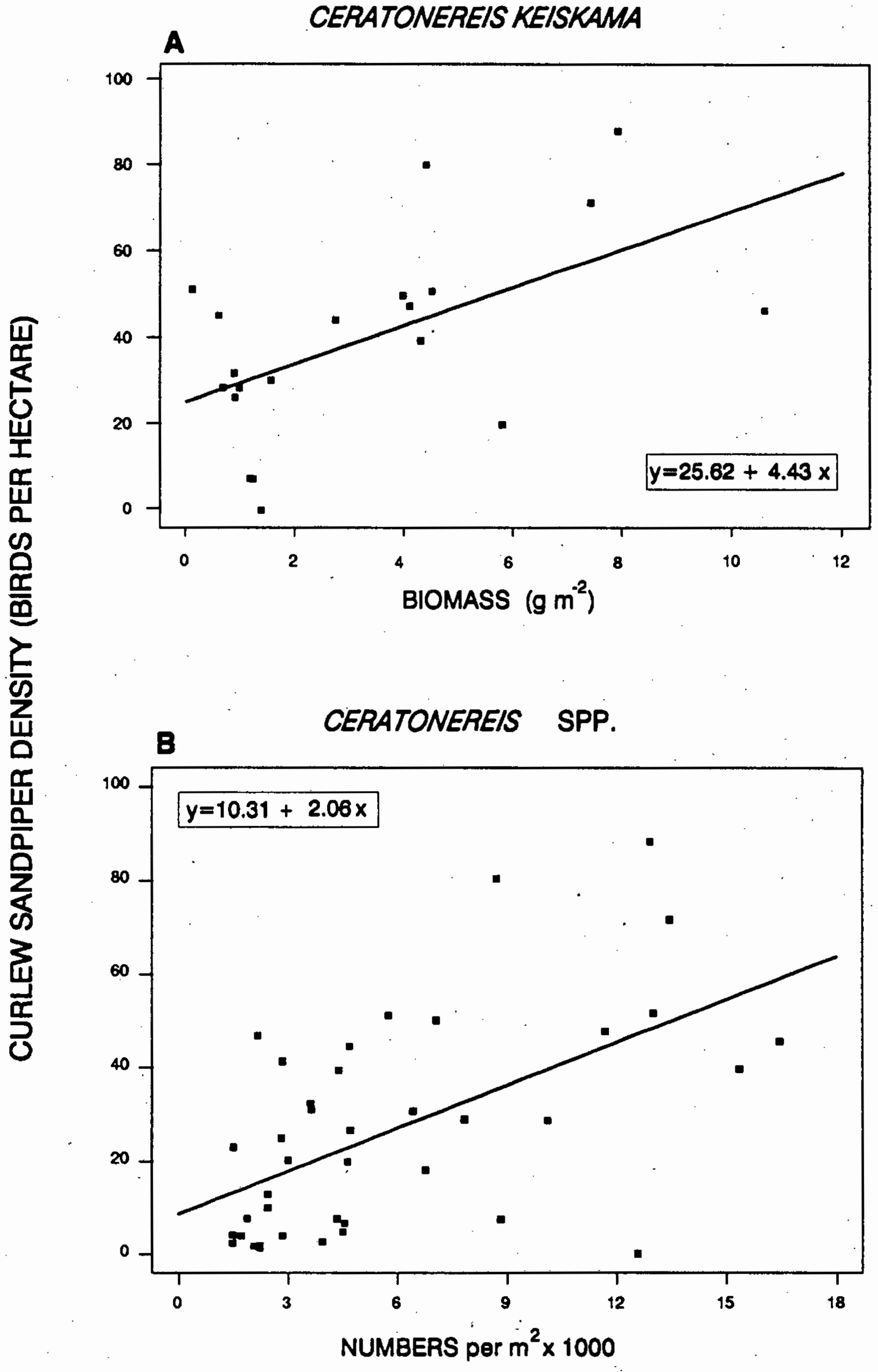


Figure 7.6. The relationships between the density of Curlew Sandpipers (birds ha^{-1}) and the biomass of *Ceratonereis keiskama* (g m^{-2}) (A) and of the combined density (numbers m^{-2}) of *Ceratonereis* spp. (B).

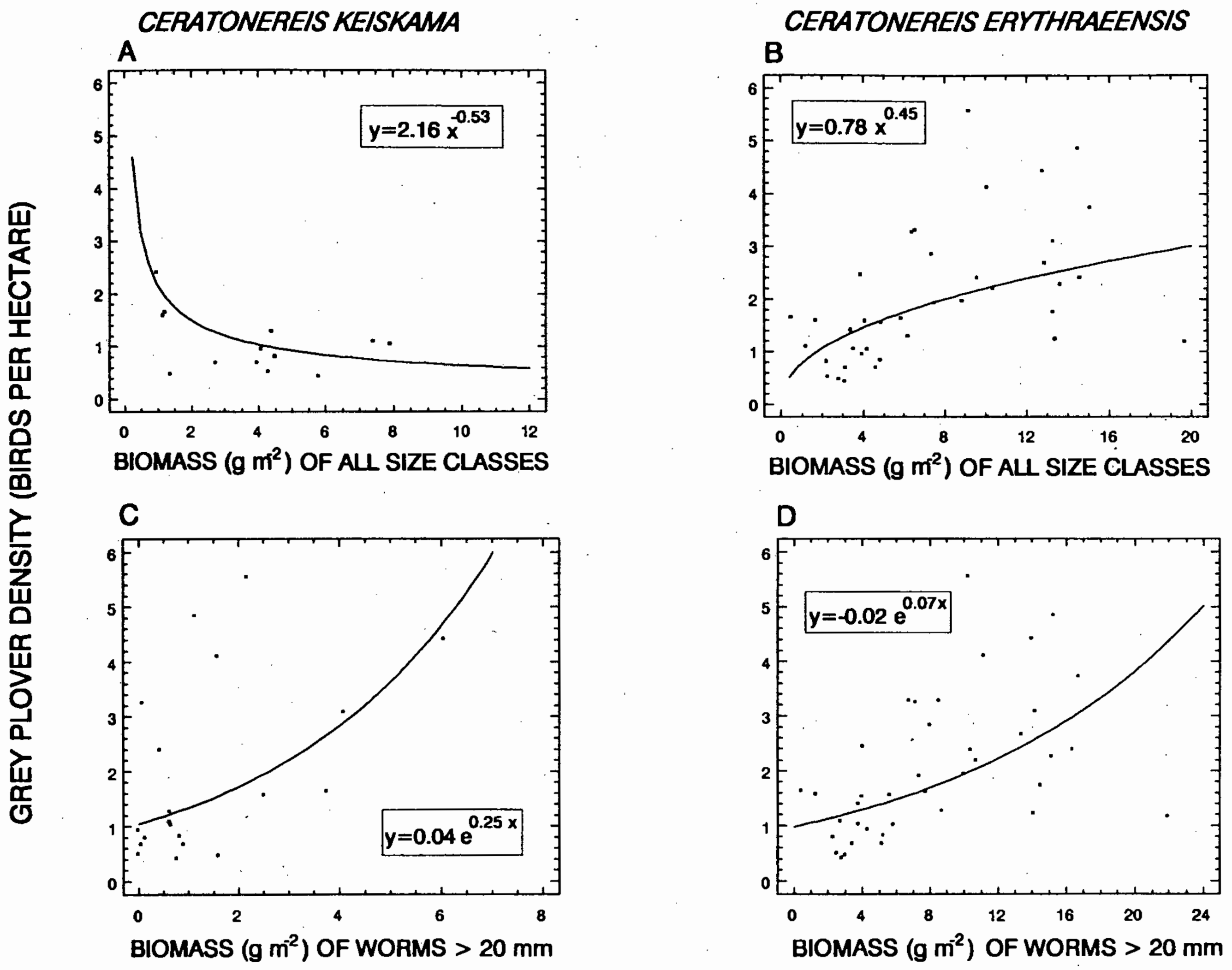


Figure 7.7. The relationships between the density of Grey Plovers (birds ha^{-1}) and total biomass (dry weight g m^{-2}) of *Ceratonereis keiskama* (A) and *C. erythraeensis* (B) and the biomasses of preferred sizes of both *Ceratonereis* species (C, D).

$p < 0.002$ - Fig 7.7B). No correlations existed between Grey Plover density and the production of *Ceratonereis* species.

Foraging efficiency of birds in relation to prey and bird density

The foraging efficiency of both Curlew Sandpipers and Grey Plovers differed between mudflats (Chapter 5 - Table 5.5).

The foraging rate of Curlew Sandpipers was independent of both bird and nereid density at all four mudflats. There was, however, a significant trend for success rate to increase as the density of nereids in the substratum increased ($r = 0.53$, $N = 32$, $p < 0.002$). A positive correlation also exists between Curlew Sandpiper success rate and the density of conspecifics, both on the estuary as a whole and at mudflat A, where this species occurs at the highest density ($r = 0.65$, $N = 30$, $p < 0.0009$; $r = 0.79$, $N = 9$, $p < 0.01$ - Fig 7.8A & B). Since Curlew Sandpiper and nereid density are correlated, partial correlation analysis was used to determine to what extent bird and prey density interact to influence the success rate of birds. When nereid density was held constant, the correlation between success rate of Curlew Sandpipers and their density was significant ($r = 0.51$, $N = 30$, $p < 0.005$). However, when bird density was held constant, the success rate of Curlew Sandpipers was not correlated with nereid density ($r = 0.24$, $N = 30$, $p > 0.05$). This implies that the density of conspecifics is a primary determinant of Curlew Sandpiper success rate.

The foraging and success rates of Grey Plovers were positively correlated ($r = 0.97$, $N = 25$, $p < 0.00001$), and both variables were positively and linearly correlated with nereid density on the estuary as a whole ($r = 0.42$, $N = 25$, $p < 0.04$; $r = 0.46$, $N = 25$, $p < 0.02$, respectively). Furthermore, the foraging rate of Grey Plovers was fastest when the density of conspecifics was lowest, and decreased as their density increased

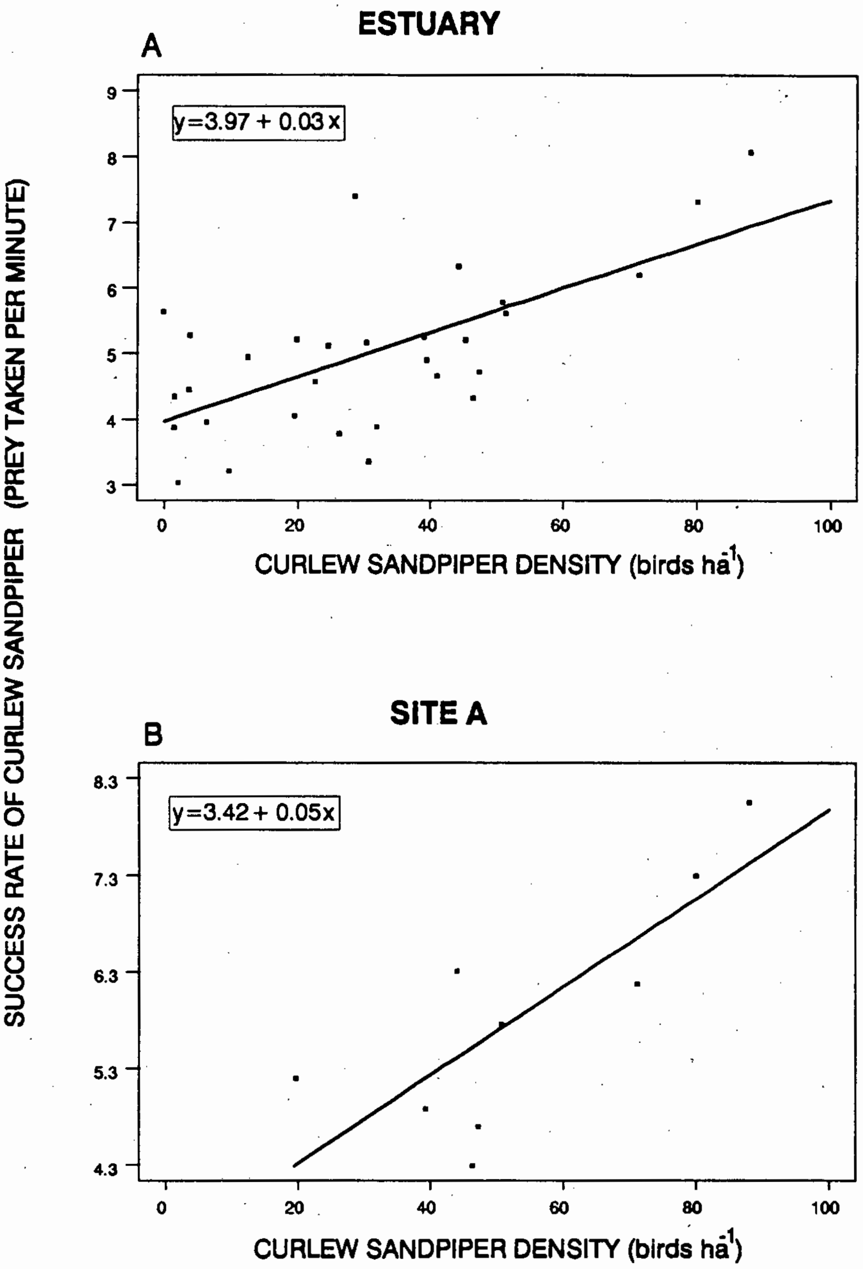


Figure 7.8. The relationships between the success rate (prey eaten per minute) of Curlew Sandpipers and their density (birds ha^{-1}) on the estuary as a whole (A) and at site A (B).

($r=-0.44$, N=24, $p<0.03$ - Fig 7.9A). By contrast, the foraging, success and intake rates of nereids by Grey Plovers were positively correlated with the total density of migrant waders and increased as their density increased ($r=0.55$, N=25, $p<0.004$ - Fig 7.9B; $r=0.55$, N=25, $p<0.005$; $r=0.58$, N=25, $p<0.002$, respectively). Stepwise variable selection analysis revealed that densities of both conspecifics and other migrant waders influenced the foraging rate of Grey Plovers ($r=0.67$, N=25, $p<0.001$), but nereid density did not.

Ingestion rate of birds in relation to prey biomass

The ingestion rate (prey weight in grams eaten per minute) of Curlew Sandpipers was not correlated with the biomass of nereid species either at mudflat A or on the estuary as a whole. By contrast, the ingestion rate of Grey Plovers was positively correlated with the biomass of *C. keiskama* in the area where it occurs and *C. erythraeensis* on the estuary as a whole ($r=0.72$, N=14, $p<0.004$; $r=0.51$, N=25, $p<0.009$ - Fig 7.10A & B).

Bird density in relation to physical characteristics of the habitat

Densities of all migrant waders combined were negatively correlated with the dry weight of vegetation on the mudflats ($r=-0.46$, N=36, $p<0.005$) (Fig 7.11). This trend, however, reflects mainly the distribution pattern of Curlew Sandpipers. The biotic factors influencing the distribution of Curlew Sandpipers and Grey Plovers on the estuary (see above) and dry vegetation cover were included in stepwise variable selection analyses to determine which factors are primarily responsible for the distribution patterns of these species on the estuary. The analysis revealed that both the combined density of two *Ceratonereis* spp., *C. keiskama* biomass and vegetation cover all influence the density of Curlew Sandpipers ($r=0.76$, df=35, $p<0.001$). For

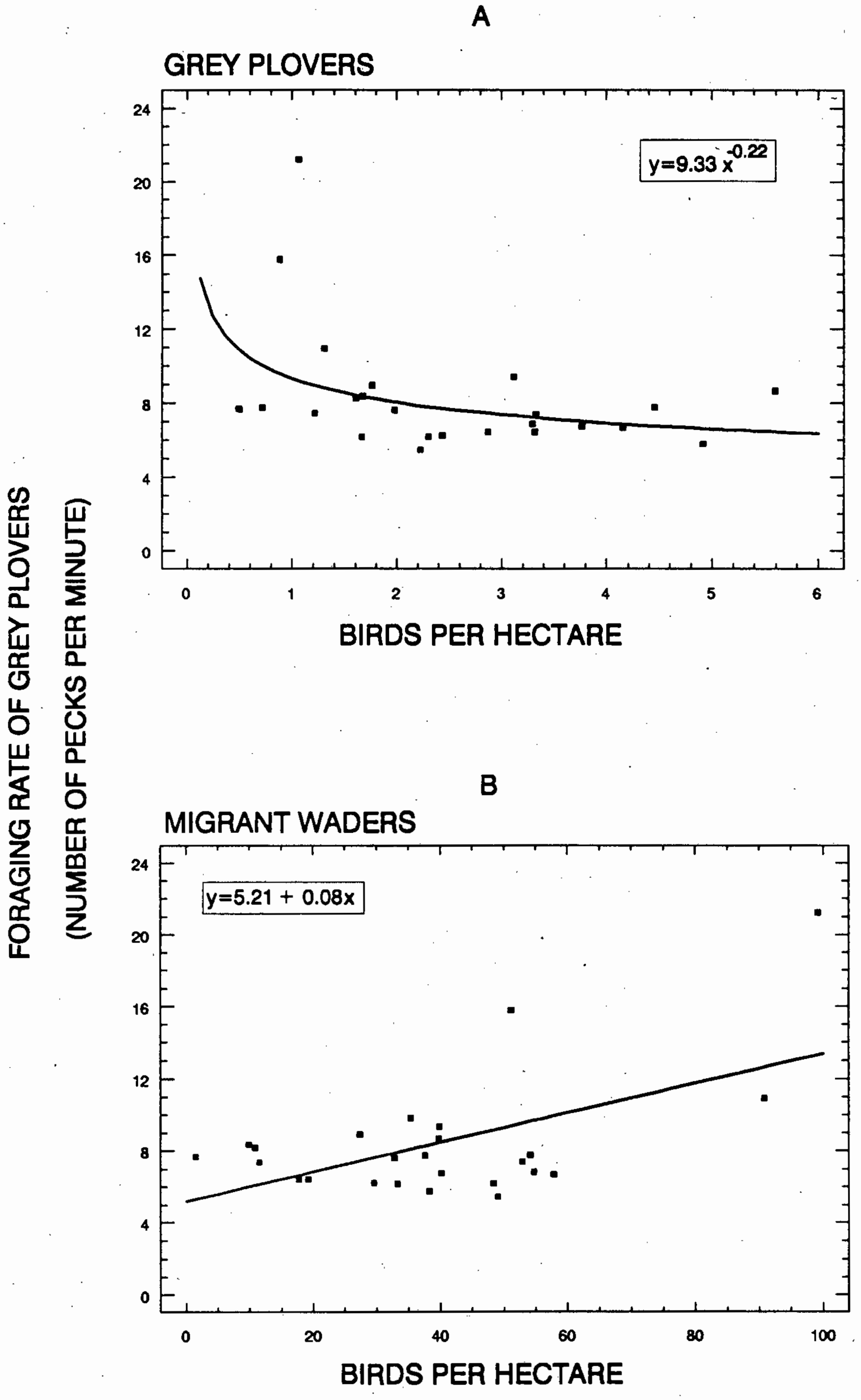


Figure 7.9. The relationships between the foraging rate of Grey Plovers (number of pecks per minute) and their density (birds ha^{-1}) (A) and the density (birds ha^{-1}) of migrant waders (B).

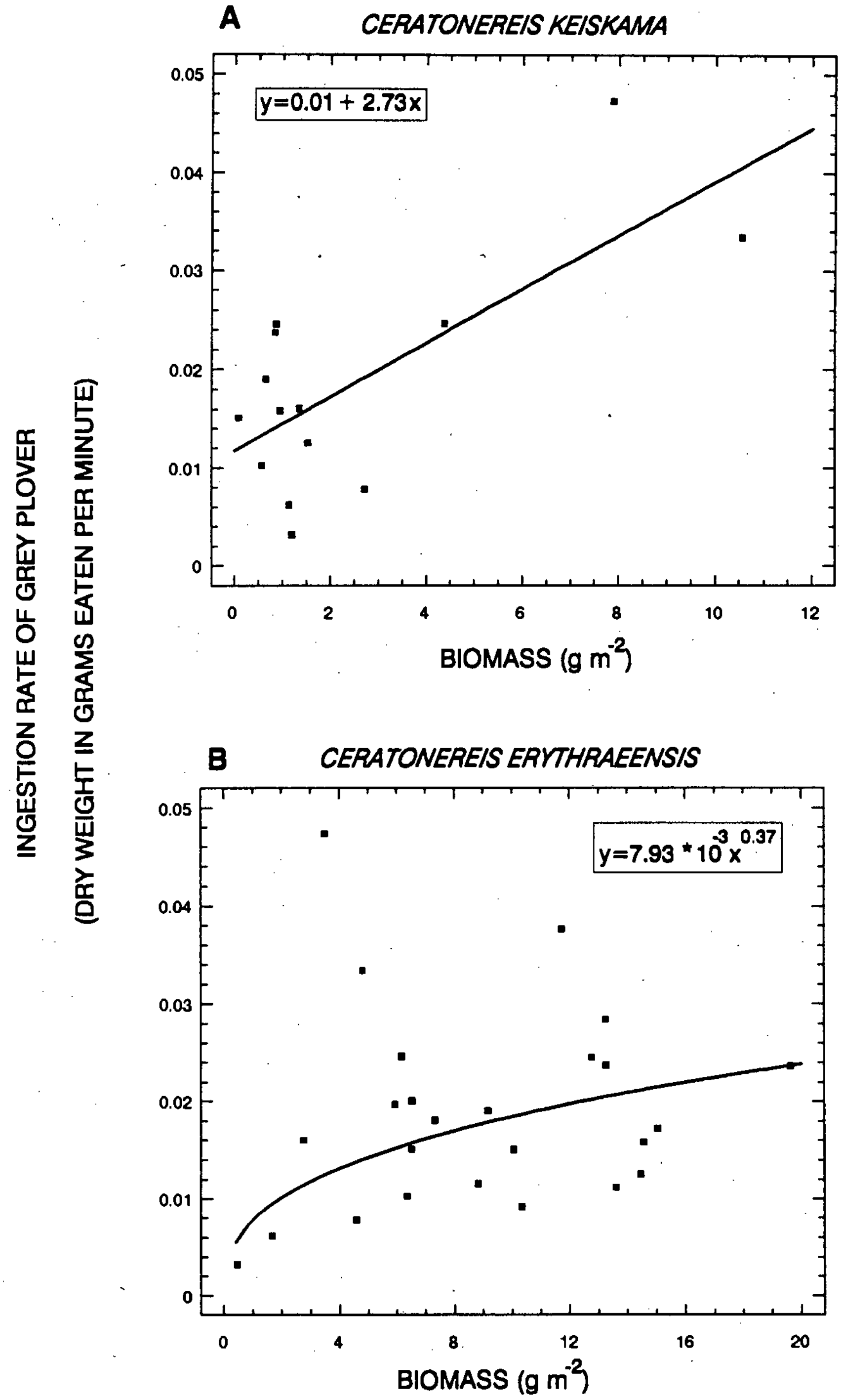


Figure 7.10. The relationships between the ingestion rate of Grey Plovers (dry weight in grams eaten per minute) and biomass (g m^{-2}) of *Ceratonereis keiskama* (A) and *C. erythraeensis* (B).

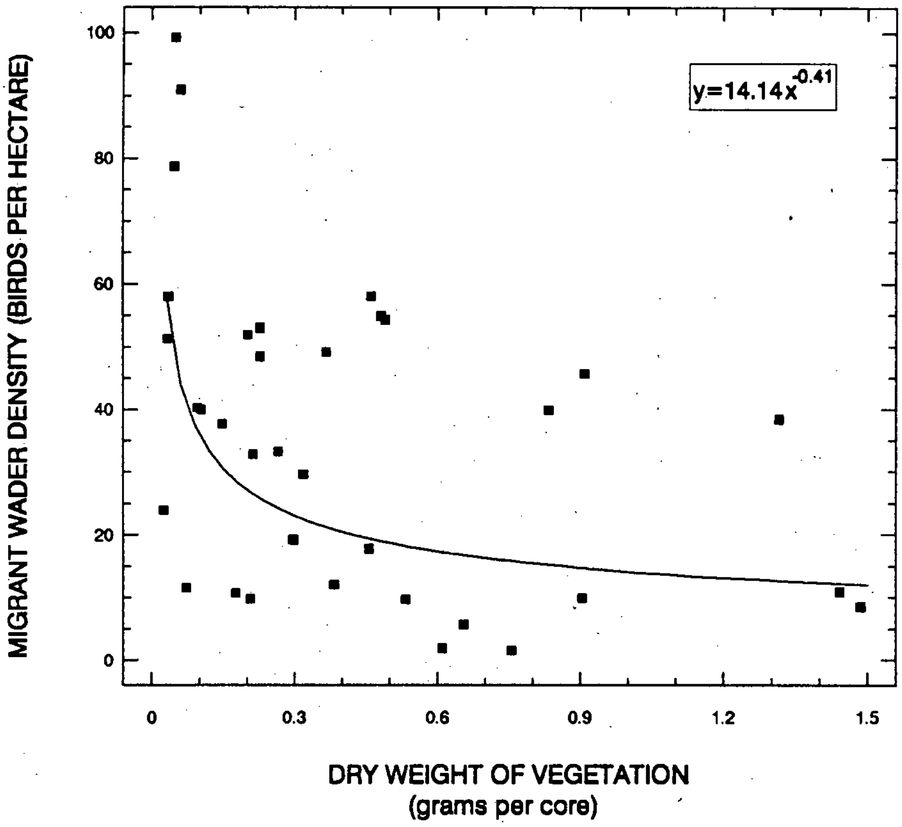


Figure 7.11. The relationship between migrant wader density (birds ha^{-1}) and the dry weight (g) of vegetation.

Grey Plovers, on the other hand, the biomass of *C. erythraeensis* and vegetation cover were identified by stepwise variable selection analysis as factors responsible for their distribution ($r=57$, $N=35$, $p<0.001$).

The density of Curlew Sandpipers on the estuary was influenced by sediment type and was highest on muddy substrata (Kruskal-Wallis Test; $H=6.0$, $df=7$, $p<0.05$). This contrasts with Grey Plovers which were distributed over the intertidal mudflats independently of sediment type ($H=5.1$, $df=7$, $p>0.05$).

DISCUSSION

Habitat preference of tactile vs visual foragers

At the Berg River estuary, the preference of waders for a particular mudflat can been linked to both biotic and abiotic influences on foraging conditions. Species with different foraging techniques and food requirements differed in their choice of foraging sites.

The closest relationships between predator and prey parameters were between Curlew Sandpipers and *C. keiskama* and between Grey Plovers and *C. erythraeensis*. This accords with the birds' diet: *C. keiskama* is the most frequently taken prey of Curlew Sandpipers whereas *C. erythraeensis* is preferred by Grey Plovers (Chapter 4). Grey Plover density was not correlated with the density of nereids, but was strongly influenced by the biomass of *C. erythraeensis* and vegetation cover. The ingestion rate of Grey Plovers was also well correlated with nereid biomass (Fig 7.10). Grey Plovers are visual foragers and select more profitable sizes of worms independently of worm abundance (Chapter 4). Their density should thus be more closely linked to worm biomass than to worm density. Mudflat B, with the highest overall density, biomass and production of all invertebrates and the greatest vegetation cover was a preferred mudflat for this species (Table 7.1, Fig 7.3). For visual foragers which are able to assess prey size and profitability prior to consuming the prey, total available food may play an important role in determining their distribution pattern on intertidal mudflats. Sediment covered with vegetation dries out more slowly than bare substratum (Chapter 2); this slows the downward movement of prey in the substratum during the low tide period. Grey Plovers, which feed on invertebrates at the surface of the substratum and rely mainly on the surface activity of their prey in order to detect them, may therefore prefer sites with vegetation and algal cover where prey appear to be more active.

By contrast, Curlew Sandpipers are tactile foragers and feed on the most abundant size classes of worms (Chapter 4). As was predicted, their density is closely linked to the total density of nereids (Fig 7.6B). Mudflat A, where *C. keiskama* occurred at its highest density, was a preferred mudflat for Curlew Sandpipers. A positive correlation between Curlew Sandpiper density and the biomass of *C. keiskama* is a consequence of a strong correlation between the density and biomass of this nereid (see methods).

Several studies have shown that sediment particle size, and hence its penetrability, may influence the availability of estuarine polychaetes to birds (e.g. Myers *et al.*, 1980). Rapid vertical migration of prey is more likely in coarse sediments than in fine ones, due to the former's lower water retention capacity (Chapter 2). Sand grains which are similar in diameter to worms may interfere with the birds ability to detect and/or capture prey (Quammen, 1982). *Calidris* species searching for food by touch will be most efficient when their chance of direct contact with prey is high (Gerritsen & van Heezik, 1985). This foraging method requires a high number of pecks/probes to detect a prey item and is energetically expensive. Curlew Sandpipers at the Berg River minimize the energy expended in single pecks by selecting mudflat A, which has a muddy, easily penetrable substratum with little vegetation cover (Fig 7.3 & Table 7.1). A similar preference for wet and soft mud, in response to prey detectability rather than prey abundance, has been shown for tactilely-foraging Dunlins *Calidris alpina* (Kelsey & Hassall, 1989).

Foraging efficiency in relation to bird density

Birds foraging visually have a greater field of view and can detect prey at greater distances than can tactile foragers. It is predictable, therefore, that visual foragers will be more susceptible to mutual interference than will tactile foragers. In order to minimize this interference they should maintain a greater individual distance (Recher & Recher, 1969; Goss-Custard, 1970). At high bird density, therefore, the foraging rate of visual foragers is more likely to decrease than is that of tactile foragers (Goss-Custard, 1976). Alternatively, because at high bird density prey are more likely retreat deeper into the substratum, visually-foraging birds would be more rapidly affected by a decrease in the availability of prey on the surface than tactile foragers, which take prey from deeper in the sediment (Goss-Custard, 1984). At the Berg River estuary, the foraging rate of Grey Plovers was highest when birds were at low density and decreased as their density increased (Fig 7.9A). By contrast, the intake rate of tactilely-foraging Curlew Sandpipers continued to increase as their density increased (Fig 7.8A & B). This result is consistent with the findings of Goss-Custard (1984) who showed that prey intake of visually-hunting Redshanks decreased as birds fed closer together; there was no such reduction in the intake rates of Redshanks or Knots which were foraging tactilely.

This study has further shown that, although the foraging rate of Grey Plovers decreased as the density of conspecifics increased, it was positively correlated with the density of other species (Fig 7.9A & B). This suggests that intraspecific competition plays a greater role in reducing foraging efficiency than does interspecific competition. By contrast, Stinson (1977) has shown that Grey Plovers use avoidance behaviour to maintain intraspecific spacing and therefore most competition for food and most aggression is directed interspecifically. Pienkowski (1980), on the other hand, suggested that plovers may avoid areas where there are high densities of other waders because the presence of larger numbers of other birds prevents full use being made of the plovers' large field of view.

Sequential occupation of mudflats

The sequential occupation of foraging areas by migrant waders found in this study has been reported for some other bird species, including European Teal *Anas crecca* (Zwarts, 1976), Knot *Calidris canutus*, European Oystercatcher *Haematopus ostralegus* (Goss-Custard, 1977a) and Redshank *Tringa totanus* (Goss-Custard, 1977b).

The term "preferred" area has been used to describe foraging grounds which are first occupied by birds (Goss-Custard, 1980). In the present study certain areas were preferred by birds because they could forage there most efficiently. Zwarts (1981) suggested that the distance from the foraging area to the roosting site is equally important in determining which sites are preferred. The Berg River estuary is relatively small and most birds can forage within 1-1.5 km of a major roost site (Chapter 1). It can be predicted that each foraging area has an upper limit to the bird density it can support, after which feeding in such areas is no longer profitable to birds (Goss-Custard, 1977b; Zwarts, 1976). Several mechanisms may determine the limit to density. Foraging efficiency is likely to decrease at high bird density because of increased interference among birds (Goss-Custard, 1977a). This, however, is influenced by the foraging techniques used by birds. Secondly, at high bird density the availability of prey might be reduced due either to direct depletion of prey by birds or to movement of prey deeper into the substratum in response to surface disturbance caused by the walking and probing birds (Goss-Custard, 1970).

To offset a decrease in their intake rate at preferred foraging sites, birds might move to alternative foraging grounds, in this study mudflats 6-11 and C, or chase away other birds. Subdominant birds which are forced to move from preferred sites are usually juveniles (Bryant, 1979). At the Berg River estuary, smaller and less abundant species, eg. Ringed Plover and resident waders, foraged in the less preferred sites.

If interspecific competition plays rôle in determining the distribution of species within the Berg River estuary and causes the observed shifts in the habitat use during the austral summer, the degree of spatial segregation between species should increase as the overall density of birds increases. No such pattern was detected at the Berg River estuary (Fig 7.5). Additionally, the degree of spatial segregation should be greater in the year of high bird numbers (1988 - Chapter 1) than in the year of low bird numbers if interspecific competition influences spacing patterns. No such difference between the years is apparent.

The present study has shown that, although the distribution of waders within the estuary can be linked to the distribution of their preferred prey, environmental factors are also important in determining dispersion patterns. A comparison of the dispersion patterns of migrant and resident waders has indicated that the former group apparently has a profound impact on the distribution of the latter. Without, however, knowing the extent of the aggressive interactions between birds it is impossible to determine whether the uneven distribution of birds and shifts in habitat use at the Berg River estuary are primarily a consequence of habitat choice; changes in the feeding conditions on the preferred sites; or, competitive interactions among birds for food and space. These possibilities are examined in Chapter 8.

REFERENCES

Bryant, D. M. 1979 Effect of prey density and site character on estuary usage by overwintering waders (Charadrii). *Estuarine and Coastal Marine Science* **9**, 369-384.

Gerritsen, A. F. C. & van Heezik, Y. M. 1985 Substratum preference and substratum related foraging behaviour in three *Calidris* species. *Netherlands Journal of Zoology*, **35**, 671-692.

Goss-Custard, J. D. 1970 Feeding dispersion in some overwintering wading birds In: *Social Behaviour in Birds and Mammals*. (Crook, J. H., ed). Academic Press, London, pp 3-35.

Goss-Custard, J. D. 1976 Variation in the dispersion of Redshank *Tringa totanus* on their winter feeding grounds. *Ibis* **118**, 257-263.

Goss-Custard, J. D. 1977a The ecology of the Wash III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology* **14**, 721-739.

Goss-Custard, J. D. 1977b Predator responses and prey mortality in the Redshank (*Tringa totanus* L.) and a preferred prey, *Corophium volutator* (Pallas). *Journal of Animal Ecology* **46**, 21-35.

Goss-Custard, J. D. 1980 Competition for food and interference among waders. *Ardea* **68**, 31-52.

Goss-Custard, J. D. 1984 Intake rate and food supply in migrating and wintering shorebirds. In: *Behaviour of Marine Animals* Vol. 6 (Burger J. & Olla, B. L., eds). Plenum Press, New York, pp 233-270.

Goss-Custard, J. D., Kay, D. G. & Blindell, R. M. 1977 The density of migratory and overwintering Redshank, *Tringa totanus* (L.) and Curlew, *Numenius arquata* (L.), in relation to the density of their prey in south-east England. *Estuarine and Coastal Marine Science* **5**, 497-510.

Kelsey, M. G. & Hassall, M. 1989 Patch selection by Dunlin on a heterogeneous mudflat. *Ornis Scandinavica* **20**, 250-254.

Myers, J. P., Wiliams, S. L. & Pitelka, F. A. 1980 An experimental analysis of prey availability for Sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. *Canadian Journal of Zoology* **58**, 1564-1574.

Pienkowski, M. W. 1980 Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. Proceedings IWRB Symposium on Feeding Ecology of Waterfowl 1977. *Verhandlungen der Ornithologischen Gesellschaft in Bayern* **23**, 105-124.

Quammen, M. L. 1982 Influence of subtle substratum differences on feeding by shorebirds on intertidal mudflats. *Marine Biology* **71**, 339-343.

Rands, M. R. & Barkham, I. P. 1981 Factors controlling within-flock feeding densities in three species of wading birds. *Ornis Scandinavica* **12**, 28-36.

Recher, H. F. & Recher, J. A. 1969 Some aspects of the ecology of migrant shorebirds. II Aggression. *The Wilson Bulletin* **81**, 140-154.

Ricklefs, R. E. & Lau, M. 1980 Bias and dispersion of overlap indices: results of some Monte Carlo simulations. *Ecology* **61**, 1019-1024.

Stinson, C. H. 1977 The spatial distribution of wintering black-bellied plovers. *Wilson Bulletin* **89**, 470-472.

Wolff, W. J. 1969 Distribution of non-breeding waders in an estuarine area in relation to the distribution of their food organisms. *Ardea* **57**, 1-28.

Zwarts, L. 1976 Density-related processes in feeding dispersion and feeding activity of Teal (*Anas crecca*). *Ardea* **64**, 192-207.

Zwarts, L. 1981 Habitat selection and competition in wading birds. In: *Birds of the Wadden Sea*. (Smit, C. J. & Wolff, W. J., eds). A. A. Balkema, Rotterdam, pp 271-278.

APPENDIX 7.1

Bird species and the two-letter codes used in Fig 7.5.

Code	Bird species
CS	Curlew Sandpiper
LS	Little Stint
RP	Ringed Plover
GP	Grey Plover
MS	Marsh Sandpiper
GR	Greenshank
KP	Kittlitz's Plover
WP	Whitefronted Plover
BP	Blacksmith Plover

CHAPTER 8

AGGRESSIVE INTERACTIONS AMONG MIGRANT AND RESIDENT WADERS AT THE BERG RIVER ESTURY, SOUTRH AFRICA

SUMMARY

Aggressive interactions between waders were studied at the Berg River estuary from December 1987 to March 1990. Interactions with conspecifics accounted for 91% of all aggressive encounters. Most aggressive interactions involved displacement chases.

Aggression indices of migrant waders varied seasonally and, for most species, were higher during the austral winter than summer. Grey Plovers had the highest aggression indices during the austral summer. Visual foragers were more aggressive than tactile foragers, and resident species were more aggressive than migrant species.

Aggression rates of tactilely-foraging Curlew Sandpipers were negatively correlated with their own density, and their feeding success decreased as their aggression level increased: the reverse was true for Kittlitz's Plovers. Aggression rates of visually-foraging Grey Plovers were positively correlated with the biomass of nereid worms in the substratum. There was also a positive correlation between the aggression rates of Grey Plovers and their own density but only in the post-migration period.

The dispersion of migrant waders within the Berg River estuary during the austral summer is determined primarily by feeding conditions at preferred foraging sites rather than by density-dependent factors and competition. Competitive interactions, however, probably take place during the winter.

INTRODUCTION

Aggressive interactions are important in influencing the spacing behaviour of shorebirds (Burger *et al.*, 1979). It has been proposed that visually-foraging birds are well dispersed on the foraging grounds because they are more susceptible to intraspecific aggression than are tactilely-foraging birds, which tend to forage in dense flocks (Goss-Custard, 1976). In support of this, it has been shown that the foraging rate of tactilely-foraging birds is unaffected at high bird density, but decreases for visually-foraging birds as their density increases (Goss-Custard, 1976; Silliman *et al.*, 1977; Chapter 7). A decrease in the intake rate of birds at high foraging densities has usually been attributed to increased aggression between the birds. However, increased pressure on food resources at high bird density might lead to a decrease in prey availability and, consequently, a decrease in the intake rate. No studies to date have shown to what extent these variables interact to influence foraging efficiency of birds.

Most studies of aggression between shorebirds have concentrated on migratory species during the nonbreeding season when they form large, mixed-species assemblages. During the nonbreeding season, migrant waders are often sympatric with resident congeners. Although coexistence between resident and migrant species has been studied with regard to diet and foraging microhabitat (Strauch & Abele, 1979), no attempts have been made to establish how aggressive interactions may influence their coexistence.

The aim of this study was to examine the aggressive interactions of both migrant and resident waders on a seasonal basis, and to assess their importance in influencing dispersion patterns of waders at the Berg River estuary. Aggressive interactions are examined in relation to density of both birds and prey, and their influence on the foraging efficiency of both tactile and visual foragers is investigated.

METHODS

The study period extended from December 1987 to April 1989. Twice a month, observations of birds were made at each of four sites, A, B, C and D, each of 2 000 m^2 (25 x 80 m) (Fig 2.1). The sample period was a daytime low tide during which the area was constantly scanned and every aggressive interaction was recorded. These included:

I Species involved.

II Which species was the aggressor and which the recipient.

III The intensity of the encounter; measured on a 5-point scale of increasing intensity:

1. *Threat*: a threatening posture only.
2. *Displacement*: one bird makes direct contact with another, causing it to move from its foraging site.
3. *Chase*: one bird chases another or both birds are involved in a run.
4. *Attack*: one bird physically attacks another either on the ground or from the air.
5. *Fight*: the recipient of an attack retaliates.

Within the study plots, the numbers of foraging and roosting birds were recorded at 20 minute intervals: average densities per season are given in Appendix 8.1. One minute focal bird observations were used to determine the foraging rate (total number of pecks) and success rate (total number of successful pecks) of foraging birds. A detailed description of the methods used is given in Chapters 4 and 5. Once a month, benthic invertebrates at the study sites were sampled. Details of the method used are described in Chapter 2.

The intra- and interspecific aggression indices per low tide for each species were calculated using the following formulae, modified from the aggression indices of Burger *et al* (1979):

$IAI=\{(1*N_1)+(2*N_2)+(3*N_3)+(4*N_4)+(5*N_5)\}/\{D_1*(T/60)\}$

$IEI=\{(1*N_1)+(2*N_2)+(3*N_3)+(4*N_4)+(5*N_5)\}/\{(D_1+D_2)*(T/60)\}$

where:

IAI = Intraspecific aggression index

IEI = Interspecific aggression index

N_1 = Total number of threats

N_2 = Total number of displacements

N_3 = Total number of chases

N_4 = Total number of attacks

N_5 = Total number of fights

D_1 = Average number of individuals of species A

D_2 = Average number of individuals of species B

T = Time of tidal exposure (min)

Each aggression index was expressed per hour. Aggression indices were averaged within a season. Winter was considered to extend from May to August and summer from September to April. All aggressive interactions of migrant and resident waders were summed over the each tidal cycle and divided by their total numbers and time of tidal exposure (in min) to give a total aggression rate per bird per minute. The average of the two monthly counts were used to provide an aggression rate per month.

Additional observations of aggressive behaviour were made in October 1989 at mudflat B and in December 1989 and March 1990 at mudflat A, during the period when migrant waders are most abundant. Birds were counted every 15 minutes over the intertidal mudflat of approximately 2.6 ha at mudflat A and 4.4 ha at mudflat B.

The area was scanned for 15 minute periods throughout the period of daytime tidal exposure and the frequency and intensity of aggressive interactions were recorded in the way described above. Feeding rates of birds were not recorded, nor were invertebrate samples collected.

RESULTS

Intra- and interspecific aggression

Intraspecific aggression indices were higher than interspecific aggression indices for both migrant and resident waders (Table 8.1). Intra- and interspecific aggression indices varied seasonally, with aggression indices during the winter being higher than during the summer for most of the species. Overall, resident waders were more aggressive than migrants during the winter.

Grey Plovers and Curlew Sandpipers had the highest aggression indices during the summer of 1987/88 and Ringed Plovers and Grey Plovers during the summer of 1988/89. Blacksmith Plovers during the winter months had the highest aggression index of all the birds.

The intensity of aggression varied between species, but chasing was the most common form of aggression during both intra- and interspecific interactions by both migrants and residents (Tables 8.2-8.4). Overall, chase and displacement predominated in the aggressive encounters among the migrant waders (75% of all encounters - $X^2=405$, $df=1$, $p<0.0001$), whereas chase and attack was most common among the residents (87% of all encounters - $X^2=442$, $df=1$, $p<0.0001$). This pattern was determined mainly by the fact that plovers predominated among the resident waders and visually-foraging plovers use chase and attack as the most common form of aggression ($X^2=840$, $df=1$, $p<0.0001$). Chase and displacement

Table 8.1. Average intra- and interspecific aggression indices (±SD) for migrant and resident waders at four study sites combined from December 1987 to April 1989. N = number of sample periods = number of low tides when birds were present; N_1 = number of low tides when aggression was recorded.

	SUMMER 1987/88					SUMMER 1988/89					WINTER 1988				
		Intraspecific Aggression		Interspecific Aggression			Intraspecific Aggression		Interspecific Aggression			Intraspecific Aggression		Interspecific Aggression	
Species	N	N_1	Index	N_1	Index	N	N_1	Index	N_1	Index	N	N_1	Index	N_1	Index
MIGRANT WADERS															
Curlew Sandpiper	23	10	0.31 (0.37)	3	0.005 (0.017)	50	26	0.07 (0.17)	3	0.002 (0.008)	7	4	1.11 (1.27)	2	0.053 (0.094)
Grey Plover	25	5	0.43 (1.01)	6	0.034 (0.100)	45	9	0.30 (1.02)	11	0.078 (0.313)	8	-	0.00	-	0.000
Greenshank	25	3	0.14 (0.43)	1	0.003 (0.014)	36	5	0.17 (0.45)	1	0.002 (0.012)	14	4	1.41 (2.47)	-	0.000
Ringed Plover	16	3	0.12 (0.34)	-	0.000	32	7	0.36 (1.65)	2	0.007 (0.029)	-	-	-	-	-
Little Stint	13	2	0.03 (0.08)	1	0.001 (0.002)	21	1	0.27 (1.21)	-	0.000	-	-	-	-	-
RESIDENT WADERS															
Kittlitz's Plover	10	3	0.10 (0.20)	2	0.027 (0.082)	26	4	0.09 (0.22)	2	0.001 (0.006)	19	15	4.52 (6.37)	3	0.031 (0.083)
Whitefronted Plover	10	1	0.21 (0.69)	3	0.297 (0.598)	34	11	1.44 (3.51)	4	0.041 (0.154)	23	10	1.90 (3.09)	1	0.010 (0.050)
Blacksmith Plover	12	1	0.23 (0.79)	-	0.000	4	-	0.00	1	3.325 (6.65)	14	7	10.68 (33.59)	4	0.590 (1.672)
Blackwinged Stilt	9	1	0.21 (0.63)	-	0.000	9	-	0.00	-	0.000	13	3	1.39 (3.15)	1	0.481 (1.733)

Table 8.2. The percentage (%) and, in parentheses, the total number of aggresive intraspecific interactions between migrant waders observed at the Berg River estuary from December 1987 to April 1989.

Intensity	Curlew Sandpiper	Grey Plover	Greenshank	Marsh Sandpiper	Ringed Plover	Little Stint	Turnstone	Whimbrel	Total
Threat	7 (13)	12 (10)	2 (1)	-	6 (1)	-	-	-	6 (25)
Displacement	40 (80)	14 (11)	27 (13)	-	12 (2)	14 (2)	-	100 (1)	27 (109)
Chase	39 (77)	42 (34)	53 (26)	91 (41)	46 (8)	65 (9)	100 (2)	-	48 (197)
Attack	7 (14)	27 (22)	12 (6)	7 (3)	18 (3)	14 (2)	-	-	12 (50)
Fight	7 (14)	5 (4)	6 (3)	2 (1)	18 (3)	7 (1)	-	-	7 (26)

Table 8.3. The percentage (%) and, in parentheses, total number of aggressive intraspecific interactions between resident waders observed at the Berg River estuary from December 1987 to April 1989.

Intensity	Kittlitz's Plover	Whitefronted Plover	Blacksmith Plover	Blackwinged Stilt	Chestnutbanded Plover	Total
Threat	-	-	13 (6)	-	-	1 (6)
Displacement	7 (23)	10 (6)	18 (9)	-	-	9 (38)
Chase	62 (197)	76 (47)	49 (24)	50 (8)	-	62 (276)
Attack	29 (91)	13 (8)	18 (9)	19 (3)	100 (1)	25 (112)
Fight	2 (5)	1 (1)	2 (1)	31 (5)	-	3 (12)

Table 8.4. The total number of the interspecific interactions between waders observed at the Berg River estuary from December 1987 to April 1989.

Aggressor	Recipient	Threat	Displacement	Chase	Attack	Fight
Migrant wader	*Migrant wader*					
Grey Plover	Greenshank	-	1	4	-	-
Grey Plover	Curlew Sandpiper	1	3	5	1	-
Grey Plover	Turnstone	1	2	5	1	-
Grey Plover	Ringed Plover	-	-	4	1	-
Curlew Sandpiper	Greenshank	-	1	3	2	-
Curlew Sandpiper	Little Stint	-	1	1	-	-
Greenshank	Marsh Sandpiper	-	-	1	-	-
Ringed Plover	Curlew Sandpiper	-	1	1	-	-
Little Stint	Curlew Sandpiper	2	-	-	-	-
Migrant wader	*Resident wader*					
Grey Plover	Blacksmith Plover	-	-	1	-	-
Grey Plover	Blackwinged Stilt	-	2	-	-	-
Grey Plover	Kittlitz's Plover	-	-	-	1	-
Grey Plover	Whitefronted Plover	-	1	2	-	-
Curlew Sandpiper	Kittlitz's Plover	-	-	1	-	-
Curlew Sandpiper	Whitefronted Plover	-	1	1	-	-
Ringed Plover	Whitefronted Plover	-	-	-	1	-
Resident wader	*Resident wader*					
Blacksmith Plover	Blackwinged Stilt	-	-	-	1	-
Blacksmith Plover	Kittlitz's Plover	-	-	6	2	-
Whitefronted Plover	Blackwinged Stilt	-	1	-	-	-
Whitefronted Plover	Kittlitz's Plover	-	-	3	-	-
Resident wader	*Migrant wader*					
Blackwinged Stilt	Greenshank	-	-	-	1	-
Blacksmith Plover	Grey Plover	-	-	-	1	-
Kittlitz's Plover	Curlew Sandpiper	-	2	2	4	-
Kittlitz's Plover	Ringed Plover	-	-	1	-	-
Whitefronted Plover	Curlew Sandpiper	-	2	4	-	-
Whitefronted Plover	Ringed Plover	-	-	2	-	-

predominated among the tactile foragers ($X^2=304$, df=1, $p<0.0001$) which were numerically dominant among the migrant waders.

Of all the interspecific aggression initiated by migrant waders, 26% was directed at residents (Table 8.4). By contrast, 58% of all interspecific aggression by resident waders was directed at migrants ($X^2=19.87$, df=1, $p<0.0001$). Although 11 species of waders were observed in 84 interspecific aggressive interactions, 44% of these involved Grey Plovers. In all except one of these interactions, a Grey Plover was the aggressor.

Temporal and spatial variations in aggression

There were spatial and temporal differences in the aggression rates of the two most abundant migrant species; Curlew Sandpipers and Grey Plovers (Fig 8.1A & B). The aggression rate of Curlew Sandpipers during the summer was highest at sites A & B. The aggression rate peaked during the winter months and pre-migration period in both years. The peaks in aggression by Grey Plovers, on the other hand, occurred in the post- and pre-migration periods. During the austral summer they were most consistently aggressive at site B.

Kittlitz's Plover, which is the most common resident wader (Chapter 1), had a pronounced peak in aggression during the winter months (May-July) (Fig 8.1C).

Aggression in relation to bird and prey density

The overall aggression rate of migrant waders was not correlated with their own density, but was negatively influenced by total invertebrate density ($r=-0.60$, $N=15$, $p<0.02$ - Fig 8.2A). The aggression rate of resident waders, on the other hand, was positively correlated with their own density ($r=0.65$, $N=16$, $p<0.007$ - Fig 8.2B).

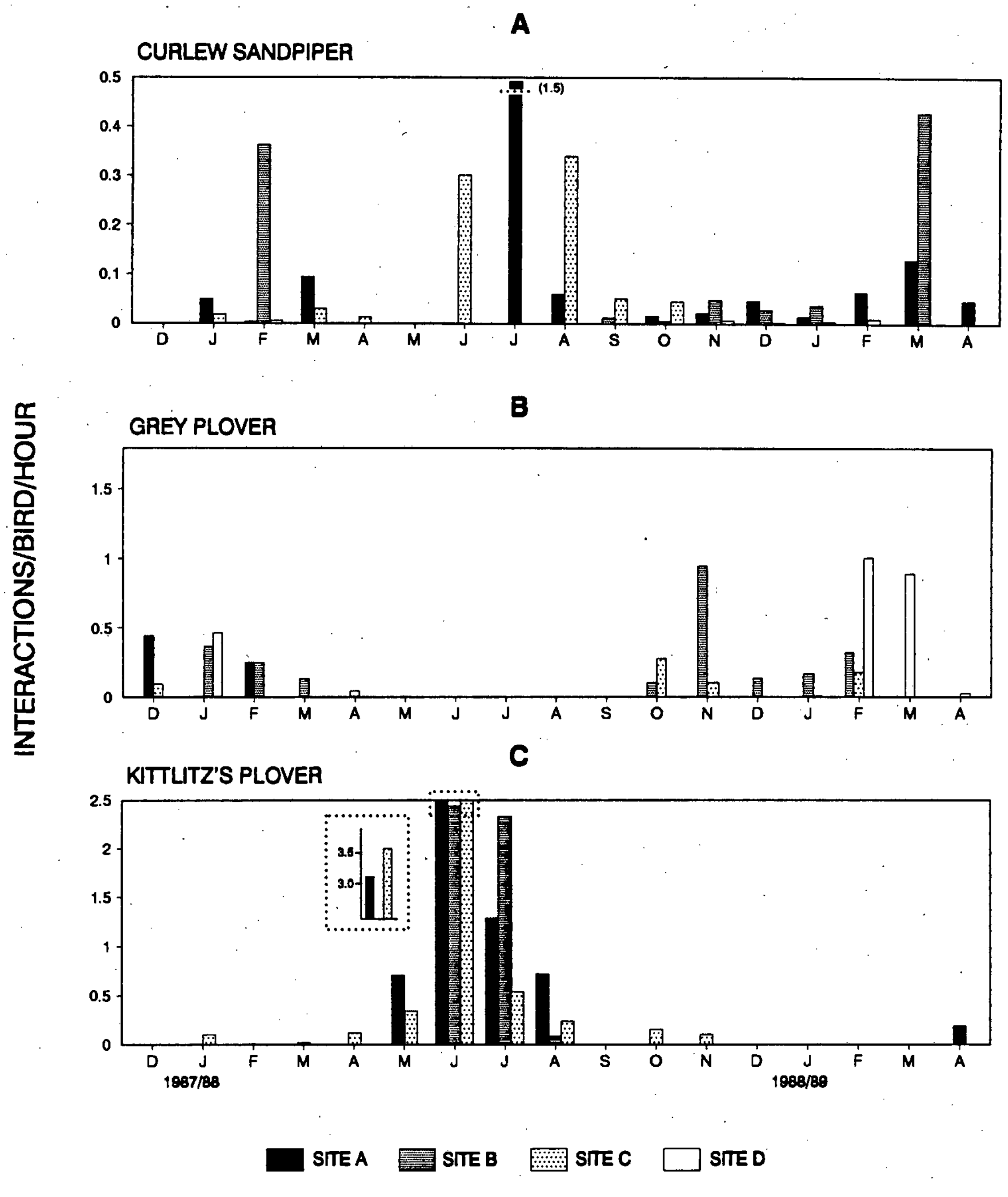


Figure 8.1. Aggression rates of Curlew Sandpipers (A), Grey Plovers (B) and Kittlitz's Plovers (C) at study sites A, B, C and D from December 1987 to April 1989.

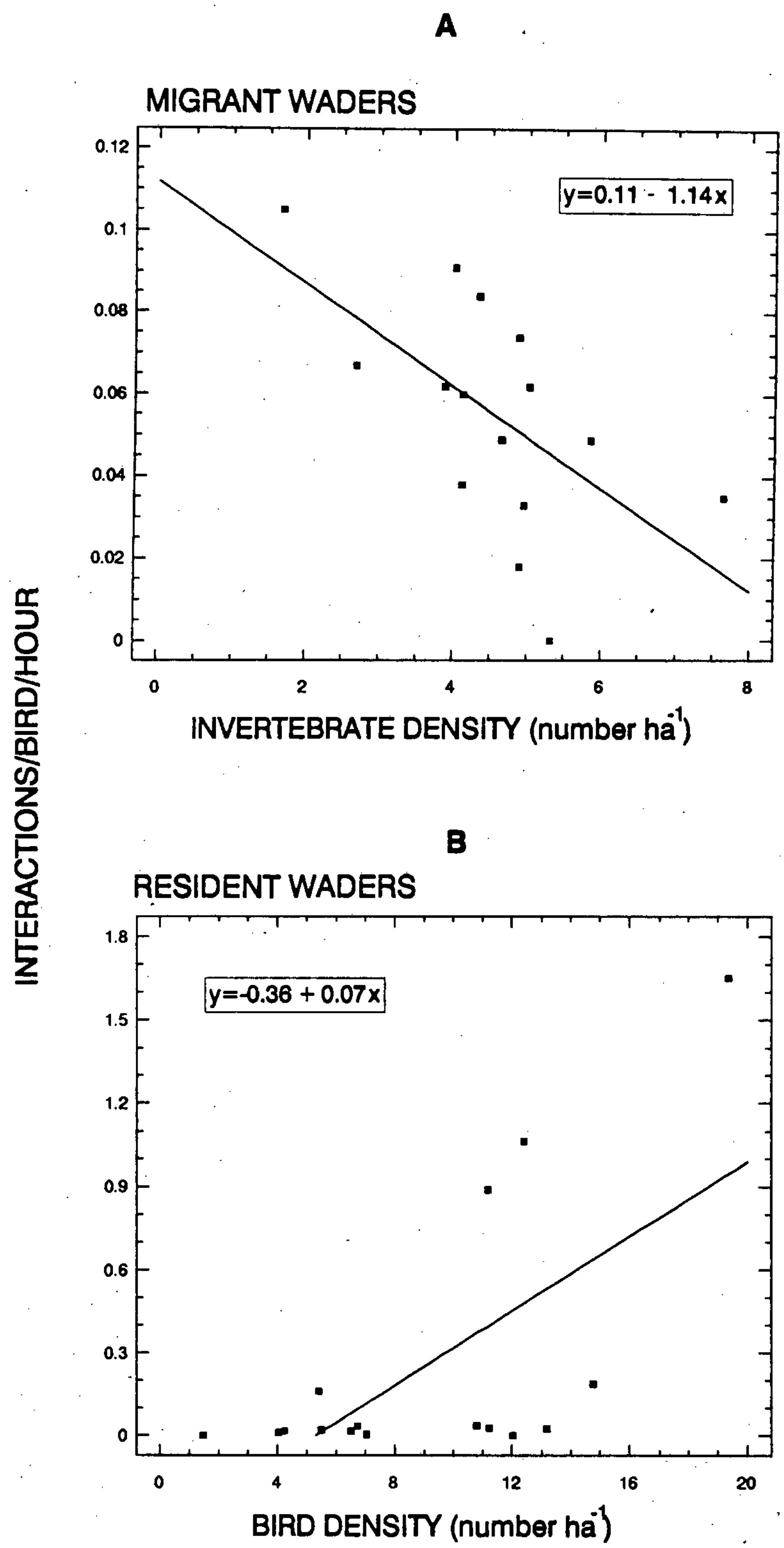


Figure 8.2. The relationships between the aggression rate of migrant waders and invertebrate density (number ha^{-1}) (A) and between the aggression rate of resident waders and bird density (number ha^{-1}) (B).

This correlation however was strongly influenced by the highest incidence of aggression among the birds in the winter months.

At mudflat A, where Curlew Sandpipers occurred at their highest density, their aggression index decreased as their own density increased, both over the entire study period ($r=-0.79$, $N=17$, $p<0.002$ - Fig 8.3) and within one low tide period in December (see methods) ($r=-0.88$, $N=8$, $p<0.004$). There was also a negative correlation between the aggression index of Curlew Sandpipers and the density of their favoured prey, *Ceratonereis keiskama* ($r=-0.53$, $N=17$, $p<0.03$). Since the density of Curlew Sandpipers is strongly correlated with the density of *Ceratonereis keiskama* (Chapter 7), partial correlation analysis was used to determine to what extent bird and prey density interact to influence the aggression of birds. When nereid density was held constant, the correlation between the aggression index of Curlew Sandpipers and the density of conspecifics was significant ($r=-0.69$, $N=17$, $p<0.05$). However, when bird density was held constant, aggression rate was not influenced by variation in nereid density ($r=-0.06$, $N=17$, $p>0.05$). This implies that the density of conspecifics is the primary determination of Curlew Sandpiper aggression.

Grey Plovers occurred at highest density at mudflat B (Chapter 7). Pooling data from the full duration of the study, there was no relationship between the density of Grey Plovers and their aggression rates or aggression indices at this site. However, when Grey Plovers arrived at the estuary in October, aggression rates at site B were strongly influenced by the density of birds ($r=0.96$, $N=7$, $p<0.0006$ - Fig 8.4A). Aggression rates between Grey Plovers were influenced by the biomass of nereids: as nereid biomass increased, so did the incidence of aggression between Grey Plovers ($r=0.62$, $N=10$, $p<0.05$ - Fig 8.4B).

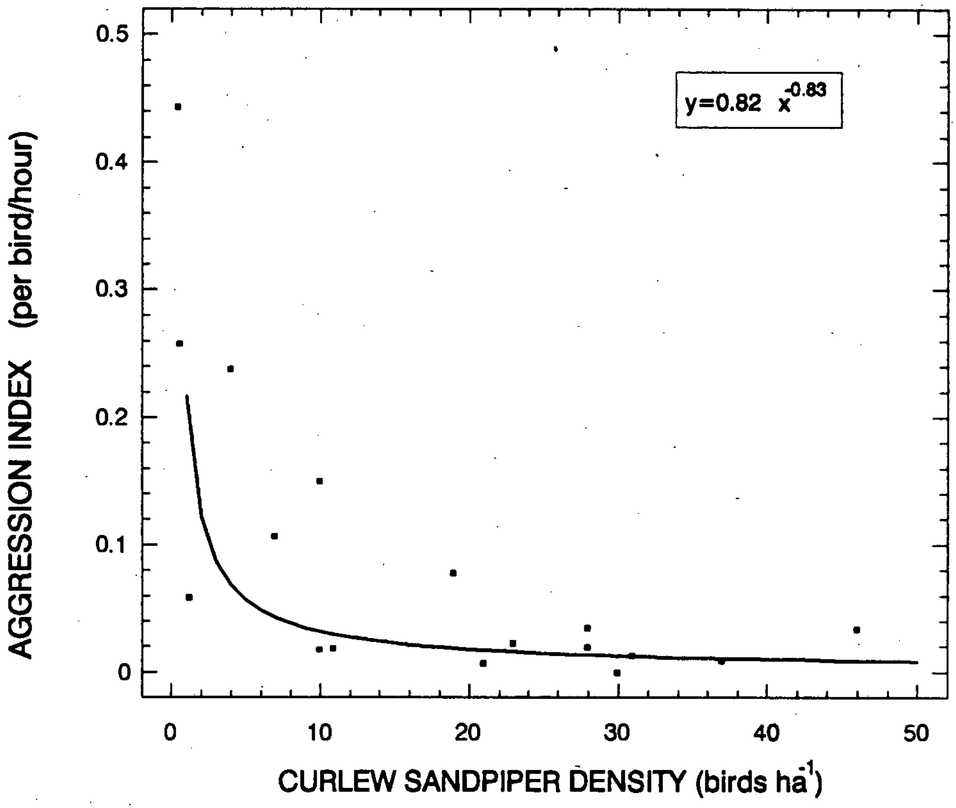


Figure 8.3. The relationship between the aggression rate of Curlew Sandpipers and their density (birds ha^{-1}).

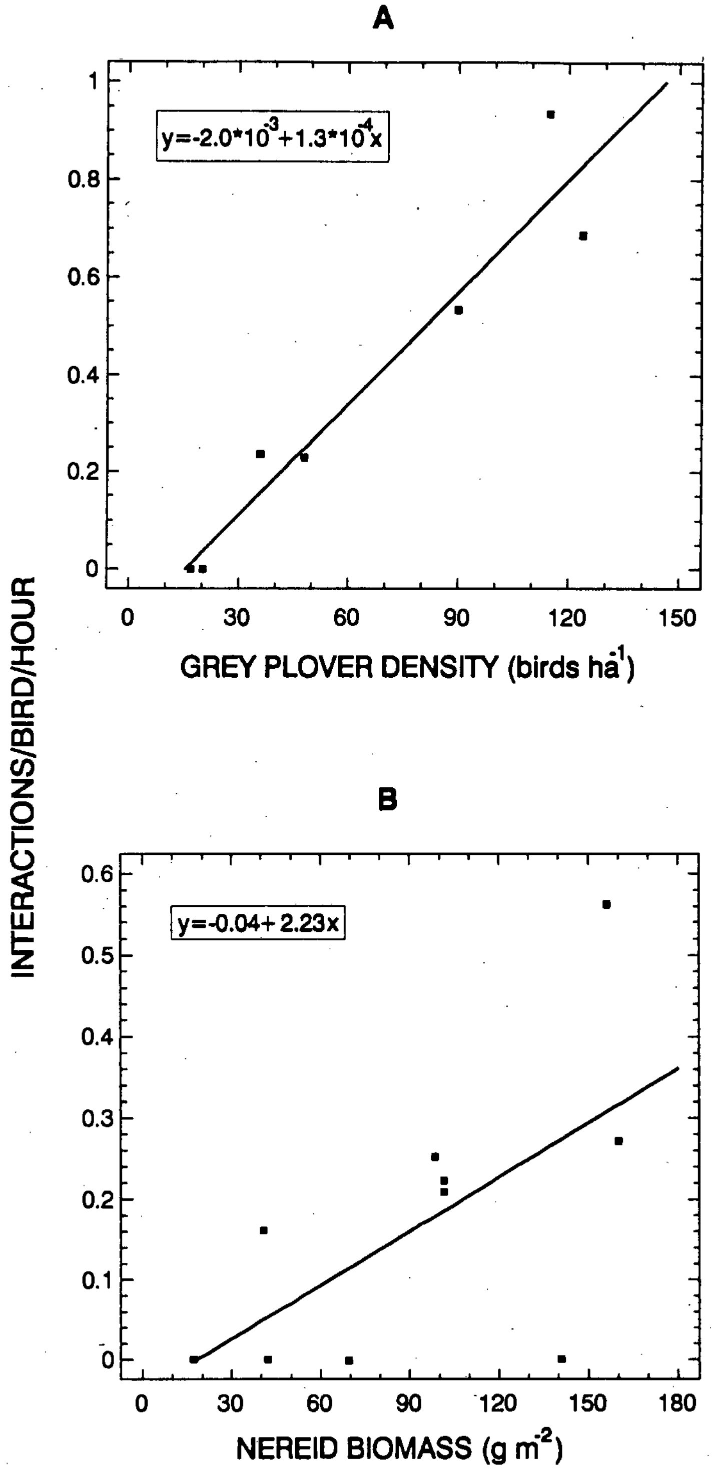


Figure 8.4. The relationships between the aggression rate of Grey Plovers and their density in October (birds ha^{-1}) (A) and nereid biomass (g m^{-2}) throughout the seventeen month study period (B).

Foraging efficiency in relation to aggression

Aggressive interactions negatively influenced the foraging rate of Curlew Sandpipers at site A ($r=-0.59$, $N=17$, $p<0.02$ - Fig 8.5A). The correlation was even more significant when the one outlying point was excluded from the regression ($r=-0.62$, $N=16$, $p<0.01$). By contrast, the foraging rate of Grey Plovers was not correlated with either their aggression rate or their aggression index (Fig 8.5B). The foraging rate of Kittlitz's Plovers, on the other hand, was not correlated with their aggression index but was positively correlated with their aggression rate ($r=0.61$, $N=15$, $p<0.02$ - Fig 8.5C).

DISCUSSION

Frequency and intensity of aggression

Morphologically similar individuals are likely to utilize similar food resources or foraging microhabitats, and are thus more likely to be involved in aggressive encounters over these resources than are morphologically dissimilar individuals (Recher & Recher, 1969). Most aggressive interactions at the Berg River estuary were between conspecifics. In the case of interspecific aggression, some studies have shown that the larger species are more likely to initiate and win an aggressive interaction (Burger *et al.*, 1979; Stawarczyk, 1984; Metcalfe & Furness, 1987). At the Berg River estuary, however, size-related dominance in aggression was not pronounced: in only 57% of all interspecific interactions was the larger species the aggressor (Table 8.4).

Because visual foragers can detect prey from a greater distance than tactile foragers, they should maintain a greater individual distance from conspecifics and be more aggressive in defence of this personal space (Recher & Recher, 1969). At the Berg River estuary, aggression indices of visual foragers, both migrants and residents,

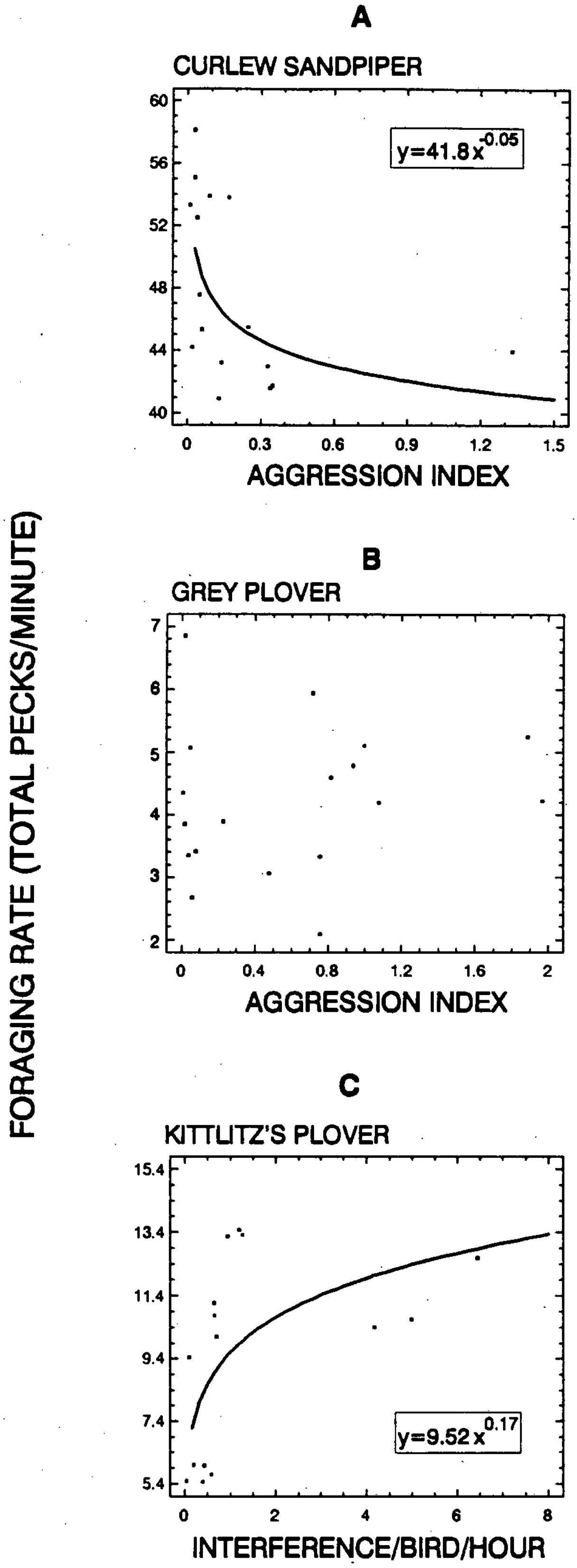


Figure 8.5. The relationships between the foraging rate of Curlew Sandpipers and their aggression index (A), the foraging rate of Grey Plovers and their aggression index (B), and the foraging rate of Kittlitz's Plovers and their aggression rate (C).

were higher than those of tactilely-foraging birds (Table 8.1). Visually-foraging birds are involved in more intense aggressive interactions than tactile foragers, and aggressive intensity, rather than frequency, may be important in influencing spacing behaviour in shorebirds (Young, 1989).

The results of the present study must be treated cautiously. Since aggression is partly influenced by the density of birds and observations were conducted within a small area, the extent of aggression might be underestimated, especially in the case of visual foragers which maintain large individual distances.

Foraging efficiency in relation to aggression

Several studies have demonstrated that the aggression rate of waders increases with increasing bird density (Recher & Recher, 1969; Goss-Custard, 1977; Burger *et al.*, 1979; Stawarczyk, 1984, Metcalfe & Furness, 1987). Recher & Recher (1969), Puttick (1981) and Stawarczyk (1984) have, however, suggested that aggression can be suppressed at very high bird densities.

An unexpected finding of this study is that the aggression index of tactilely-foraging Curlew Sandpipers decreased with increasing bird density (Fig 8.3). The potential advantages gained by birds from foraging in a flock, such as localization of patches of abundant food in a habitat where prey are distributed unevenly, or learning from other birds how to exploit prey in the most profitable way, have been detailed by several authors (e.g. Murton, 1971; Krebs *et al.*, 1972). However, there is limited evidence that flocking by birds enhances foraging efficiency *per se* (Young, 1989). A major advantage to tactilely-foraging birds in joining a flock is the reduction of time spent in vigilant behaviour, hence a higher proportion of the available time can be devoted to foraging (Tolman, 1968; Silliman *et al.*, 1977). Because Curlew Sandpipers are non-selective predators of nereids, feeding on the most abundant size classes (Chapter 4), they can achieve a high foraging success at high prey density. At high prey densities, Curlew Sandpipers may tolerate the close proximity of conspecifics if the predator detection advantage they gain from flocking outweighs any advantage they could gain from aggressive displacement of neighbours. African Marsh Harriers *Circus ranivorus*, and Peregrine and Lanner Falcons *Falco peregrinus* and *F. biarmicus* regularly hunt over the intertidal mudflats at the Berg River estuary. Curlew Sandpipers, by reducing aggression, increase their intake rate (Fig 8.5A) as their density increases (Fig 7.8A & B - Chapter 7). Curlew Sandpipers at Langebaan Lagoon in South Africa, on the other hand, suppress their aggression when foraging at dense aggregations of dipteran larvae, presumably in order to enhance foraging efficiency and capitalize on the availability of a rich food supply (Puttick, 1981).

Although visually-foraging Grey Plovers are more subject to mutual interference than are tactile foragers, their aggression was independent of bird density over the entire residence period. However, a significant correlation between aggression rate of Grey Plovers and density of conspecifics existed during the post-arrival period, in October, when new territories are established (Fig 8.4A). The negative correlation between the foraging rate of Grey Plovers and the density of conspecifics (Chapter 7 - Fig 7.9A) might therefore be a direct consequence of the increased incidence of aggression among the territorial birds.

Grey Plovers become more aggressive as the biomass of their preferred prey increases (Fig 8.4B). Myers *et al.*, (1979) suggested that territories are more likely to be established where prey density is high. Grey Plovers at the Berg River estuary are selective foragers and take the larger sizes of prey independently of their abundance (Chapter 4). Furthermore, their ingestion rate is positively correlated with the biomass of the preferred sizes of nereids in the substratum (Fig 7.10 - Chapter 7).

Grey Plovers at the Berg River estuary apparently obtain control of profitable patches by being more aggressive and territorial.

Are the dispersion patterns of waders at the Berg River estuary shaped by competition?

It has been shown in Chapter 7 that birds on the Berg River estuary select mudflats where the density or biomass of their preferred prey is highest and where they can feed most efficiently. Although the aggression rate of both Curlew Sandpipers and Grey Plovers is highest in these preferred sites (Fig 8.1), the aggression rate of Curlew Sandpipers decreases with increasing bird density and that of Grey Plovers is independent of their density. This implies that shifts in habitat use by these species on the Berg River estuary, detailed in Chapter 7, might not be density-dependent, but rather a response to other factors. I suggest that feeding conditions at the birds' preferred sites are responsible for the observed movement of birds within the estuary for the following reasons.

Deposition of algae *Cladophora* sp. occurred on the Berg River estuary in the summers of 1987/88 and 1988/89. Deposition in the latter summer was, however, much more extensive than in the summer of 1987/88 (Fig 2.2 - Chapter 2). Algae have a profound impact on the population dynamics of invertebrates and can cause substantial changes in their numbers and distribution (Chapter 2). Additionally, heavy deposition of algae might restrict access of birds to certain invertebrate prey in the substratum. The distribution of *Cladophora* within the estuary varied between mudflats with respect to both the time and extent of deposition (Fig 2.2 - Chapter 2). Birds responded to these temporal changes in feeding conditions by moving between mudflats in search of suitable foraging areas. In December 1987, when the deposition of algae peaked, birds abandoned site B (Fig 7.2 & 7.3 - Chapter 7) and the overall numbers of birds on the estuary also fell (Chapter 1). The coefficients of variation (CV) in foraging densities of Curlew Sandpipers and Grey Plovers in five sections of the estuary gradually decreased during the austral summer of 1987/88 (Fig 8.6). No clear pattern in the CV of any species occurred during the winter or during the summer of 1988/89. This suggests that equalization in the density of Curlew Sandpipers and Grey Plovers, respectively the most abundant and most aggressive species on the estuary, occurred during the summer of 1987/88 but not in the following seasons. The CV in the density of both *Ceratonereis* spp. also decreased during the summer of 1987/88 but did not follow this pattern during the winter or the following summer (Fig 8.7). A possible explanation for these patterns is that the relatively small amounts of algae deposited in summer 1987/88 may have prevented birds from foraging in a few of the most profitable sites, but still enabled them to track closely the distribution and abundance of their preferred prey, leading to an equalization of nereid density across the estuary. In the following year, the heavier deposition of algae resulted in more preferred areas being unavailable to birds and the influence that algae had on bird distribution was greater than the influence of prey density. In January 1989 the CV of all bird species increased considerably, reflecting an immediate response by the birds to changes in feeding conditions on the mudflats caused by the disappearance of algae from the estuary and an overall increase in the availability of prey (Chapter 2). A decrease in the numbers of Curlew Sandpipers in the suboptimal foraging mudflats and their subsequent increase at a preferred mudflat (A) was particularly evident (Fig 7.3 - Chapter 7). A high reproductive output of their preferred prey *Ceratonereis keiskama*, at mudflat A in the summer of 1989 promoted higher densities of Curlew Sandpipers at this site than in the previous summer, when the reproductive output of nereids was much lower (Chapters 2 & 3).

Taken together, the findings of this study indicate that distribution of migrant waders on the Berg River estuary during the austral summer is determined by the feeding conditions at preferred sites rather than by density-dependent factors

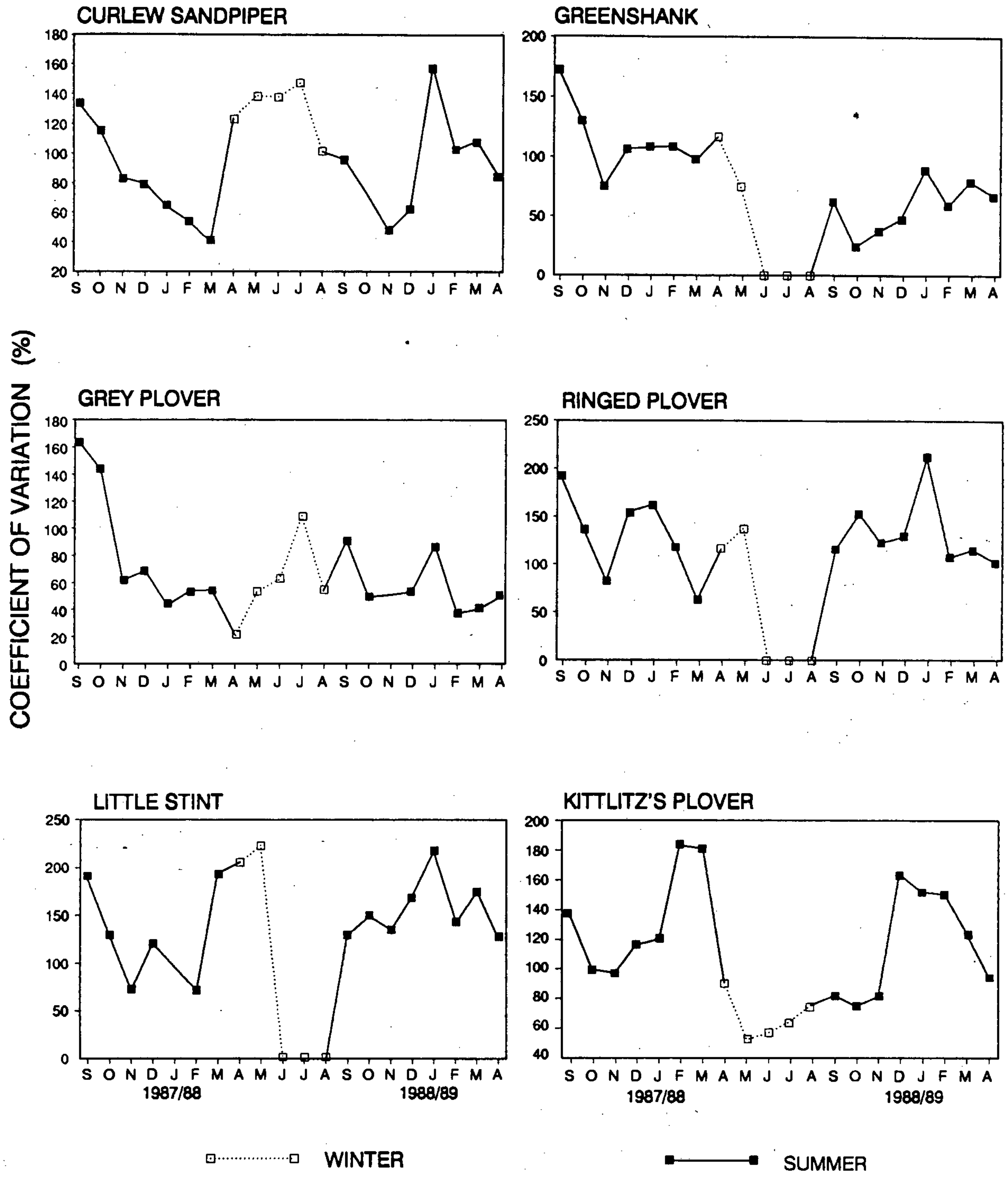


Figure 8.6. Coefficients of variation (%) in the foraging density of Curlew Sandpipers, Grey Plovers, Greenshanks, Little Stints, Ringed Plovers and Kittlitz's Plovers.

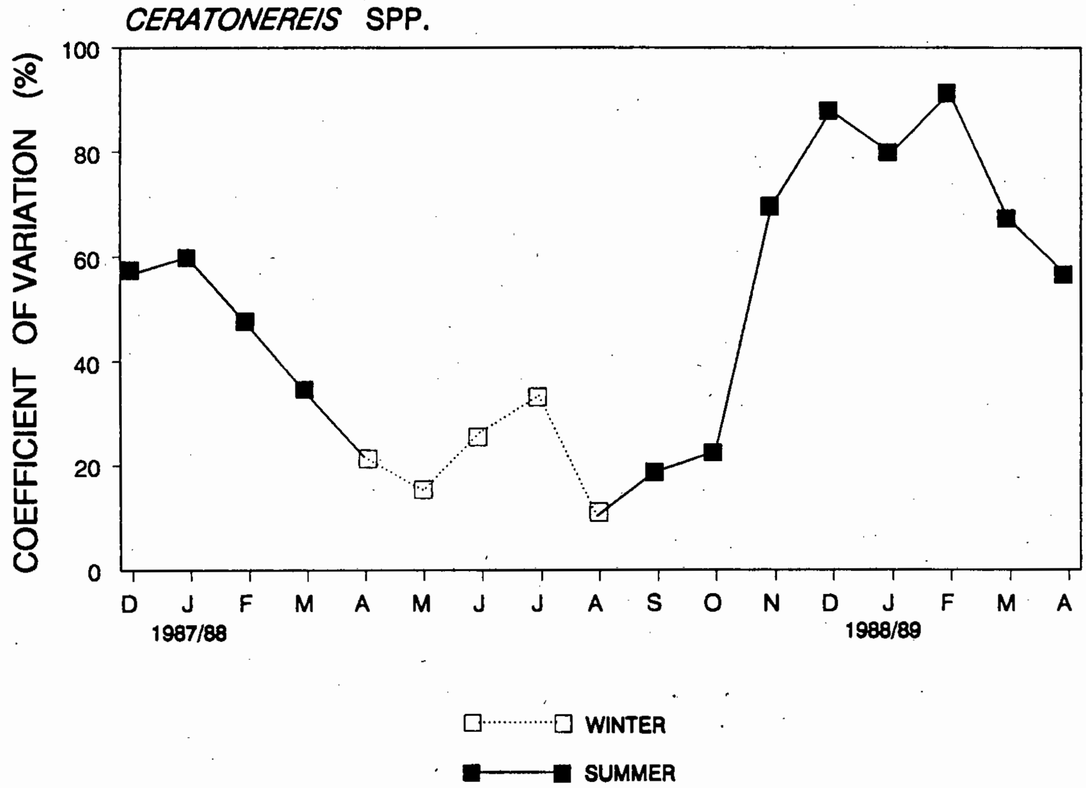


Figure 8.7. Coefficient of variation (%) in the density of *Ceratonereis* spp. across five sections at the Berg River estuary.

mediated by competition. In summer 1987/88 when feeding conditions were little influenced by algal deposition, equalization of prey density and bird density occurred across the estuary. Although the aggression level of migrant waders is unknown for much of the residence period in the austral summer of 1987/88, it is believed that the equalization of prey and bird density should reduce aggressive interactions between the birds. In both years, however, the aggression rates of Curlew Sandpipers peaked in the pre-migration period. This is believed to be influenced by the hormonal changes prior to migration and breeding, as prey availability is high at this time of year (Chapter 2 & 3).

Competitive interactions however, may take place during the winter months when the highest aggression indices of birds coincide with the lowest prey availability (Chapter 3). Resident waders were displaced from the optimal foraging areas by migrant waders during the austral summer (Chapter 7). During the winter months however, when the number of migrant waders on the estuary dropped, resident waders moved to these optimal foraging areas. Since resident waders are more abundant during winter than summer, and are more aggressive than migrant species, some competition may take place between them.

REFERENCES

Burger, J., Hawn, D. C. & Chase, J. 1979. Aggressive interactions in mixed-species flocks of migrating shorebirds. *Animal Behaviour* **27**, 459-469.

Goss-Custard, J. D. 1976 Variation in the dispersion of Redshank *Tringa totanus* on their winter feeding grounds. Ibis 118, 257-263.

Goss-Custard, J. D. 1977 The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology* **14**, 721-739.

Krebs, J. R., MacRoberts, M. H. & Cullen, J. M. 1972 Flocking and feeding in the Great Tit *Parus major* - an experimental study. *Ibis* **114**, 507-530.

Metcalfe, N. B. & Furness, R. W. 1987 Aggression in shorebirds in relation to flock density and composition. *Ibis* **129**, 553-563.

Murton, R. K. 1971 The significance of a specific search image in the feeding behaviour of the Wood-pigeon. *Behaviour* **40**, 10-42.

Myers, J. P., Connors, P. G. & Pitelka, F. A. 1979 Territoriality in non-breeding shorebirds. *Studies in Avian Biology* **2**, 231-246.

Puttick, G. M. 1981 Sex-related differences in foraging behaviour of Curlew Sandpipers. *Ornis Scandinavica* **12**, 13-17.

Recher, H. F. & Recher, J. A. 1969 Some aspects of the ecology of migrant shorebirds. II. Aggression. *The Wilson Bulletin* **81**, 140-154.

Silliman, J., Millis, G. S. & Alden, S. 1977 Effects of flock size on foraging activity in wintering Sanderlings. *The Wilson Bulletin* **89**, 434-438.

Stawarczyk, T. 1984 Aggression and its suppression in mixed-species wader flocks. *Ornis Scandinavica* **15**, 23-37.

Strauch J. G. & Abele, L. G. 1979 Feeding ecology of three species of plovers wintering on the Bay of Panama, Central America. *Studies in Avian Biology* **2**, 217-230.

Tolman, W. C. 1967 The feeding behaviour of domestic chicks as a function of rate of pecking by a surrogate companion. *Behaviour* **29**, 57-62.

Young, A. D. 1989 Spacing behaviour of visual- and tactile-feeding shorebirds in mixed-species groups. *Canadian Journal of Zoology* **67**, 2026-2028.

APPENDIX 8.1

Average density (birds ha^{-1}) of migrant and resident waders at the four study sites.

	AVERAGE DENSITY (birds ha^{-1}) (±SD)		
	Summer 1987/88	Summer 1988/89	Winter 1988
MIGRANT WADERS			
Curlew Sandpiper	53.00	51.00	0.56
	(69.80)	(54.20)	(1.35)
Little Stint	7.15	3.15	0.00
	(15.80)	(9.53)	
Ringed Plover	5.01	4.01	0.00
	(10.10)	(8.63)	
Marsh Sandpiper	2.31	0.42	0.01
	(7.31)	(1.34)	(0.08)
Greenshank	3.67	1.76	1.49
	(4.29)	(3.50)	(3.87)
Grey Plover	3.92	2.99	0.22
	(2.90)	(2.87)	(0.50)
Bartailed Godwit	0.03	0.17	0.00
	(0.20)	(0.73)	
Whimbrel	0.14	0.09	0.02
	(0.37)	(0.26)	(0.08)
Turnstone	0.00	0.21	0.00
		(0.66)	
Sanderling	0.00	<0.01	0.01
		(0.04)	(0.08)
Ruff	0.00	<0.01	0.00
		(0.03)	
Curlew	0.00	<0.01	0.00
		(0.02)	
RESIDENT WADERS			
Kittlitz's Plover	6.99	1.75	9.02
	(13.20)	(3.93)	(14.50)
Whitefronted Plover	0.67	3.69	2.13
	(1.52)	(7.60)	(2.16)
Blackwinged Stilt	0.59	0.28	1.19
	(1.28)	(0.93)	(2.87)
Blacksmith Plover	0.68	0.03	0.86
	(1.18)	(0.14)	(1.55)
Avocet	0.00	0.05	0.04
		(0.31)	(0.27)
Chestnutbanded Plover	0.01	0.00	0.27
	(0.06)		(0.40)
Threebanded Plover	0.00	<0.01	0.18
		(0.03)	(0.66)

CHAPTER 9

ARE DISPERSION PATTERNS OF PALEARCTIC WADERS SHAPED BY COMPETITION?

INTRODUCTION

Many species of Holarctic-breeding waders exhibit "leap-frog" migration patterns, whereby populations which breed at high latitudes migrate farther and spend the nonbreeding season in more southerly areas than populations which breed at temperate latitudes, the former generally being smaller birds (Salomonsen, 1955; Boland, 1990). In species with distinct sexual dimorphism, the smaller sex, usually females, migrate farther south than the larger males (Mayr, 1939; Myers, 1981).

Hypotheses have been put forward to explain this phenomenon which can be grouped into two categories: those which invoke competition as a forcing mechanism and those which do not.

In the latter category two hypothesis have been erected. It has been suggested that larger birds should winter farther north, because physiologically they are better adapted to withstand cold temperatures than small birds (Bergmann's Rule). However, this does not provide an adequate explanation of wader dispersion patterns (Myers, 1981; Ketterson & Nolan, 1983). A second hypothesis predicts that survivorship of migrants during the nonbreeding season is evolutionarily linked to the length of the breeding season (Greenberg, 1980). There is a strong selection pressure for birds breeding at high latitudes to migrate further away from the breeding areas to more "benign" wintering sites where their survival rate is high. According to Greenberg (1980), the benefits of increased survival exceed the costs of long distance migration and compensate for relatively low productivity. Although this model received strong criticism in respect to waders (Pienkowski & Evans, 1985), no conclusive evidence has been presented to reject its predictions.

A second group of hypotheses supposes that competition for resources during either the breeding or non-breeding season is an important factor in explaining the phenomenon of "leap-frog" migration.

Alerstam and Hogstedt (1980) proposed that birds which breed at temperate latitudes, where the onset of spring is unpredictable, should remain, during the nonbreeding season, in the same climatic region as their breeding sites in order to respond quickly to favourable breeding conditions. According to this hypothesis, Arctic-breeding species may migrate further away from their breeding grounds and still return at the optimal breeding time by using their 'circannual clock'. The underlying assumption of this hypothesis is that the onset of spring at Arctic latitudes is more predictable than at temperate latitudes. However, evidence has been presented that this is not the case, and the model has been criticized for incorrect assumptions (Slagsvold, 1982; Pienkowski *et al.*, 1985).

An alternative "winter competition" model proposed by Pienkowski and Evans (1984, 1985) predicts that it is advantageous for all birds to stay as close to the breeding grounds as possible during the nonbreeding season but that some are prevented from doing so by competition. A prediction of this model is that competition for winter resources (food) during the nonbreeding season should be greater at north temperate sites than in tropical and south temperate areas. To satisfy this prediction it needs to be shown that the intensity of competition decreases with increasing distance from the breeding grounds. The intensity of competition at the Berg River estuary should thus be demonstrably lower than that at estuaries in northwestern Europe.

In this Chapter, the results of my studies at the Berg River estuary are summarized and discussed in the light of current models for dispersion patterns of migratory shorebirds.

Impact of birds on their prey populations

The density of Palearctic-breeding migratory waders at the Berg River estuary during the austral summer is one of the highest on the east Atlantic seaboard (Chapter 1). The rate of prey removal consequently is high (404 g $ha^{-1}d^{-1}$). However, due to the high productivity of the estuary, the cumulative predation by waders represents only 17% of the annual production of intertidal prey. A bird-exclusion experiment established during the three months prior to northward migration confirmed that the birds have little measurable impact on their prey populations (Chapter 6). This contrasts with the results from north temperate estuaries where, despite relatively low bird densities, substantial reductions in the densities of prey have been reported (O'Connor & Brown, 1977; Evans, 1979; Quammen, 1984).

Although some migratory waders at the Berg River estuary apparently experience a negative energy balance throughout most of the austral summer if they feed only on intertidal mudflats, these energy deficits are less that those reported from localities in western Europe. The evidence indicates that birds meet their increased energy requirements for pre-migratory weight gain by increasing the duration, and perhaps intensity, of nocturnal foraging, and by the use of supplementary feeding grounds during the daytime high tide period.

Partitioning of food resources

Interspecific competition for food may result in the partitioning of food and space resources and the withdrawal of species to exclusive niches in which they will exploit the resources more efficiently than other birds, because they are better adapted to do so (Schoener, 1982). Such specialization and narrowing of niches should occur when food resources become scarce (Holmes & Pitelka, 1968). When food resources are abundant a high degree of dietary overlap is predictable. Migratory sandpipers seem better adapted to exploiting limited resources on their nonbreeding grounds in Florida, where they exhibit a low niche breadth, than to exploiting abundant summer resources in the Canadian Arctic (Baker & Baker, 1973).

At the Berg River estuary, dietary overlaps between species were high. However, there was clear separation between species in the preferred size classes of their principal prey, nereid worms. Visually-foraging plovers fed on the largest nereids regardless of their abundance. Curlew Sandpipers, predominantly tactile foragers, consumed different sized worms in proportion to their occurrence in the substratum.

Although it was impossible to establish the degree of dietary overlap between morphologically similar species, it was shown that Grey and Blacksmith Plovers included different proportions of two nereid species in their diet in areas where they co-occurred. Seasonal variations in the diet of birds were well linked to seasonal changes in the availability of their prey rather than to interspecific interactions as well as the low prey diversity.

Habitat segregation

The dispersion patterns of birds at the Berg River estuary can be linked to the distribution of their preferred prey as well as to abiotic factors which affect their foraging efficiencies. Birds preferred those sites where they could feed most efficiently. Tactile foragers preferred mudflats with high densities of nereids, muddy substrata and minimal vegetation cover. These conditions allowed them to reduce the cost of energetically expensive tactile foraging. For visual foragers, which can assess the sizes of prey prior to consuming them, the biomass rather than density of their preferred prey was important in determining their distribution. The extent of vegetation cover on the mudflats also influenced their choice of foraging site, presumably in relation to variations in the surface activity of prey.

If competition plays a rôle in determining the distribution of species within the estuary during the austral summer, the degree of interspecific spatial segregation between competing species should increase as the overall density of birds increases within the estuary. The degree of spatial segregation should also be greater in years of high bird numbers than in years of low bird numbers. At the Berg River estuary no species pairs showed a clear pattern of decreasing spatial overlap as bird numbers increased over the four first months of their residence. In addition, there was congruence between the indices of habitat overlap among the majority of species pairs in a year of high bird numbers as well as in a year of relatively low bird numbers.

At the Berg River estuary, therefore, the observed patterns of resource partitioning in terms of both food and space are consequences of inter-specific differences in foraging techniques, and could be explained without invoking direct competition *per se*.

Shifts in the habitat use

Several studies in northern hemisphere estuaries have demonstrated a sequential occupation of mudflats by birds: first arrivals occupy the most profitable sites and once carrying capacity is reached in these sections of the estuary, subdominant birds are forced, by competition, to move to suboptimal foraging grounds (Zwarts, 1976; Goss-Custard, 1977). Alternatively, the redistribution of birds might be caused by local depletion of food resources or by increased interference among the birds, both of which will reduce their intake rate (Goss-Custard, 1977). Redistribution of birds when local densities are high can therefore be seen as a consequence of increased competitive interactions among the birds.

Early occupation of profitable sites by migrant waders during the austral summer was recorded at the Berg River estuary. The redistribution of waders as summer progressed, and numbers of birds on the estuary increased, was, however, well synchronized with the deterioration of feeding conditions on their preferred sites due to deposition of algae *Cladophora* spp. In the summer, when relatively little algae was deposited, equalization of numbers of two bird species (Curlew Sandpipers and Grey Plovers, respectively the most common and most aggressive waders on the estuary) and nereid density occurred across the estuary. This pattern was not repeated in the following summer when heavier deposition of algae resulted in a more patchy distribution of birds and prevented them from tracking the density of their prey across the whole estuary. If an equalization of bird numbers is simply a response to competition, it should be most pronounced when bird numbers are highest. When algal deposition was heavy, and bird numbers were greatest, higher ceiling densities of foraging birds occurred on favoured mudflats.

I conclude, therefore, that redistribution of birds within the Berg River estuary is a response to changes in feeding conditions at different mudflats rather than to density-dependent factors mediated by competition.

Aggression

Aggression is recognized as a direct measure of competitive interaction among birds (Burger *et al.*, 1979). At high bird density, the pressure on food and space resources is also relatively high, resulting in more frequent aggressive interactions between individuals. Thus, if competition sets an upper limit to density, aggressive interactions should increase as the density of birds increases. At the Berg River estuary, the aggression index of tactilely-foraging Curlew Sandpipers decreased as their density increased, whereas that of visually-foraging Grey Plovers was independent of the density of conspecifics. In the immediate pre-migration period, however, there was an increase in the aggressive interactions which coincided with birds' increased energy demands. However, since food is most abundant at this time of the year, it is unlikely that the increased aggression levels are a consequence of exploitative competition: they may simply be due to hormonal changes and the readiness of birds to migrate and breed (Johns, 1964; Schlinger & Callard, 1990).

A considerable increase in the amount of aggression, especially among resident waders, occurred during the winter months. This was paralleled by a movement of resident waders to the optimal foraging areas which had been occupied by migrants during the austral summer. During the winter, resident waders were numerically dominant and migrant species (immature individuals) occupied suboptimal sites. This suggests that competition between waders may take place during the winter months when the availability of prey is at a minimum.

The possible rôle of competition in determining migratory patterns of shorebirds has been identified by several authors (Myers *et al.*, 1985; Cox, 1968), but a scarcity of data from the southern hemisphere has weakened the empirical basis of these models and hypotheses.

The results of this study indicate that, despite an exceptionally high density of migratory shorebirds during the austral summer at the Berg River estuary, competitive interactions are not a major force determining their distribution. The most important factor mediating their coexistence on the estuary is the superabundant availability of food throughout most of their residence period (Chapter 2). Although temporal deterioration in feeding conditions may occur due to the deposition of algae on the intertidal mudflats, the highest production of benthic invertebrates coincides with the highest energy demands of birds in the period prior to migration (Chapter 5). This contrasts with north temperate estuaries where benthic invertebrates do not reproduce until spring when most migrant waders have departed (Smit & Wolff, 1981). Despite much lower densities of birds, competition for food is more likely to occur at high northern latitudes where food resources are relatively unpredictable, scarce and where their availability may additionally be limited during spells of cold weather (Pienkowski, 1983; Evans, 1979). The carrying capacity of estuaries for waders at high latitudes might therefore be lower than those further south. If north temperate estuaries have relatively limited food resources and there is an additional risk involved in death from cold (either directly or through starvation - Davidson & Evans, 1982), then it is difficult to accept a fundamental assumption of the winter competition model that north temperate estuaries should be favoured over more southerly estuaries, unless there is a very high risk attached to the migration process itself. Although this study confirmed one of the predictions of the winter competition model, namely that competition was lower at a south temperate estuary than at estuaries further north, this observation alone still fails to prove whether long-distance migrations are undertaken by choice or are necessitated by competitive displacement. If it is advantageous for all birds to stay as close to breeding grounds as possible then the estuaries further north should always be close to their carrying capacities and consequently, the interannual variability in bird numbers during the nonbreeding season should increase in proportion to distance away from breeding grounds. Furthermore, if competition displaces birds from north temperate estuaries, the proportion of subordinate individuals (e.g. juveniles) should be less variable at north temperate estuaries than at estuaries further south. According to Hockey (in prep) the coefficient of variation in total bird numbers over a ten year period in Great Britain and South Africa are similar. Comparative data on the proportion of juvenile birds overwintering in South Africa and Great Britain also indicate little latitudinal difference.

Production of benthic invertebrates is positively correlated with mean ambient temperature and negatively with latitude, decreasing with increasing distance from the equator (Chapter 2). This suggests that a lack of extreme temperatures in the southern hemisphere might allow prolonged reproduction of invertebrates. Although data on the invertebrate productivity of tropical intertidal mudflats are lacking, observed productivity exceeds predicted productivity at all three South African localities included in the analysis (Chapter 2). It could be predicted that migratory patterns of shorebirds might be determined primarily by the productivity of invertebrate prey. The benefits of superabundant food supplies and concomitantly reduced competition in the southern hemisphere might therefore outweigh the costs of long distance migration. If there is a benefit of increased survivorship determined by favourable feeding conditions at more distant wintering localities, the findings of this study will support Greenberg's time-allocation model. If however the annual survival rate of long distance migrants is lower than the survival rate of short distance migrants, then no matter how beneficial the southern temperate estuaries are in terms of food supply, the long distance migrants have to be considered as subordinate birds displaced from north temperate estuaries by competition. Unfortunately, no comparable data on the survival rate in relation to migration distance of shorebirds from the same breeding localities are yet available (Pienkowski & Evans, 1985).

On the basis of the above evidence, it is apparent that, as yet, there is insufficient empirical data to support any of the current models of shorebird migratory patterns. A study of the intra- and interspecific survival rates of migratory shorebirds in relation to migration distance is essential for testing any of these hypotheses. The findings at the Berg River estuary throw new light on shorebird-prey relationships and interspecific competition in the southern hemisphere. I propose that a combination of high prey abundance and productivity and a reduced level of competition in the southern hemisphere may outweigh the costs incurred in long-distance migration. Studies of invertebrate productivity and shorebird-prey relationships in tropical estuaries are now required to test whether the density of migratory shorebirds is linked to invertebrate productivity across the full range of latitudes occupied by waders during the nonbreeding season.

REFERENCES

Alerstam, T. & Hogstedt, G. 1980 Spring predictability and leap-frog migration *Ornis Scandinavica* **11**, 196-200.

Baker, M. C. & Baker, A. E. 1973 Niche relationships among six species of shorebirds on their wintering and breeding ranges. *Ecological Monographs* **43**, 193-212

Boland, J. M. 1990 Leapfrog migration in North American shorebirds: intra- and interspecific examples. *The Condor* **92**, 284-290.

Burger, J., Hawn, D. C. & Chase, J. 1979 Aggressive interactions in mixed-species flocks of migrating shorebirds. *Animal Behaviour* **27**, 459-469.

Cox, G. W. 1968 The rôle of competition in the evolution of migration. *Evolution* **22**, 180-192.

Davidson, N. C. & Evans, P. R. 1982 Mortality of Redshanks and Oystercatchers from starvation during severe weather. *Bird Study* **29**, 183-188.

Evans, P. R. 1979 Adaptations shown by foraging shorebirds to cyclical variations in the activity or availability of their invertebrate prey. In: *Cyclic Phenomena in Marine Plants and Animals* (Naylor, E. & Hartnoll, R. G., eds. Pergamon Press, Oxford, pp 357-366.

Holmes, R. T. & Pitelka, T. A. 1968 Food overlap among coexisting sandpipers on the northern Alaskan tundra. *Systematic Zoology* **17**, 305-318.

Goss-Custard, J. D. 1977 The ecology of the Wash III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology* **14**, 721-739.

Greenberg, R. 1980 Demographic aspects of long-distance migration. In: *Migrant Birds in the Neotropics: Ecology, Behaviour, Distribution and Conservation* (Keast, A. & Morton, E. S., eds). Smithsonian Institution, Washington D. C., pp 493-504.

Johns, J. E. 1964 Testosterone-induced nuptial feathers in phalaropes. *The Condor* **66**, 449-456.

Ketterson, E. D. & Nolan, V. 1983 The evolution of differential bird migration. In: *Current Ornithology* Vol. I (Johanston, R. F., eds) Plenum Press, New York & London, pp 357-402.

Mayr, E. 1939 The sex ratio in wild birds. *American Naturalist* **73**, 156-179.

Myers, J. P. 1981 A test of three hypotheses for latitudinal segregation of sexes in wintering birds. *Canadian Journal of Zoology* **59**, 1527-1534.

Myers J. P., Maron, J. L. & Sallaberry, M. 1985 Going to extremes: why do Sanderlings migrate to the tropics? *Ornithological Monographs* **36**, 520-534.

O'Connor, R. J. & Brown, R. A. 1977 Prey depletion and foraging strategy in the Oystercacher *Haematopus ostralegus*. *Oecologia* **27**, 75-92.

Pienkowski, M. W. 1983 Changes in the foraging pattern of plovers in relation to environmental factors. *Animal Behaviour* **31**, 244-264.

Pienkowski, M. W. & Evans, P. R. 1984 Migratory behaviour of shorebirds in the western Palearctic. In: *Behaviour of Marine Animals, Vol 6. Shorebirds: Migration and Foraging Behaviour* (Burger, J. & Olla, B. L., eds). Plenum Press, New York & London, pp 73-123.

Pienkowski, M. W. & Evans, P. R. 1985 The role of migration in the population dynamics of birds. In: *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (Sibly, R. M. & Smith, R. H., eds). Blackwell, Oxford, pp 321-352.

Quammen, M. L. 1982 Predation by shorebirds, fish and crabs on invertebrates in intertidal mudflats: an experimental test. *Ecology* **65**, 529-537.

Salomonsen, F. 1955 The evolutionary significance of bird migration. *Det Kongelige Danske Videnskabernes Selskab, Biolgiskie Meddelelser* **22**, 1-62.

Schlinger, B. A. & Callard, G. V. 1990 Aggressive behaviour in birds: an experimental model for studies of brain-steroid interactions. *Comparative Biochemistry and Physiology* **97**, 307-316.

Schoener, T. W. 1982 The controversy over interspecific competition. *American Scientist* **70**, 586-592.

Smit, C. J. & Wolff, W. J. 1981 *Birds of the Wadden Sea*. A. A. Balkema, Rotterdam, pp 308.

Slagsvold, T. 1982 Spring predictability and bird migration and breeding times: a comment on the phenomenon of leap-frog migration. *Ornis Scandinavica* **13**, 145-148.

Zwarts, L. 1976 Density-related processes in feeding dispersion and feeding activity of Teal (*Anas crecca*). *Ardea* **64**, 192-207).