THE COMPARATIVE BIOLOGY
OF
NEW ZEALAND OYSTERCATCHERS

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by

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

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Chapter 1

INTRODUCTION

1.1 GENERAL

Oystercatchers comprise a distinctive group of mollusc-eating shorebirds. They form an extremely uniform monogeneric family which has not undergone any major adaptive radiations into a diversity of ecological niches, but rather has dispersed from original centres of distribution to occupy identical niches in new geographical localities. The uniformity of structure and habit displayed within the group has been attributed by Larson (1957) to a high ecobiotic specialisation with centripetal selection involved. Throughout their range, oystercatchers exploit identical ecological niches which require specialised habits for successful utilisation. The specialised feeding habits of oystercatchers are well documented (Murphy, 1925; Dewar, 1940; Larson, 1957; Tinbergen and Norton-Griffiths, 1964; Dare, 1966), and a natural consequence of this specialisation is that it is restrictive to adaptive radiation.

1.2 TAXONOMY

The Order Charadriiformes is composed of 13 families of wading birds. Oystercatchers belong to the Family Haematopodidae which is represented by a single genus *Haematopus* Linnaeus, 1758. Peters (1934) recognised four species (1-4 below), but contemporary taxonomists (Mayr and Amadon, 1951) describe six species as follows:-

(1) *Haematopus ostralegus* Linnaeus - World wide distribution
(2) *Haematopus leucopodus* Garnot - Southern South America
(3) *Haematopus fuliginosus* Gould - Southern and Northern Australia
(4) *Haematopus ater* Vieillot and Oudart - Central and Southern South America
(5) *Haematopus unicolor* Forster - New Zealand

(6) Haematopus bachmani Audubon - West coast of North America from California to Alaska.

The limited speciation described above is due in part to high ecobiotic specialisation. Many races of oystercatcher have been described: Peters (1934) has listed 19 subspecies and Mayr and Amadon (1951) 21. The formation of local races appears to be correlated with discontinuity of littoral distribution (Murphy, 1936). Continental races are better considered as geographical isolates of a population continuum, as subspecific characters appear to be attributable to geographical variation.

1.3 NOMENCLATURE ADOPTED FOR NEW ZEALAND SPECIES

For comparative purposes, standard nomenclature had to be adopted. It was convenient to use the nomenclature of the Check-list of New Zealand Birds (1953) as follows:

170. Haematopus ostralegus finschi Martens, 1897
South Island Pied Oystercatcher
171. Haematopus unicolor reischeki Rothschild, 1899
Variable Oystercatcher
172. Haematopus unicolor unicolor Forster, 1844
Black Oystercatcher
173. Haematopus unicolor chathamensis Hartert, 1927
Chatham Island Oystercatcher.

1.4 SPECIES CHARACTERISATION

Detailed descriptions of the species given by Oliver (1955) are summarised as follows:-

(1) South Island Pied Oystercatcher - Haematopus ostralegus finschi.

The South Island Pied Oystercatcher has very stable plumage characters which serve as distinguishing features (Plate 1.1). Williams (1963) lists three main ways of positively identifying this subspecies:

(a) when in flight, broad white bands (alar bars) may be seen along the upperwings and appear almost continuous with a white rump patch extending in a bright wedge into the middle of the back;

(b) boundaries between black and white areas are sharply defined; and,

(c) the white recess on the shoulder in the front of the wing is unique to the species.

(2) Variable Oystercatcher - Haematopus unicolor reischeki

The plumage of birds of this race is extremely variable, ranging between pied and wholly black phases (Plate 1.2). Between these two extreme phases, a great number of intermediates exist, which do not appear to have any fixed plumage patterns. Pied birds can be distinguished from H. ostralegus finschi by:

(a) the alar bar on the wing and the rump patch being restricted and not so conspicuously white;

(b) the boundaries between black and white areas being blurred with smudgy markings, especially on the breast; and,

(c) the absence of a white recess on the shoulder in front of the wing.

Entirely black forms of this race appear to be indistinguishable from typical H. unicolor unicolor. Falla, Sibson and Turbott (1966) commented, "It has been stated that the black form of reischeki is a browny black and lacks the purple gloss of the true unicolor, but this needs verification."

(3) Black Oystercatcher - Haematopus unicolor unicolor:

The plumage of this oystercatcher is entirely black. Pigment saturation within the New Zealand species reaches a maximum in this race, adults having a distinctive glossy appearance (Plate 1.3).

(4) Chatham Island Oystercatcher - Haematopus unicolor chathamensis:

The Chatham Island Oystercatcher is a pied form (Plate 1.4).

Plate 1.1

South Island Pied Oystercatcher (*Haematopus ostralegus finschi*) showing the white recess in front of the wing, the distinct boundary between the black and white areas of the plumage, and the extensive white alar bar on the wing.

Plate 1.2

Variable Oystercatcher (*H. unicolor reischeki*).
Pied phase showing mottling of the breast at the junction of black and white areas of the plumage, and the complete absence of a white recess in front of the wing. Black and "smudgy" intermediate phases are also common (from Moon, 1967).

Plate 1.3

Black Oystercatcher (*H. u. unicolor*)

Plate 1.4

Skin of Chatham Island Oystercatcher (*H. u. chathamensis*) showing the mottling of the breast at the junction of black and white areas of the breast, and the white rump patch which is intermediate in size between that of *H. ostralegus finschi* and *H. unicolor reischeki*.

Ventral view (left), dorsal view (right).

It closely resembles the pied phase of the Variable Oystercatcher of mainland New Zealand, differing only in its stouter short bill and unusually large feet. The distinctions between this form and *finschi* all involve additional dark elements as follows:

(a) the alar bar is less extensive than that of *finschi*;

(b) the boundary between black and white on the chest is indistinct; and,

(c) the area of white on the rump and lower back is reduced.

The species and races of New Zealand oystercatchers can thus be distinguished on plumage characters (except for black forms of *H. unicolor reischeki* and *H. unicolor unicolor*).

1.5 HISTORY OF NEW ZEALAND TAXONOMY

The nomenclature of the New Zealand species of oystercatcher has had a checkered career, as indicated by the following history: The earliest reference to N.Z. oystercatchers is by Latham (1785, cited by Oliver, 1955) from a pied specimen collected by one of Cook's expeditions. Gray (in Dieffenbach, 1843) recorded pied birds as common in New Zealand. The Black Oystercatcher was first discovered by Forster at Dusky Sound in 1773, but his description was not published until 1844. Pied birds breeding in inland Canterbury were referred by Potts (1870) to *Haematopus longirostris* Vieillot, the type locality of which is New South Wales. Travers (1872) used this name for specimens collected at the Chatham Islands, and Buller (1872, 1888, and 1905) subsequently applied it to all New Zealand pied oystercatchers. Rothschild (1899) gave the name *reischeki* to birds of plumage intermediate between black and pied. Martens (1897) gave a specimen from Saltwater Creek near Timaru distinctive species status *finschi*, which Mathews (1913) subsequently applied to all New Zealand pied birds as subspecies of *Haematopus ostralegus*. He restricted *longirostris* as a subspecific name for an Australian race. This classification was accepted by Hartert (1921) who later (1927) ascribed the Chatham Islands bird to

Haematopus ostralegus chathamensis. Stresemann (1927) considered black oystercatchers to be melanistic mutants of the pied *Haematopus ostralegus*, and submerged all the New Zealand oystercatchers except *chathamensis* under *Haematopus ostralegus unicolor* Forster. This synonymy was accepted by Peters (1934, 253). Falla's review (1939) retained *finschi*, *reischeki* and *unicolor* as full species and raised Hartert's *chathamensis* to species status. On the basis of plumage, voice, and general habits, Sibson (1945) referred *finschi* to a subspecies of *Haematopus ostralegus*. The Checklist of New Zealand Birds (1953) accepted this reference and tentatively placed the other pied and black birds under a single species *Haematopus unicolor* Forster with the following reservation: "It has yet to be determined whether black examples of *H. unicolor reischeki* are distinct from the typical *H. u. unicolor*. Apparently *H. unicolor* is a polymorphic species with pied birds commoner in the north (*H. u. reischeki*) and the black strain dominant in the south (*H. u. unicolor*)." Oliver (1955) considered the Checklist's classification unacceptable as it constituted excessive lumping. He described four types of oystercatcher:

(1) a smaller pied migratory species - *Haematopus ostralegus finschi*;

(2) a larger pied non-migratory species - *H. longirostris chathamensis*;

(3) a black non-migratory species - *H. unicolor unicolor*; and,

(4) birds with plumage intermediate between (2) and (3).

Oliver contended that birds in (4) were hybrids between *H. longirostris chathamensis* and *H. unicolor unicolor* because these intermediates lack fixed plumage patterns, and occur where the range of the two species overlap.

Finally, Falla et al. (1966) restored *finschi*, *reischeki*, *unicolor* and *chathamensis* to species status on the grounds that they are "strong" races.

In summary, it is evident from the views expressed above that the taxonomic status of the New Zealand oystercatchers is uncertain.

Major controversy is centred on the exact status of the coastal Variable Oystercatcher (black and large pied of Oliver, 1955). Three acceptable possibilities are outlined by Heather (1966):

(1) the black form is distinct from and tending to interbreed with a northern pied form;
(2) clinal variation is occurring within one single form; and,
(3) the northern pied birds have strong melanistic tendencies and are distinct from the southernmost black form.

1.6 AIMS OF THE STUDY

In reviewing the biological species concept Maslin (1968) considered that well-defined species should be characterised by:

A. differences involving morphology, physiology, ecology, and ethology;
B. reproductive isolation in nature from other species; and,
C. interbreeding freely within itself.

Although Mayr (1963) was opposed to including in a species definition criteria that are applicable to other taxonomic categories, such a restriction would seriously affect the efficacy of the biological species concept since it would preclude all criteria except reproductive isolation and interbreeding. The use of a wide range of criteria seems justifiable where the validity of the specific status of organisms is reinforced. The aim of this study then, was to critically examine, on a comparative basis, selected aspects of the biology of New Zealand oystercatchers to clarify their present confused taxonomic status.

Chapter 2

DISTRIBUTION AND ABUNDANCE OF WINTERING POPULATIONS

2.1 INTRODUCTION

Much of the taxonomic splitting which has occurred in the past has been the direct result of considering various forms in isolation. In some cases world-wide distribution patterns have been completely ignored and geographic relationships thus obscured. For this reason the distribution of New Zealand oystercatchers was firstly related to world patterns, and then analysed in detail within the country. The main aim of the analysis was to establish clearly the ranges of the various races. Estimates of abundance were made to determine the numerical status and dynamics of wintering populations.

2.2 METHODS

Records of distribution and estimates of abundance were extracted from several sources: (i) the early literature of ornithological discovery in New Zealand; (ii) Classified Summarised Notes (in New Zealand Bird Notes and Notornis); (iii) the Recording Scheme of the Ornithological Society of New Zealand; and, (iv) personal records and communications. Wherever possible, all population estimates were based on figures for 1967; when these were absent or unobtainable the next most recent data were used. To minimise discrepancies in counts due to seasonal fluctuations in populations, all figures were taken from censuses made in the winter months of May, June, and July by which time post-breeding dispersal and migration had ceased. Personal records were obtained by counting individual birds in flocks at high water roosts. Large flocks of more than 500 birds were counted several times and the figures accepted only if the error between successive counts was less than 5% of the total. No estimate of reliability could be placed on data from other sources so they were accepted in good faith.

2.3 WORLD DISTRIBUTION

Oystercatchers are widely distributed throughout the world and occur on most tropical, temperate and subpolar seacoasts of continents. They are absent from Polynesia and other remote oceanic islands. The northerly and southerly limits of the family range are most extensive in the breeding season when they are, respectively, Iceland and Cape Horn. Some Old World forms show a tendency to move inland, penetrating far up the valleys of great river systems. The majority of forms, however, are confined to a littoral distribution. The world distribution of oystercatcher species is shown in Fig 2.1. It is noteworthy that birds with pied plumage are the only forms that exist in the immediate neighbourhood of the Equator (nos. 3, 5, 6, 17), and that they alone extend into the cold region (nos. 10, 11). The significance of this differential colour phase distribution will be dealt with later.

2.4 NEW ZEALAND DISTRIBUTION AND ABUNDANCE

A. Ranges

The distribution of oystercatchers in mainland New Zealand is unique in that all three races have coincident ranges. This is probably due to the limited extent of the land mass which has resulted in condensed ranges (in comparison with continental forms) for resident birds. The ranges, distribution, and abundance of the New Zealand races of oystercatcher are shown in Figs 2.2, 2.3, and 2.4.

B. Distribution and Abundance

The distribution patterns of the two New Zealand species of oystercatcher are remarkably different. South Island Pied Oystercatchers (*Haematopus ostralegus*) are much more abundant than either

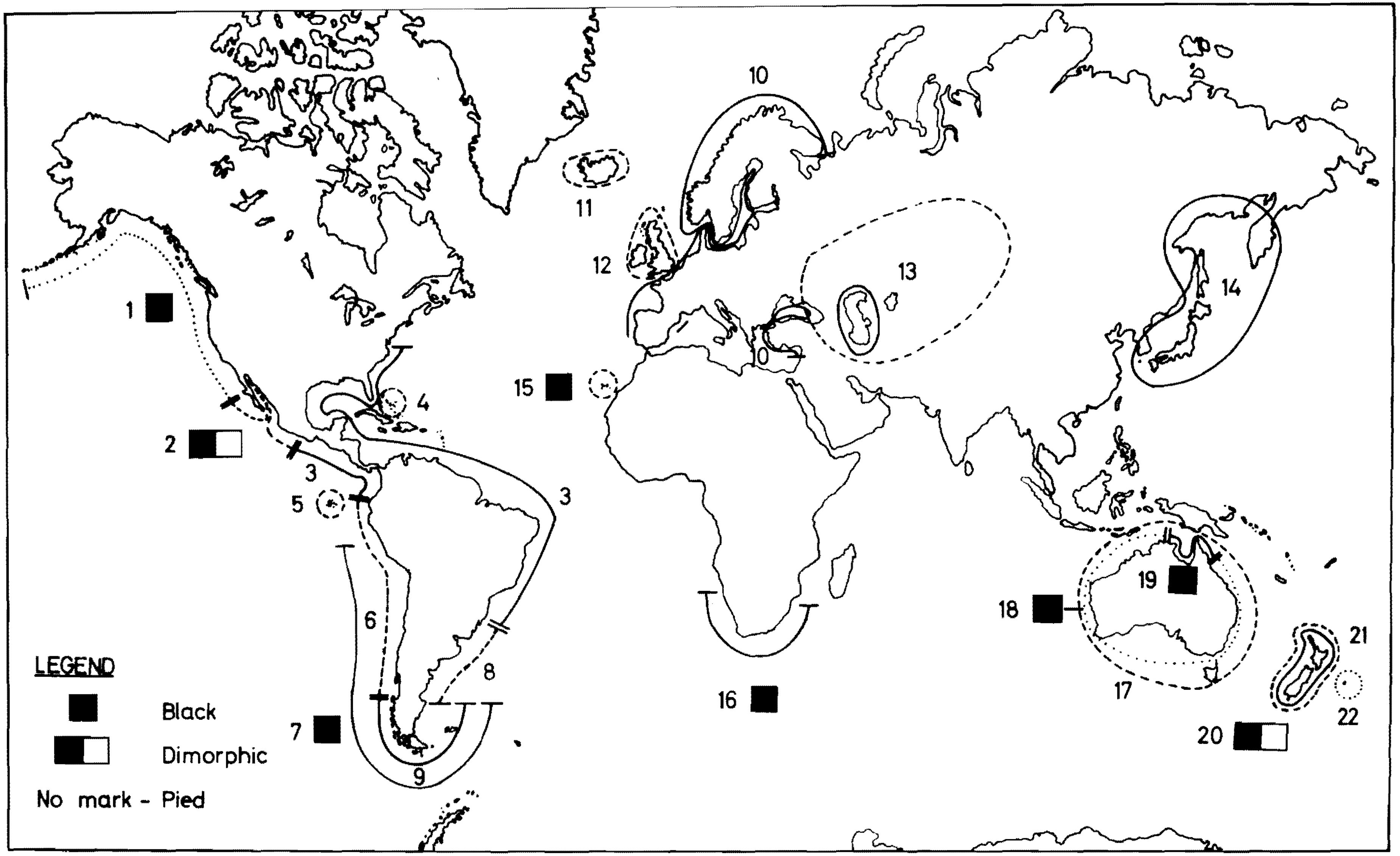

10
11
12
13
14
1
2
3
4
15
5
3
6
8
16
19
18
21
17
22
20
7
9
LEGEND
Black
Dimorphic
No mark - Pied

Figure 2.1

World distribution of oystercatchers (Modified after Larsen, 1957).

Key to species:

1. *Haematopus bachmani*
2. *H. o. frazari*
3. *H. o. palliatus*
4. *H. o. pratti*
5. *H. o. galapagensis*
6. *H. o. pitanay*
7. *H. o. durnfordi*
8. *H. leucopodus*
9. *H. ater*
10. *H. o. ostralegus*
11. *H. o. malacophaga*
12. *H. o. occidentalis*
13. *H. o. longipes*
14. *H. o. osculans*
15. *H. o. meade-waldoi*
16. *H. o. moquini*
17. *H. o. longirostris*
18. *H. o. finschi*
19. *H. f. fuliginosus*
20. *H. f. opthalmicus*
21. *H. unicolor unicolor* - *H. u. reischeki*
22. *H. u. chathamensis*

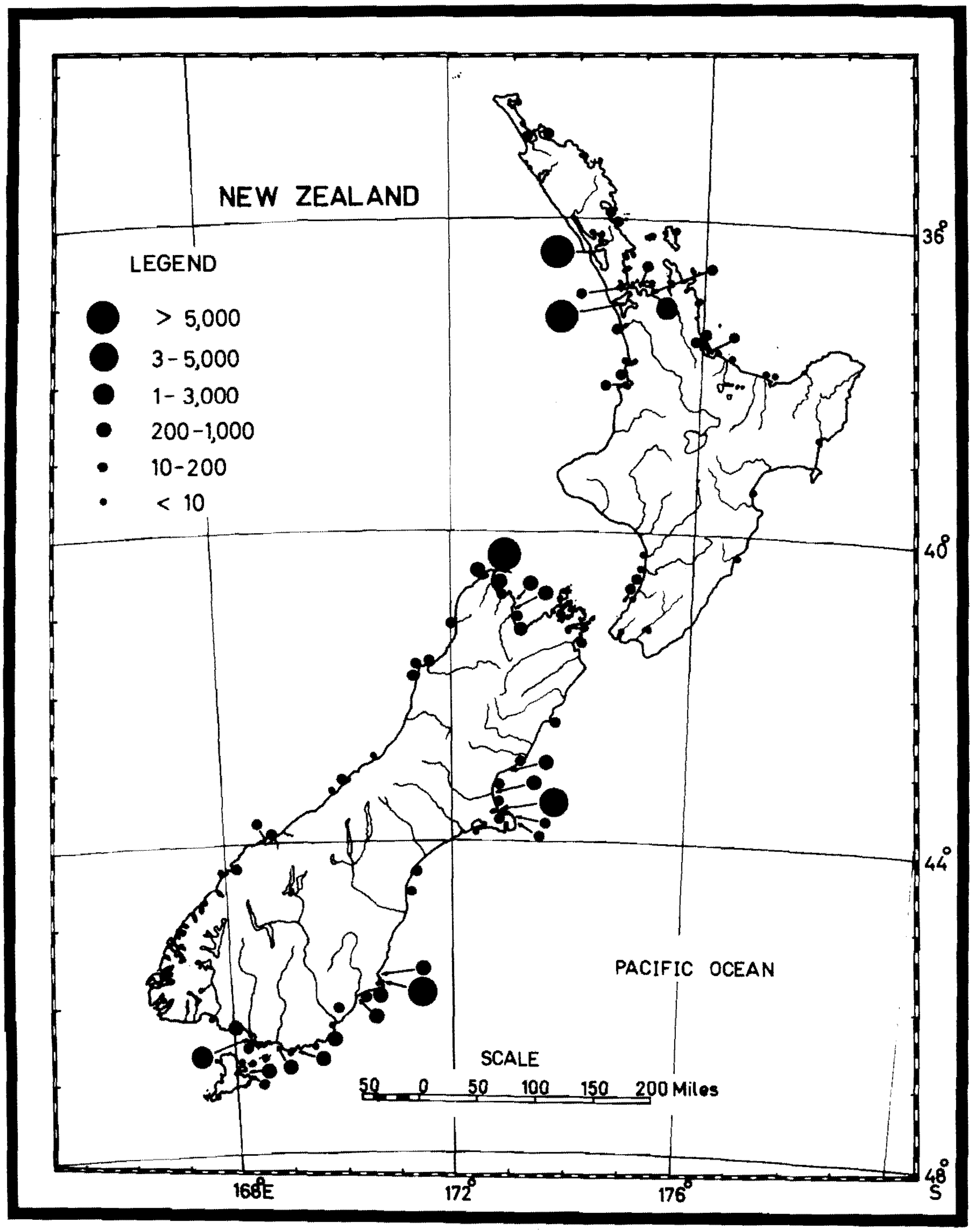

NEW ZEALAND
LEGEND
● > 5,000
● 3 - 5,000
● 1 - 3,000
● 200 - 1,000
• 10 - 200
• < 10
PACIFIC OCEAN
SCALE
50 0 50 100 150 200 Miles
36°
40°
44°
48° S
168°E
172°
176°

Figure 2.2

Range, distribution, and abundance of the South Island Pied Oystercatcher.

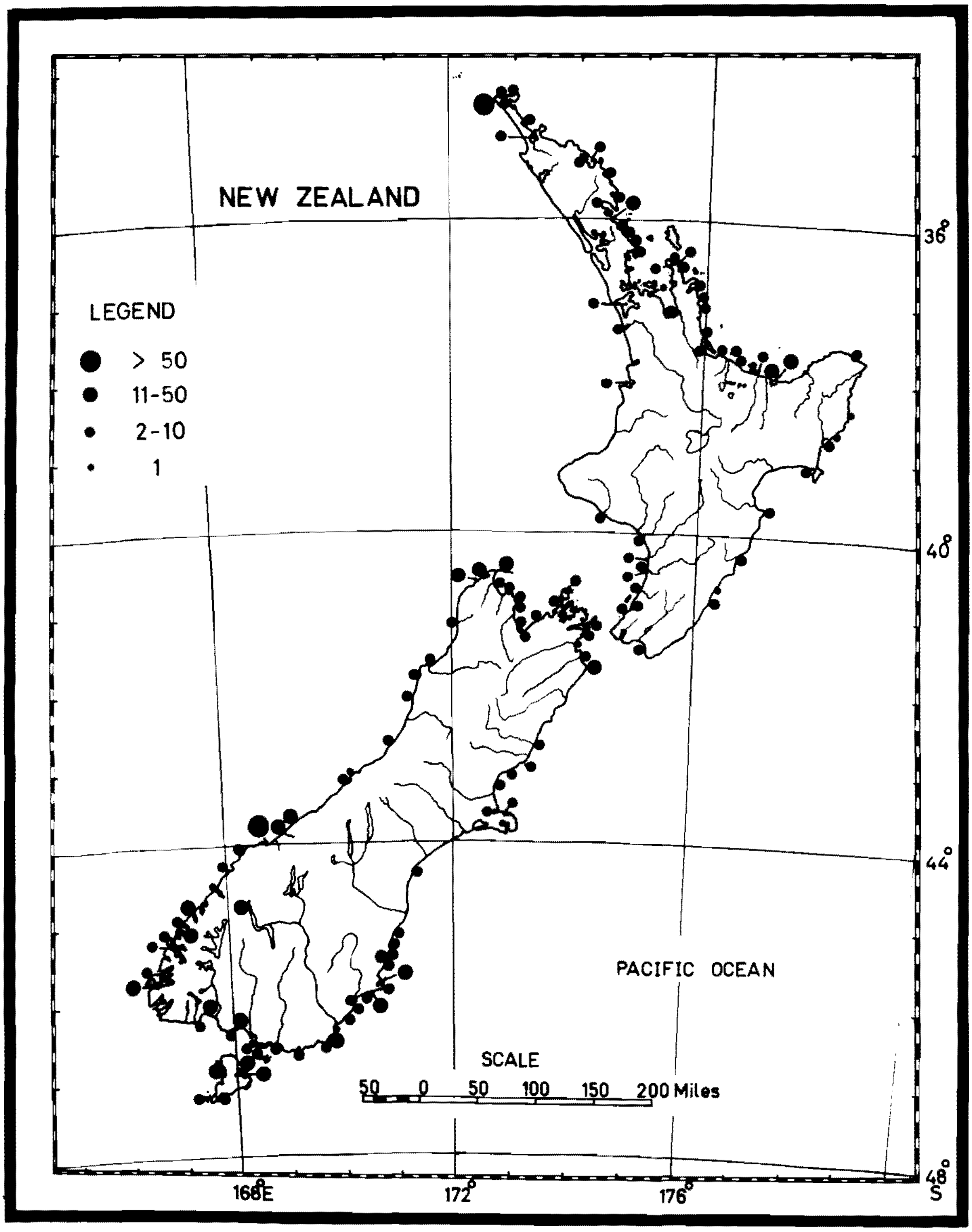

NEW ZEALAND
LEGEND
● > 50
● 11-50
• 2-10
· 1
PACIFIC OCEAN
SCALE
50 0 50 100 150 200 Miles
36°
40°
44°
48° S
168°E
172°
176°

Figure 2.3

Range, distribution, and abundance of the Black Oystercatcher.

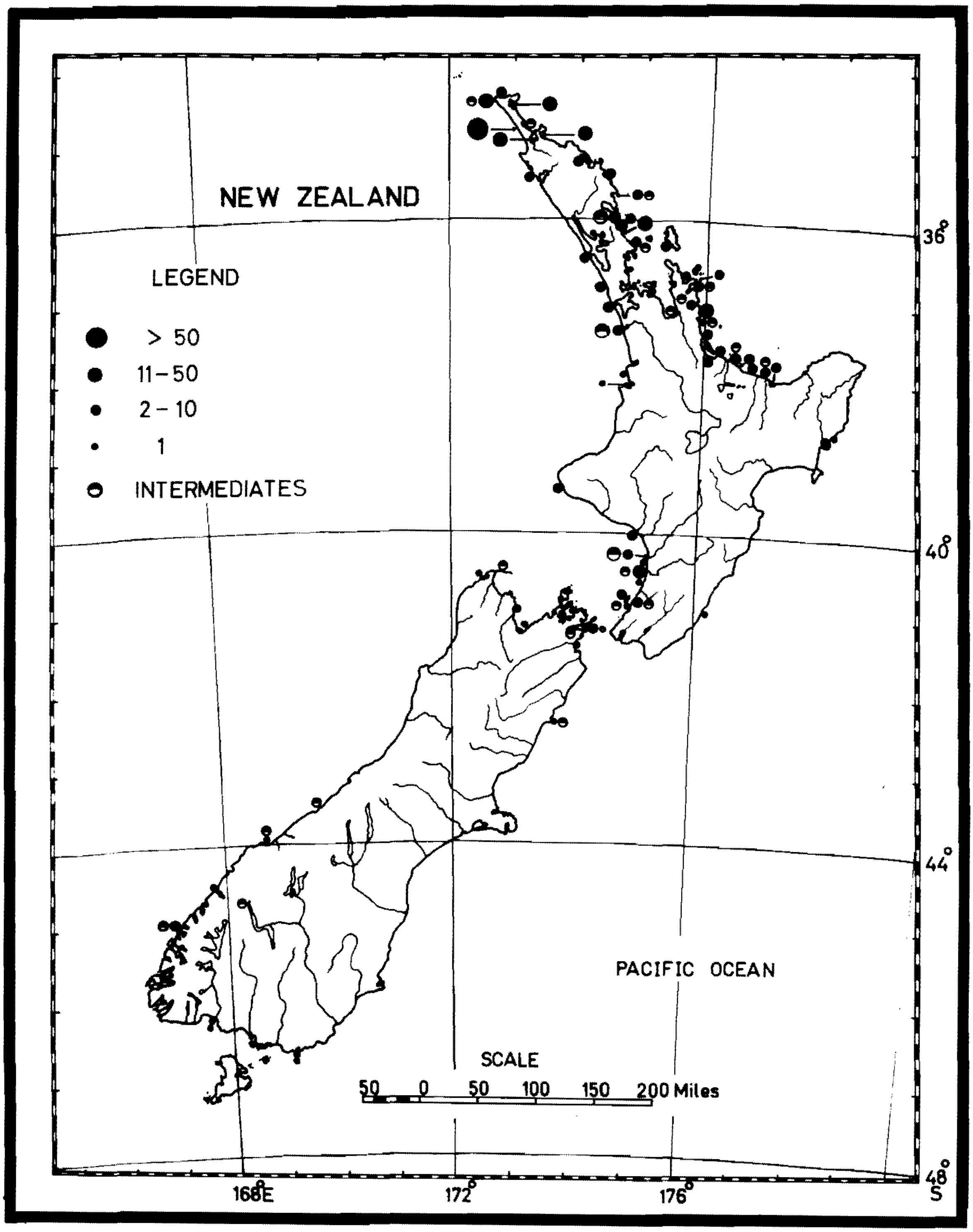

NEW ZEALAND
LEGEND
● > 50
● 11–50
● 2 – 10
• 1
◓ INTERMEDIATES
PACIFIC OCEAN
SCALE
50 0 50 100 150 200 Miles
36°
40°
44°
48° S
168°E
172°
176°

Figure 2.4

Range, distribution, and abundance of the Variable Oystercatcher. Intermediate phase birds are indicated by the half-blacked circles.

Black or Variable Oystercatchers (H. unicolor subspp.), but they occur at fewer localities. A feature of their distribution is the occurrence of large flocks of birds at major harbours, bays and estuaries. These flocks result from the well developed gregarious behaviour in this species, and it follows that such flocks can only exist in localities where adequate food supplies are present. Smaller flocks occur around the coastline usually where rivers discharge into the sea, forming small estuaries in which bivalve molluscs are locally abundant (see Fig 2.2). South Island Pied Oystercatchers are notably absent or scarce in regions where rocks predominate in the littoral zone e.g. Coromandel Peninsula, Bay of Plenty, west coast of the North Island from East Cape south, and Fiordland.

Black and Variable Oystercatchers have a much more scattered distribution than their smaller pied congener. Larger flocks of these birds, nowhere exceeding 150 individuals, occur in the parts of their range where they are either allopatric with or numerically dominant to South Island Pied Oystercatchers. Small widely dispersed flocks occur in regions where the littoral zone is characterised by rock platforms. Black and Variable Oystercatchers are allopatric to South Island Pied Oystercatchers at various localities in the North Auckland Peninsula, Coromandel Peninsula, the west coast of the North Island from East Cape south, and Fiordland. Where black and variable birds are sympatric with South Island Pied Oystercatchers, the former two races occur in very small numbers. The marked disjunctions which occur in the distribution of the races are directly attributable to changes in the continuity of littoral distribution e.g. the scarcity of records from the Taranaki coastline are due to the barren gravel beaches of this region.

Black and Variable Oystercatchers are not uniformly distributed throughout their range, their frequency of occurrence varying considerably with latitude. As Black Oystercatchers (H. u. unicolor) and black phases of the Variable Oystercatcher are phenotypically indistinguishable, and since field observations have been unable to accurately ascribe sightings to one race or the other, it is impossible to delimit their ranges. For this reason the distribution of all black birds has been plotted on the same map, and all frequency calculations made for "black" oystercatchers irrespective of their race. The distribution of the colour phases of H. unicolor with respect to latitude is shown in Table 2.1, all figures being expressed as percentages to prevent numerical bias from small samples.

TABLE 2.1 PERCENTAGE FREQUENCY OF COLOUR PHASES OF HAEMATOPUS UNICOLOR WITH LATITUDE

Latitude Grouping	Colour Phase		
	Black	Smudgy	Pied
34° - 39° S.	46.6%	7.9%	45.5%
39° - 44° S.	81.2%	8.6%	10.2%
44° - 48° S.	95.7%	3.0%	1.3%

"Black" oystercatchers predominate in the southern part of the South Island although small numbers of pied and smudgy intermediate-plumaged birds exist at these latitudes also. On transition northwards "black" phases decrease in frequency, whereas smudgy and pied phases increase until pied and black phases reach approximately equal frequency in the far north. This type of colour phase frequency gradient with black phases predominating in colder higher latitudes and pied phases predominating in warmer lower latitudes is not unique to New Zealand, a parallel case existing on the coast of southern California (see Fig 2.3). As Larsen (1957) has pointed out, these two colour phase gradients occur at approximately the same latitudes, representing the northern and southern limits of the palms. This suggests that the distribution of the various colour phases may be correlated with temperature. The greater extent of the North American continent has allowed a clearer pattern to emerge;

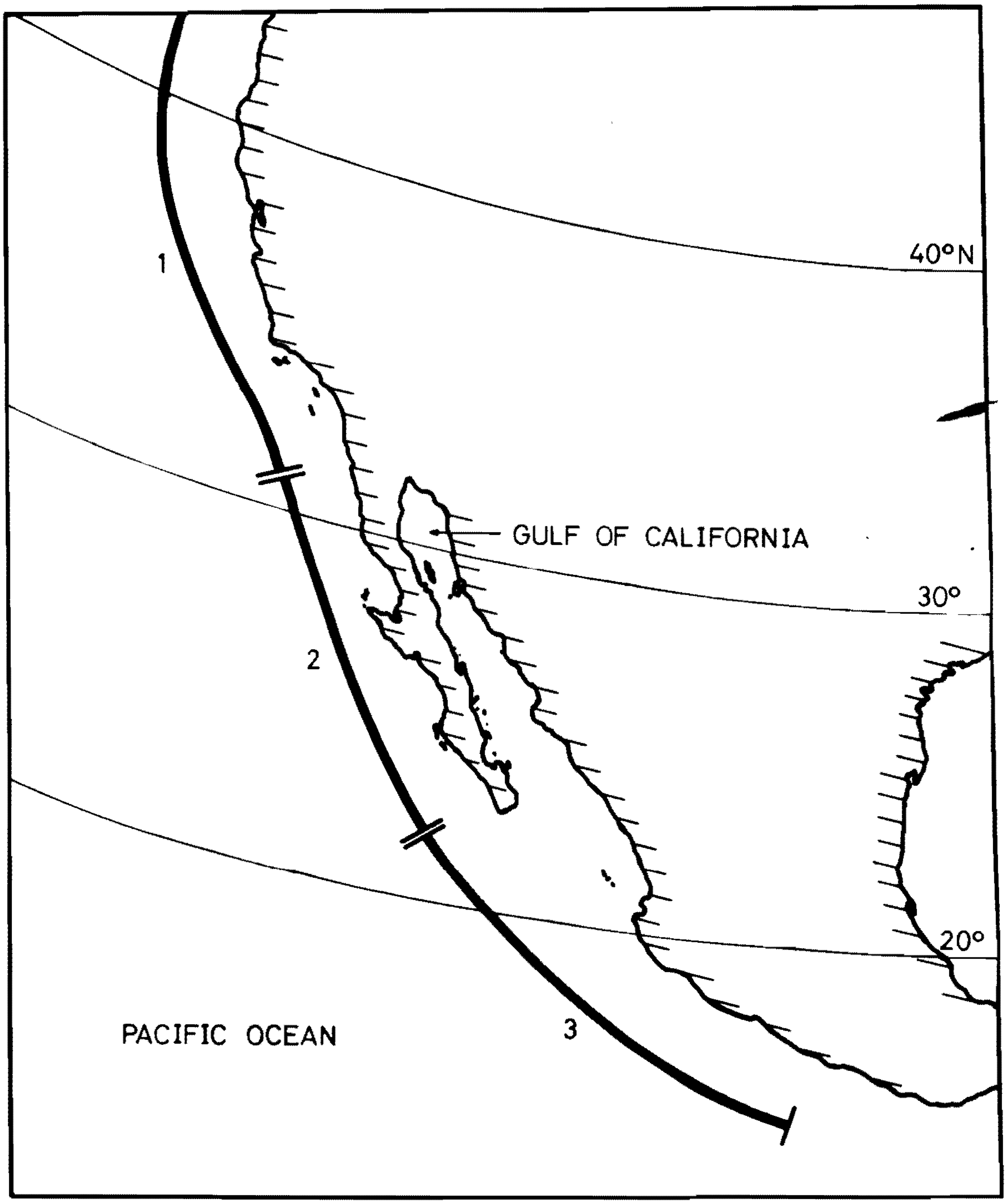

1
40° N
GULF OF CALIFORNIA
30°
2
20°
PACIFIC OCEAN
3

Figure 2.5

Colour phase gradient existing where the American Black Oystercatcher (*H. bachmani*) meets the Frazar Oystercatcher *H. ostralegus frazari*).

Key to numbers:

1. wholly black birds;
2. intermediate smudgy-plumaged birds; and,
3. pied birds.

black oystercatchers alone occur from Alaska south to southern California, they then merge and interbreed with pied and intermediate smudgy birds, and finally on the Mexican coast of the Gulf of California pied birds reach a frequency of 100%. Presumably, if the New Zealand mainland extended into lower latitudes nearer the Equator, then the pied phase of H. unicolor would also reach an exclusive frequency.

Variable Oystercatchers with smudgy plumage intermediate between black and pied phases have an interesting distribution. In all but two instances they occur where "black" and pied phases of H. unicolor are sympatric, and in the two remaining cases they occur well within dispersal range of regions where mixed matings were known to occur (see Figs 2.3 and 2.4). Smudgy-plumaged oystercatchers are nowhere abundant, the maximum number at any one locality never exceeding 20 birds.

C. Recent Trends in Distribution and Abundance

South Island Pied Oystercatchers have been abundant in New Zealand for at least the last 100 years. Potts (1869) recorded large flocks of pied birds on estuarine mudflats, and the same author recorded a flock of several thousand birds at the Heathcote-Avon estuary in 1885. This was confirmed by Buller (1888), who also noted that Black and Variable Oystercatchers were widespread but nowhere abundant. Travers & Travers (1872) recorded oystercatchers of pied plumage on the Chatham Islands at that time. Thus Black, Variable and Chatham Oystercatchers have probably remained at low population levels in recent times, whereas South Island pied birds have been comparatively abundant. Since 1941, wintering populations of the latter have undergone a spectacular irruption, especially in the northern New Zealand wintering haunts (see Fig 2.6). This population increase has been attributed by Sibson (1966) to the passing of legislation in 1940 prohibiting the shooting of shorebirds. Population levels at major wintering areas in the South Island have shown only small increases in comparison with their northern counterparts (see Fig 2.7). The differential

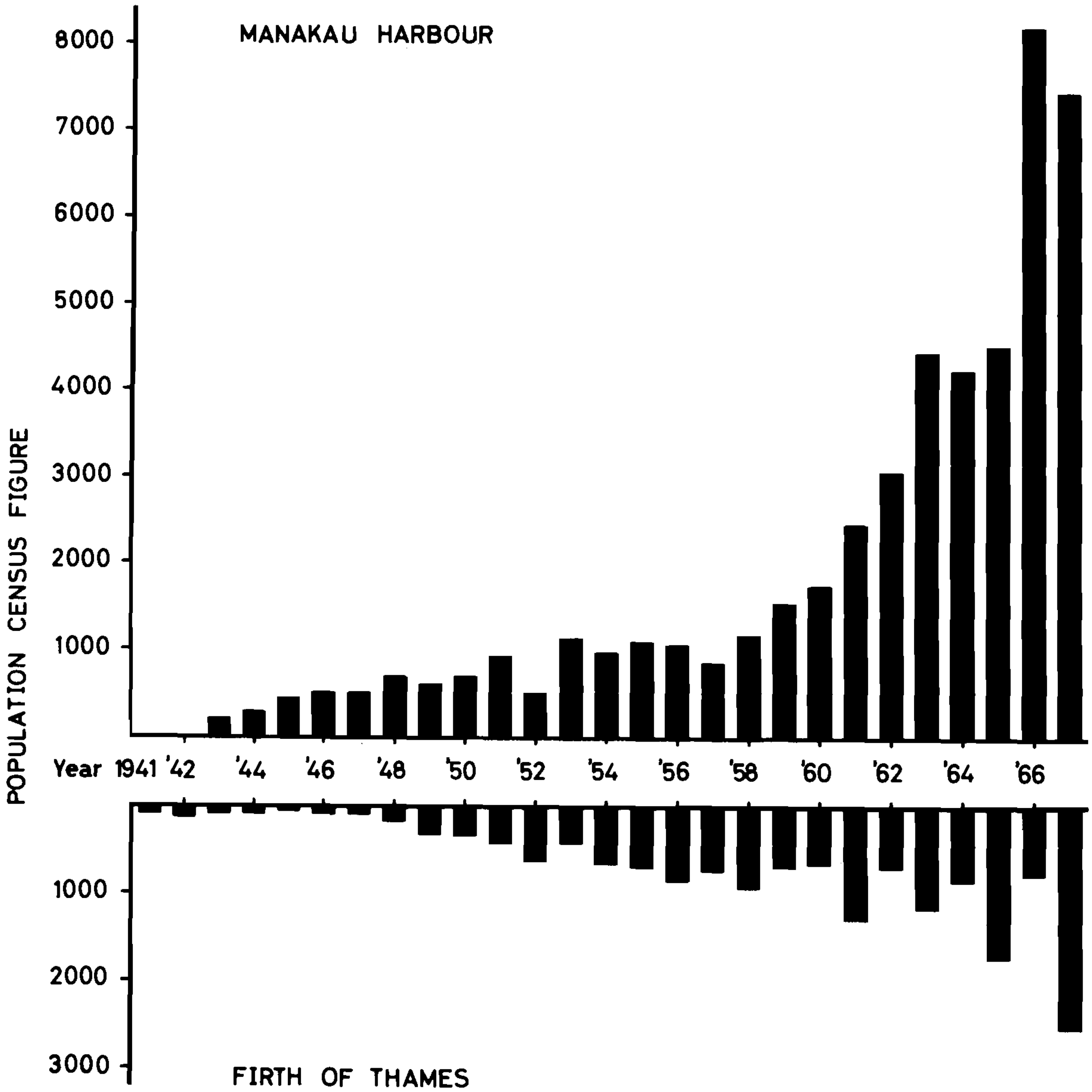
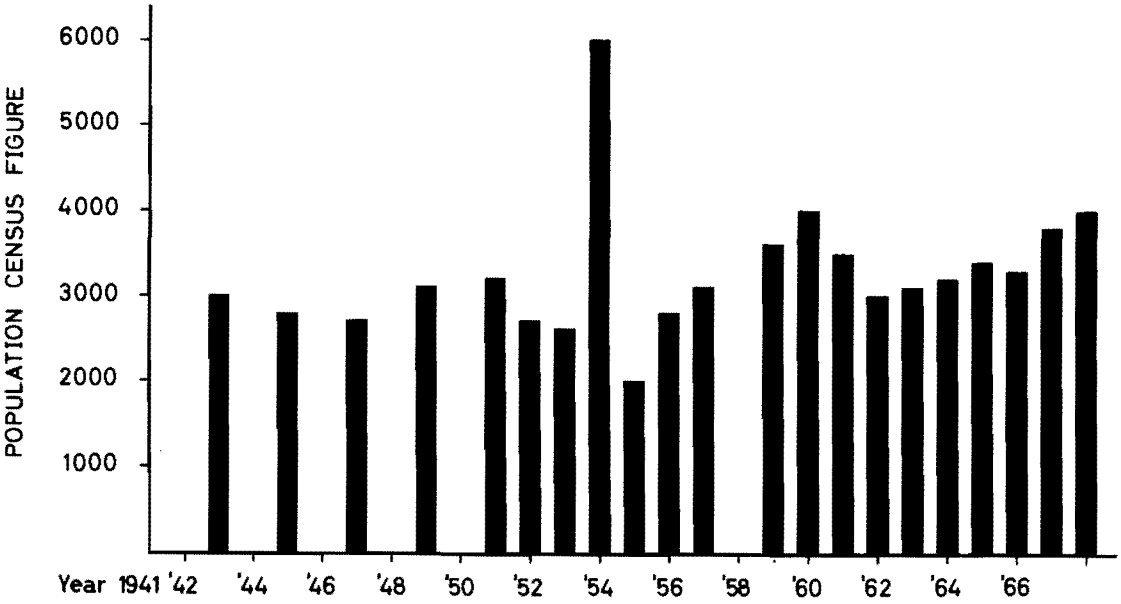

MANAKAU HARBOUR
8000
7000
6000
5000
4000
3000
2000
1000
POPULATION CENSUS FIGURE
Year 1941 '42 '44 '46 '48 '50 '52 '54 '56 '58 '60 '62 '64 '66
1000
2000
3000
FIRTH OF THAMES

Figure 2.6

Population expansion of South Island Pied Oystercatchers as indicated by increasing numbers of birds wintering at northern New Zealand wader haunts.



POPULATION CENSUS FIGURE
6000
5000
4000
3000
2000
1000
Year 1941 '42
'44
'46
'48
'50
'52
'54
'56
'58
'60
'62
'64
'66

Figure 2.7

Population levels of the South Island Pied Oystercatcher at the Heathcote - Avon estuary.

population expansion within wintering haunts can be ascribed to three main factors:

(1) previous to 1940, northern harbours and estuaries containing vast supplies of food, were not utilised by shorebirds and thus represented a vacant niche;

(2) also previous to 1940; southern harbours and estuaries were able to adequately support the smaller populations of birds inhabiting them; and,

(3) ecological pressure from population expansion since 1940 has forced birds to migrate northwards in search of new feeding areas. Since the migratory instinct is best developed in juvenile first-year birds (Buxton, 1957), they have tended to colonise northern New Zealand harbours and estuaries (Sibson, 1945; Falla et al., 1966). With population levels of South Island Pied Oystercatchers still rising, saturation appears imminent within the next decade, and should be followed by typical density-dependent predator-prey oscillations.

2.5 SUMMARY

The New Zealand species and races of oystercatcher have identical ranges, but their distribution and abundance within these ranges are very different. South Island Pied Oystercatchers are concentrated on large harbours and estuaries in the North and South Islands. "Black" oystercatchers are the dominant phase of H. unicolor in the South Island, but the frequency of the pied phase increases on transition northwards until the two reach approximately equal proportions in northern New Zealand. Black and Variable Oystercatchers have a scattered distribution with flocks never exceeding 150 birds. Smudgy-plumaged oystercatchers occur where black and pied phases of H. unicolor are sympatric. The two species of oystercatcher, H. ostralegus and H. unicolor, are largely allopatric in their winter ranges. Where the two species are sympatric one or the other is numerically reduced, often existing only as an odd pair. Species segregation is therefore quite marked though by no means absolute. Black, Variable and Chatham Oystercatchers have probably maintained their present numbers over the past 100 years, but during the same period South Island Pied Oystercatchers have increased their numbers, irrupting spectacularly since 1940 when the shooting of shorebirds was prohibited. Increasing numbers of these birds have migrated to harbours and estuaries in northern New Zealand in search of new feeding grounds. At the present rate of expansion, this species will probably reach a population level in the next decade where it will come under density-dependent control.

Chapter 3

THE FEEDING ECOLOGY OF NEW ZEALAND OYSTERCATCHERS

3.1 INTRODUCTION

The specialised and evolutionally conservative feeding habits of oystercatchers have attracted the attention of ecologists and students of animal behaviour (see Ch.1.1). Two aspects of feeding have been investigated in detail; namely methods of taking food, and behavioural patterns associated with these methods. Most of the earlier research (Dewar, 1908, 1910, 1913, 1915, 1922, 1940; Bayne, 1941; Webster, 1941; Tomkins, 1947; Legg, 1954) was directed at descriptions of food and feeding habits, with only subjective attempts to estimate the proportions and amounts of the various foods eaten. Following the successful application of quantitative techniques to the study of the feeding habits of the Rock Pipit (Anthus spinoletta) by Gibb (1956), and with the concern at the predation by oystercatchers (Haematopus ostralegus) on commercial cockle beds in Great Britain, later research was directed at determining the amount of food eaten by individual birds over known periods of time (Drinnan, 1957, 1958a, 1958b; Davidson, 1967). The inheritance and ontogeny of complex behaviour patterns associated with special feeding habits have been described by Tinbergen & Norton-Griffiths (1964) and Norton-Griffiths (1967).

In the present study, quantitative techniques were used wherever possible. Research was confined to wintering populations as gregarious behaviour was best developed at this time of the year, resulting in the formation of large approachable feeding flocks. Comparable feeding studies were undertaken because it is well known that forms which are morphologically indistinguishable (H. unicolor unicolor and the black phase of H. u. reischeki) can often be separated by their differing ecological requirements (Cain, 1966). According to this view, such groups constitute biological races, and are particularly evident among groups with specialised food requirements.

3.2 METHODS

The study areas (see Ch.3.3) were kept under surveillance by the author from January 1967 to January 1968, and in addition, the Heathcote-Avon estuary was regularly visited from March to September 1966 in the course of a B.Sc. Honours research project. Observations of feeding birds were made at distances of 10 to 50 metres through 7 X 50 mm fieldglasses. This combination of distance, magnification and field of view proved adequate to give good definition of feeding habits and foods taken.

The feeding habits of South Island Pied Oystercatchers were studied in detail at the Heathcote-Avon estuary, and comparative observations were made at Jackson Bay, Golden Bay and Kaikoura. Similar studies were made on Black and Northern Variable Oystercatchers at Westhaven Inlet, Cape Farewell, Kaikoura and Jackson Bay. For convenience, the description of observational methods and quantitative techniques employed in this study have been grouped under the following headings:-

A. HABITAT SELECTION

Many localities with contrasting substrates were visited during the course of this study. In each case, the extent and nature of the various substrates were recorded. Preferences for particular substrates in heterogeneous habitats were determined by calculating the percentage of each subspecies of oystercatcher utilising different substrates. Representative habitats were selected for detailed study (see Ch.3.3).

B. FEEDING BEHAVIOUR

1. General Behaviour

The pattern of movement from high water roosts to feeding grounds was plotted on 1" : 10 chain maps at each study area. The rhythmical nature of this behaviour was investigated in detail only at the Heathcote-Avon estuary, mainly because of its convenient situation and large winter population of oystercatchers. Movements to and from the feeding grounds were assessed quantitatively by counting the number of birds at various localities in the study area, and mapping their distribution. Observations were made at half-hourly intervals throughout complete tidal cycles, and were repeated once a month for 12 months. Further recordings were taken during the transition from neap to spring tides to detect any effects changing tidal levels might have on general flocking behaviour.

2. Specific Feeding Behaviour

Records of feeding behaviour were made for individual birds at selected sites in the study areas. Observations were made over a wide range of physical and climatic conditions in order to analyse their possible effects on feeding behaviour. Complete tidal cycles were covered, and the occurrence of each type of feeding behaviour recorded over 10 min periods. The hammering of holes in the umbo region of shells of certain bivalve molluscs was thought to be correlated with shell thickness at this point. This relationship was investigated by measuring the umbo thickness of a large sample of shells using an engineer's micrometer. Half of the shell sample was collected from an area where hammering occurred regularly, and half from an area where hammering was not observed by the author.

C. ESTIMATION OF FOOD INTAKE

1. Feeding rates

The rate of food intake was determined by direct observation. Recordings were confined to one bird at a time because of the difficulty of keeping more than one bird in the field of view of the fieldglasses. Each bird was observed for a 10 min period during which the number of probes in search of food were recorded, the number of successful probes marked, and food taken identified where possible. To minimise observer fatigue, each observation period was followed by a 10 min rest period, and then the process was repeated until a tidal cycle was completed. Whenever possible, observations were taken in areas where a particular prey, which the birds were preferentially taking, was locally abundant. This enabled the anomalous effects of differential feeding rates resulting from variation in diet to be eliminated (Hartley, 1948).

Feeding rates were recorded over four tidal cycles per month for a year so that a large number of data could be accumulated and seasonal trends in feeding noted. The variation in feeding rates of individual oystercatchers during the course of a tidal cycle was recorded using birds which had previously been mist-netted and colour-banded.

2. Factors affecting feeding rates

Four main factors affecting the rate of food intake by oystercatchers were investigated:

a. Food availability.

The effect of food availability on feeding rates was determined by recording the feeding rates of birds at areas where prey densities had been determined by a sampling programme (see section 3.2 D).

b. Age or feeding experience of the bird.

Feeding rates were recorded for colour-banded birds of different age classes. The age classes were determined by noting progressive changes in plumage, bill, iris and leg colour of marked birds during the study (see Ch.4.5).

c. Physical and Climatic factors of the environment.

The effect of these factors was evaluated by recording feeding rates over a range of conditions. Nocturnal feeding was neglected because of the difficulty of observation.

d. Competition.

Feeding rates of birds at high and low densities were recorded and compared.

As all of the above factors are interdependent, it was necessary to minimise interactions between them in order to measure individual effects on the rate of food intake. As far as was practicable, this was achieved by gathering all data, for any one subspecies of oystercatcher, at one study site.

3. Determination of Food Requirements

The daily food requirements of oystercatchers were determined by calculating the mean volume of food ingested per bird per day. The mean volume of food ingested per bird per day was given by the product of the mean feeding rate and the mean volume of the prey. All volume measurements were made with apparatus accurate to 0.1 mm.

D. ESTIMATION OF FOOD AVAILABILITY

The supply of food available to oystercatchers at each study area was determined by sampling programmes. Sampling was confined to the prey species which constituted the major part of the birds' diet. The method of sampling was as follows:-

The area to be sampled was mapped on a scale of 1" : 10 chain, and subdivided using a system of co-ordinates to form a grid. Sampling sites were selected using a set of random numbers (Fisher and Yates, 1957) so that statistical estimates of reliability could be placed on resultant estimations of prey populations. The location of each sampling site was determined by scaling actual measurements off the map, and applying them to the study area with a tape measure.

At the point of intersection of the grid co-ordinates, a quadrat 30 cm square was placed with its top right hand corner at the exact location. In study areas where the prey species burrowed in soft substrates, samples were extracted using a specially made 30 cm wide spade. Samples were taken to a depth at which no further prey species were found, which was often indicated by a black sulphide layer. The depth of each sample was recorded in the excavation rather than from the core as the former is not subject to compaction error.

All samples were sorted in the field using a sieve with a mesh of 4 mm. This mesh size was selected as it corresponded to the smallest-sized prey species found (Drinnan, 1957) and also because it allowed rapid sieving. Each faunal sample was placed in numbered plastic bags and taken back to the laboratory for counting and measurement.

Prey populations on rocky surfaces were sampled in a similar manner to that already described. Counting and measurement of individual prey specimens was carried out in the field.

The number of samples taken at each study site was dependent on its area, with never less than 30 samples being taken at any one site. This magnitude of sampling was selected as a minimum one because a range of 20 - 40 replications is considered sufficient to allow statistical analysis of data (Snedecor, 1956).

E. ESTIMATION OF PREDATION

The number of prey eaten per year was estimated by multiplying together the mean feeding rate, the mean number of birds feeding in the area per year, and the total time spent feeding per year.

Preferences for certain-sized prey were investigated by collecting opened shells and measuring their length along the anterior-posterior axis. The frequency distribution of these sizes was compared with the frequency distribution of sizes for the live prey population (from the food availability samples).

F. DETERMINATION OF DIET

The range of foods taken and the food preferences of oystercatchers were determined using three methods:-

1. Observation of feeding Birds

By observing birds at areas where specific prey species were known to occur, a preliminary range of foods eaten by oystercatchers was charted. Extension of these observations to localities where several potential food organisms were known to be abundant enabled food preferences to be determined.

2. Gut analysis

Shooting of birds for gut analysis was severely limited because most habitats frequented by large flocks of oystercatchers are adjacent to cities or other densely populated areas. Twenty gut samples were collected from the Heathcote-Avon estuary in 1966 for a B.Sc. Honours research project, but in this case the birds were mist-netted and chloroformed. During the present study 20 birds were shot at isolated Golden Bay beaches, and a further five at the Kaikoura Peninsula.

Immediately the birds were shot, formalin was sprayed through the bill gape into the alimentary canal to prevent further digestion of the gut contents. The entire gut was removed and stored in alcohol after the upper oesophagus and rectum had been tied off with cotton.

3. Faecal smears

Faeces were collected from all study areas for analysis. Their organic content was investigated by low power monocular examination of smears prepared on glass slides. Where the faeces were exceptionally bulky or desiccated, they were diluted with water and examined under a binocular microscope.

3.3 THE STUDY AREAS

A. HEATHCOTE-AVON ESTUARY

The estuary of the Heathcote and Avon rivers is situated at latitude 43° 33' South and longitude 172° 44' East (see Fig 3.1). Geologically it is a tiny remnant of the marine channel that formerly separated Banks Peninsula from the Southern Alps of the South Island of New Zealand. This channel was gradually filled by material eroded from the mountain chain. Oceanic currents flowing around this fill built up spits to eventually form the lagoons of Lake Ellesmere and the Heathcote-Avon estuary.

The estuary is bounded at its seaward aspect by a large sandbar which limits its exit to a width of about 200 m. The former occupies an area of approximately 5.6 km^2. The boundaries of the estuary form a rough triangle; the northern vertex of the triangle

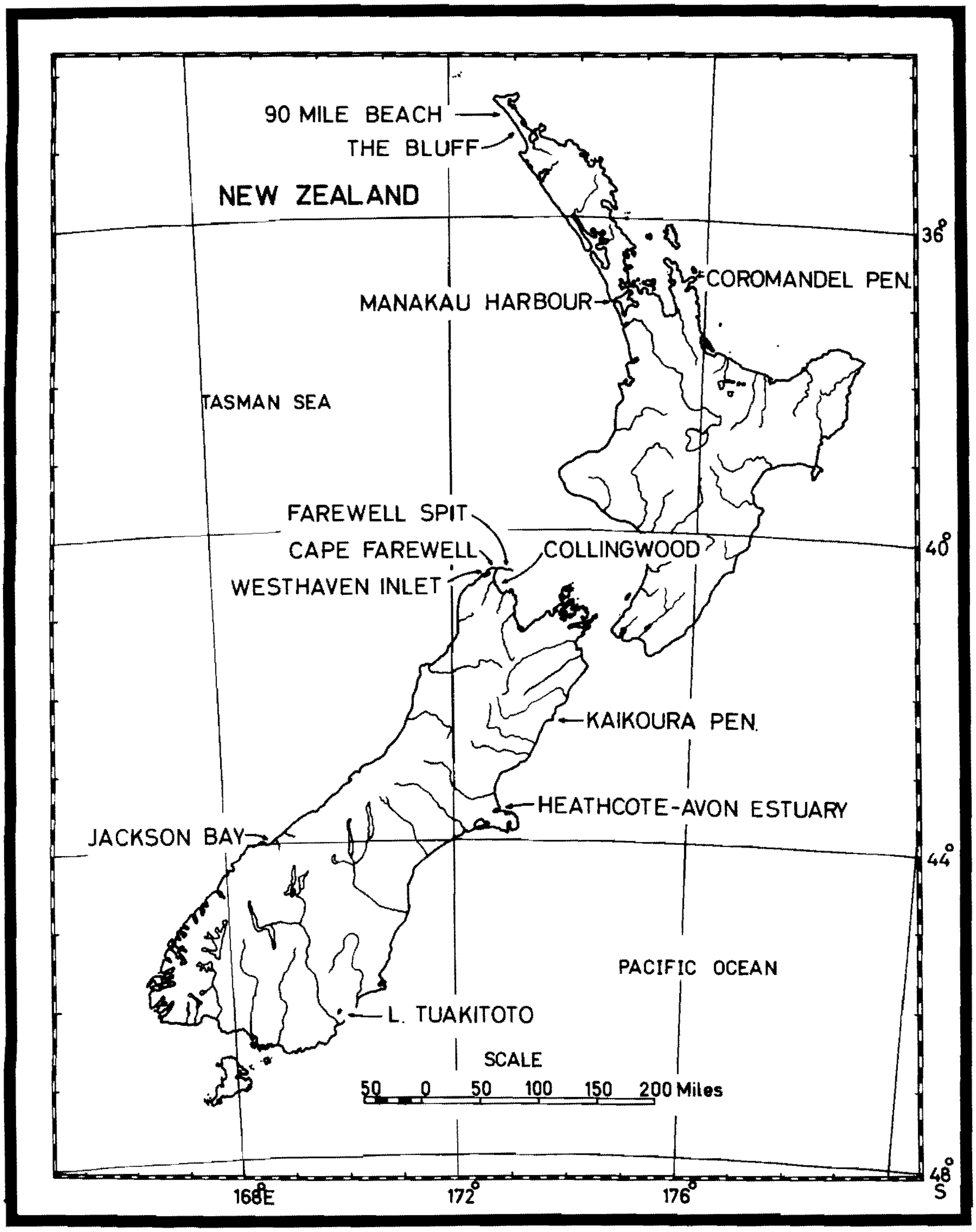

NEW ZEALAND
90 MILE BEACH
THE BLUFF
MANAKAU HARBOUR
COROMANDEL PEN.
TASMAN SEA
FAREWELL SPIT
CAPE FAREWELL
WESTHAVEN INLET
COLLINGWOOD
KAIKOURA PEN.
HEATHCOTE-AVON ESTUARY
JACKSON BAY
PACIFIC OCEAN
L. TUAKITOTO
SCALE
50 0 50 100 150 200 Miles
36°
40°
44°
48° S
168°E
172°
176°

Figure 3.1

Map of New Zealand showing the location of the study areas and other localities mentioned in the text.

is the point of entry of the Avon river, the western corner is the point of entry of the Heathcote river, and the remaining corner marks the mouth of the estuary where it enters Pegasus Bay (see Plate 3.1).

The substratum of the estuary grades from sand at the mouth to fine-grained muds at the points of river entry, the ratio of mud-dominant substrates to sand-dominant substrates being approximately fourteen to one, based on surveys made previous to the present study (Baker, 1966). At low water during spring tides the entire estuary is exposed to the air except for two narrow river channels and associated drainage canals, which merge into one near the mouth. During low water at neap tides the area of Monck's Bay from Shag Rock to about 400 m up the mouth is submerged.

The channels in the estuary have a very constant pattern (Linzey, 1944; Estcourt, 1962) and Plate 3.1 taken in 1954 is still essentially correct.

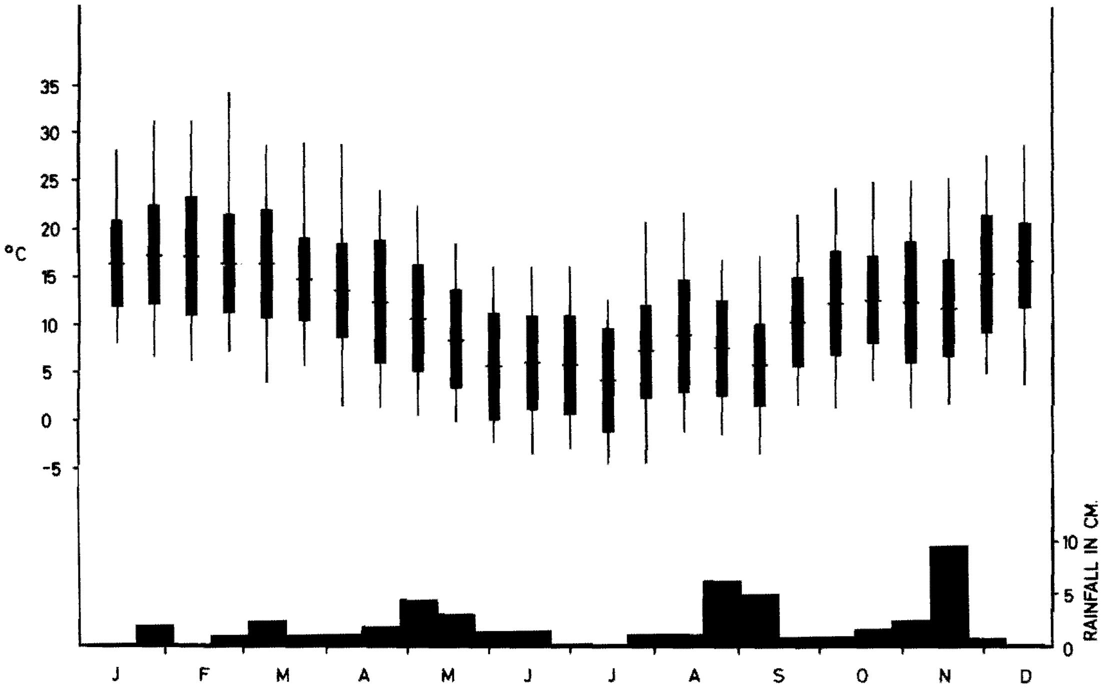
Vegetation is almost entirely lacking from the estuarine substrate except in summer when a settlement of Ulva occurs. Flats covered by rushes are limited to small areas near the mouth of the Avon and Heathcote rivers.

Thompson (1929) and Estcourt (1962) have shown that air temperatures at the estuary are slightly more equable than those at Christchurch approximately 8 km inland. However, Estcourt has also shown that estuarine temperature data fall neatly inside mean maximum and mean minimum temperature limits for Christchurch. For this reason, it seems more appropriate to use accurately recorded climatic data from the Harewood Meteorological Station, provided that ranges are indicated. Temperature and rainfall data for Christchurch are shown in Fig 3.2 (from Coleman, 1968). Air temperatures are maximal in January and February, and minimal in June and July. Rainfall occurs mainly in the periods April to May and August to November.

Study sites within the estuary are described briefly below:-

Plate 3.1

Aerial photograph of the Heathcote-Avon estuary taken at low water to show the channel system.


35
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RAINFALL IN CM.
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Figure 3.2

Temperature and rainfall data recorded at the New Zealand Meteorological station at Harewood International Airport. The solid portion of each temperature entry shows fortnightly mean temperature range; the upper limit the mean maximum and the lower limit the mean minimum, with the mean temperature indicated by the horizontal line. The vertical line extension indicates the extreme mean daily maximum and minimum (adapted from Coleman, 1968).

1. Monck's Bay Study Site

This study site (see Fig 3.3) comprises approximately 0.4 km^2 of sand-dominated substrates. The combined channels of the rivers closely follow the southern shore of the estuary and therefore do not cover a wide area at low water. As the tide ebbs, a bar in mid-channel is the first sizeable area of the estuary which is exposed. Of the three study sites this is the only one affected by heavy seas, but the outflowing river current reduces the swell considerably in the region of the mouth. The porous nature of the substrate facilitates rapid drainage and surface compaction, especially on fine hot days.

2. Mid-estuary Bars Study Site

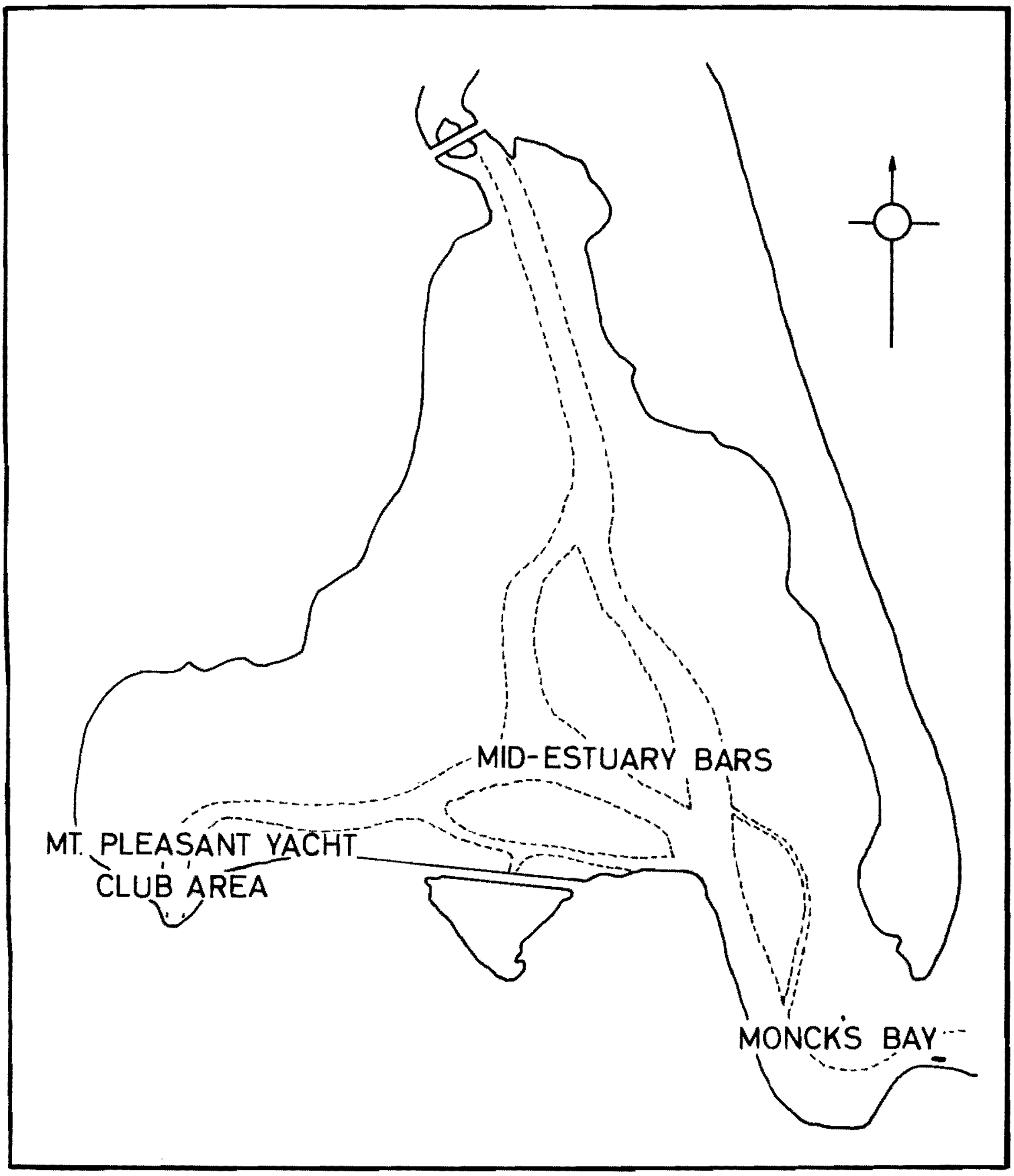
The bars in mid-estuary (see Fig 3.3) occupy an area of approximately 0.8 km^2. The substratum grades from coarse-grained sandy muds in the east to fine-grained muds in the west. Numerous drainage channels intersect the bars so that surface waters are generally absent at low water. The surface of the substratum varies from a firm consistency to a holding softness.

3. Mount Pleasant Yacht Club Study Site

The study site at the Mount Pleasant Yacht Club (see Fig 3.3) covers an area of approximately 0.05 km^2. The substrate is composed entirely of fine-grained muds underlain by a black sulphide layer of rotting detritus. Drainage is poor and the surface is dotted with small pools of water at low water. The soil near the surface is completely saturated with water when exposed, and thus presents a very soft exterior which is consolidated in patches by aggregations of cockle shells.

B. KAIKOURA PENINSULA

Kaikoura Peninsula (see Fig 3.4) is located between 42° 25' and 42° 23' South latitudes and between 173° 39' and 173° 44' East longitudes, on the east coast of the South Island of New Zealand. It is made up of a narrow isthmus approximately 1.8 km long and


MID-ESTUARY BARS
MT. PLEASANT YACHT
CLUB AREA
MONCK'S BAY

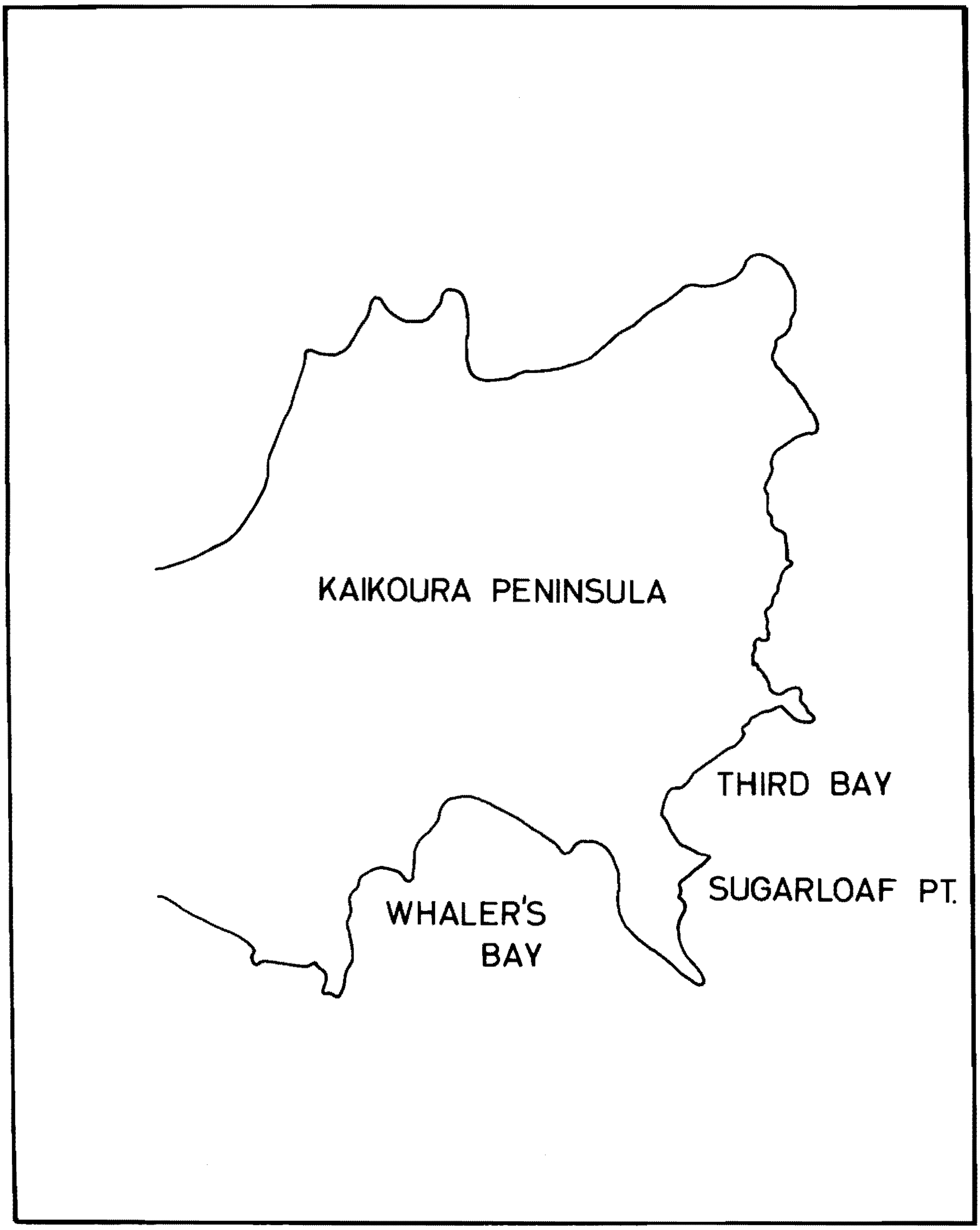

KAIKOURA PENINSULA
THIRD BAY
SUGARLOAF PT.
WHALER'S BAY

Figure 3.3

The Heathcote-Avon estuary showing the location of study sites.

Figure 3.4

Kaikoura Peninsula showing the location of study sites.

1.2 km wide at its narrowest point, and the peninsula proper which forms a rough equilateral parallelogram with a side of approximately 2.4 km. The shores of the isthmus are similar to that of the adjacent coast, being composed chiefly of shingle beach.

The peninsula proper is a hilly plateau with an average elevation of approximately 100 m. Its shoreline is rather attenuated, being drawn out into numerous points and bays. The area of the peninsula proper is approximately 4.4 km^2; whereas the littoral shelf, to which this study was confined, represents approximately 0.77 km^2 (Rasmussen, 1965).

Limestone and siltstone platforms alternate along the littoral zone of the northeast and southwest faces of the peninsula due to the existence of two synclines and an intermediate anticline orientated at right angles to the long axis of the peninsula. Repeated folding of the limestone has led to the formation of steep ridges with rough broken surfaces. The softer siltstone has been eroded by constant wave action, resulting in broad smooth platforms which slope gently towards the sea.

The primary study site in this study area involved Whaler's Bay and Third Bay on either side of Sugarloaf Point (see Fig 3.4). By far the greater portion of the substrates of these bays is limestone, with only the tips of the headlands being siltstone. Those parts of the shore in which birds fed were inhabited by a diverse biota, among which chitons (Sypharochiton pelliserpentis) and limpets (Cellana spp.) were dominant. During the Spring, the red alga (Porphyra columbina) occurred as a dense blanket over the substrate, often obscuring the fauna.

The climate of Kaikoura Peninsula is relatively mild. Frosts are rare along the shore and where they occur they are of short duration. Winter temperatures reach a minimum of approximately 4° C during June and July. Summers are warm although hot spells are infrequent. Temperatures at this time of the year reach a maximum of approximately 26° C. Rainfall occurs throughout the year, the heaviest falls being recorded in the period July to August and the lightest during January to February. At the primary study site winds were recorded from all quarters, but most arose from the southeast and were frequently in the 1 - 10 knot range. Strong on-shore winds at low water caused strong wave action (Class V of Rasmussen, 1965).

C. FAREWELL SPIT

Farewell Spit lies at latitude 40° 31' South and between longitudes 172° 45' and 173° 10' East. It is essentially a sandspit, being gradually elongated with time from the top northwest corner of the South Island of New Zealand (see Fig 3.1). Sand in suspension is carried northwards along the west coast of the South Island, and is eventually deposited on Farewell Spit where it meets a countering current originating in Golden Bay. Sheltered water in the lee of the spit in Golden Bay has allowed the Aorere River to form vast areas of mudflat (c. 31 km^2). The northern windward beach is exclusively sandy. At its landward base, Farewell Spit widens to join the projecting landmass. The northernmost point of this base is Cape Farewell which is characterised by rocky cliffs extending to form smooth platforms in the littoral zone.

The climate is usually mild. Rainfall is recorded mainly in the Spring, and shows a rapid drop-off from 227 cm at the base of the Spit to 152 cm at the tip. Prevailing winds blow from the southwest, but gales are infrequent. Small sand storms along the northern beach are characteristic of summer months.

D. WESTHAVEN INLET

Westhaven Inlet is located at 40° 36' South, 172° 35' East. It is a large inward extension of the Tasman Sea approximately 13 km southeast of Cape Farewell (see Fig 3.1). The inlet comprises an area of about 18 km^2 of mudflat. Its climate is essentially similar to that described for Farewell Spit except that annual rainfall is higher (c. 320 cm).

E. JACKSON BAY

This study area is situated at 43° 58' South, 168° 40' East on the west coast of the South Island of New Zealand. Jackson Bay extends approximately 25 km from a southern rock promontory, Jackson Head. The promontory marks the transition from the rocky shores of Fiordland to the sand and gravel beaches of Westland.

The climate of Jackson Bay is classified by McLintock (1960) as mild, but rainfall is generally high (c. 500 cm) and temperatures low. Prevailing winds come from the southwest, but much of their force is buffered by Jackson Head, making the bay relatively sheltered.

The study site in this area was Neil's Beach, a small, narrow 1.5 km stretch of sand and shingle deposited by the Arawata River where it enters the sea (see Plate 3.2). Neil's Beach has an average width at low water of approximately 200 m, and covers an area of approximately 0.3 km^2. Wave refraction around Jackson Head prevents heavy wave action on the beach except during stormy weather.

3.4 HABITAT SELECTION

Oystercatchers are essentially birds of the sea coast. Wintering populations show strong selection for littoral feeding habitats, with only two continental races of *Haematopus ostralegus* showing a tendency to move inland to utilize fully terrestrial habitats (see Fig 2.1). New Zealand populations of wintering oystercatchers exhibit strong habitat selection, feeding chiefly in marine littoral zones.

South Island Pied Oystercatchers (*H. o. finschi*) show a marked preference for habitats with soft substrates, such as estuaries, mudflats and sandy beaches. Where they occupy habitats heterogeneous with respect to substrate, they show a strong selection for soft substrates (see Fig 3.5). Habitat selection by the Black Oystercatcher (*H. unicolor unicolor*) is in marked contrast to that of the pied bird above. Black Oystercatchers are characteristic inhabitants of South Island rocky shores for which they show a very strong selection (see Plate 3.3). Black, pied and intermediate colour phases of the Variable Oystercatcher (*H. u. reischeki*) display

Plate 3.2

Neil's Beach, the study site at Jackson Bay.
August, 1967.

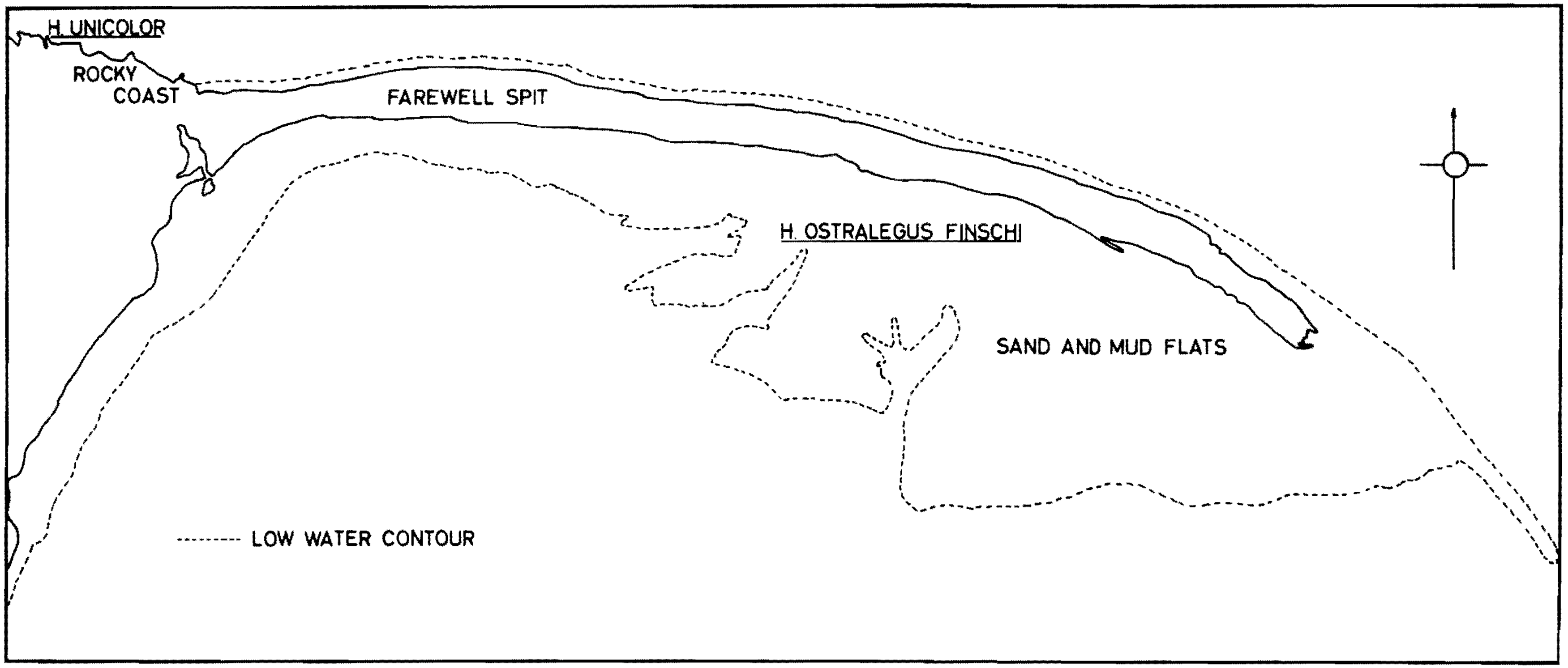

H. UNICOLOR
ROCKY COAST
FAREWELL SPIT
H. OSTRALEGUS FINSCHI
SAND AND MUD FLATS
LOW WATER CONTOUR

Figure 3.5

Habitat selection by South Island Pied and Black Oystercatchers at Farewell Spit in mid-winter, 1967.

a positive selection for habitats which have sandy beaches alternating or intermingling with rocky stretches of coastline. Where the habitat is made up of a variety of substrates, selection favours rocky areas, although Falla et al. (1966) noted the extensive use of sandy beaches as feeding habitats in northern New Zealand. The apparent difference in habitat selection between H. u. unicolor and H. u. reischeki does not appear to be significant, as it can be satisfactorily accounted for in terms of habitat availability and interspecific competition, rather than rigorous subspecific habitat selection. Wherever H. o. finschi is locally abundant, both Black and Variable Oystercatchers are restricted to rocky parts of the coast. When, however, the South Island Pied Oystercatcher is absent or is present only in small numbers, the other two races spread onto beaches and estuaries adjacent to rocky parts of the coast. Hinde (1966) considered that this was strong evidence of competition for feeding habitats, and he commented, "When one or two closely related species which occupy different habitats within the same general area is locally absent, the other may spread to occupy both habitats". Thus direct interspecific competition for food is largely prevented by differential habitat selection in regions of species overlap.

New Zealand oystercatchers fall into two natural groups on the basis of habitat selection:

(1) those which frequent habitats with soft substrates, such as sandy beaches, mudflats and estuaries, i.e. H. ostralegus; and,

(2) those which frequent habitats with hard substrates, like rocky shores and gravel beaches, i.e. H. unicolor.

From this grouping, a correlation can be made between habitat selection and plumage pattern, with birds of stable pied plumage (H. ostralegus) showing selection for habitats with soft substrates, and birds of black and unstable pied plumage (H. unicolor) selecting habitats with hard substrates. The rest of the world's oystercatchers also fall into these two habitat groupings which are again correlated with the same plumage types. All oystercatchers

Plate 3.3

The small rock platform at the base of Farewell Spit where Black Oystercatchers constantly fed in the winter of 1967. Even though these rocks are immediately adjacent to extensive beaches of the Spit, the birds rarely left the platform to feed.

with black or unstable pied plumages show a distinct preference for rocky habitats. Pied oystercatchers with clear-cut stable plumages inhabit sandy beaches, mudflats and estuaries.

The selection of rocky habitats by black oystercatchers has been attributed to predator selection (Bancroft, 1927). This view contended that melanistic plumages gave protective colouration against dark rocky backgrounds, while white-bellied forms were less conspicuous on sandy beaches. Evidence to support this view is lacking. Adult oystercatchers have very few natural predators, and no records of predation of wintering birds were detected in the literature. Black oystercatchers in New Zealand do not show any selection for dark rocks and frequently feed on white limestone outcrops in the littoral zone. Further, as already mentioned, oystercatchers with unstable pied plumage also show a preference for rocky habitats. The Chatham Island Pied Oystercatcher (*H. unicolor chathamensis*) is exclusively rock-dwelling in habit (Fleming, 1939), and certainly does not select habitats which would give its plumage the function of protective colouring. Where cryptically coloured substrate races occur among animal groups, they show exclusive selection for matching substrates. The darkly coloured South African lark *Mirafra sabota* is restricted to dark soils of southwest Africa, while its reddish congener *M. africanoides* inhabits the red Kalahari sand. Substrate selection is rigorous even where the two substrates intermingle, and it is thought to be the result of predator selection (Niethammer, 1940).

Habitat selection has been shown to have a strong genetic component by Harris (1952) who found that individuals of forest and prairie subspecies of the deermouse *Peromyscus maniculatus*, bred and raised in standard laboratory cages, differ in their preference for various artificial habitats. *P. m. bairdi* preferred habitats that resembled grasslands, *P. m. gracilis* such as resembled woodland. The extremely narrow and conservative range of habitat selection shown by oystercatchers is strong evidence for an associated genetic component. The young of the South Island Pied

Plate 3.4

South Island Pied Oystercatchers foraging in coastal fields near the Heathcote-Avon estuary following overnight rainfall which had brought earthworms to the surface.

Oystercatcher, raised on inland riverbed breeding sites, show a remarkable innate capacity to undertake their own migratory flights to suitable winter habitats (see Ch 4.11). The recognition and selection of these habitats by juvenile oystercatchers is instinctive.

In recent years, South Island Pied Oystercatchers have shown greater flexibility and partial change in habitat selection. Following heavy rain, and often coinciding with spring tides, flocks of oystercatchers leave marine littoral feeding areas and forage in coastal fields (see Plate 3.4). An increasing tendency for birds to feed in these fields outside the breeding season has been noted in the past ten years (Urquhart, 1965; Poppelwell, 1965; Hamel, 1965; Falla et al., 1966). Black Oystercatchers (Haematopus u. unicolor) have also been recorded feeding in coastal fields in South Westland (A. Williams, pers. comm.). A similar tendency to feed inland during winter has been described by Dare (1966) for the European Oystercatcher in Great Britain. He considered that terrestrial feeding at this time of the year was probably an extension of roosting behaviour, especially during the very wet or stormy weather when low-lying fields were partly flooded. Earthworms forced to the surface by this water provided a temporarily plentiful source of food. Dare suggested that from picking up these surfacing worms to actively probing for them would be but a short step, particularly for those birds which were already inland breeders, and any temporary shortage of normal shellfish foods would tend to accelerate the adoption and spread of this feeding habit. Whether this new behaviour will become firmly established and increase further, or whether terrestrial foods will continue merely to supplement the normal shellfish diet and serve as a valuable emergency food supply, remains to be seen.

In summary, the dichotomy of habitat selection shown by New Zealand oystercatchers would appear to be the result of a genetic component modified by interspecific competition. Habitat selection resulting from predator selection can be discounted as natural predators are unknown in this country. South Island Pied Oystercatchers in particular have shown an increasing tendency in recent years to supplement marine foods with terrestrial ones, and this presumably indicates an increasing flexibility in habitat selection. As Mayr (1963) has pointed out, habitat selection is a conservative factor in speciation since it reduces the probability that new isolates will be established beyond the present species border. The extremely limited speciation within the genus Haematopus is no doubt a reflection of this rigorous selection.

3.5 FEEDING BEHAVIOUR

A. Daily Activity and General Feeding Rhythms.

The daily routine of wintering flocks of oystercatchers is well documented, being described in detail for the European Oystercatcher (Haematopus ostralegus (L.)) (Dewar, 1915; Drinnan, 1957; Davidson, 1967). The New Zealand species and races of oystercatcher follow the same general pattern, but this pattern is apparent for Black and Variable Oystercatchers only where they occur in sizeable groups.

The behaviour of oystercatchers follows a regular tidal cycle. At high water, the birds congregate on high water roosts or refuges (see Plate 3.5), while low water periods are spent feeding. When the tide is at its maximum ebb, the birds often concentrate into low water roosting flocks along the edges of drainage channels, particularly when weather conditions are adverse. From these low water roosts, the birds again disperse to feed as the tide rises. They gradually retreat before the flood and gather into large "intermediate sand flocks" * on the more elevated parts of the feeding grounds. When driven off these flocking areas by the tide, the oystercatchers return to the high water roost on the supralittoral region of the shore.

The period of high water is a time of general inactivity, the time being spent resting, preening and bathing. Roosting flocks

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* name given to pre-roosting flocks by Drinnan (1957).

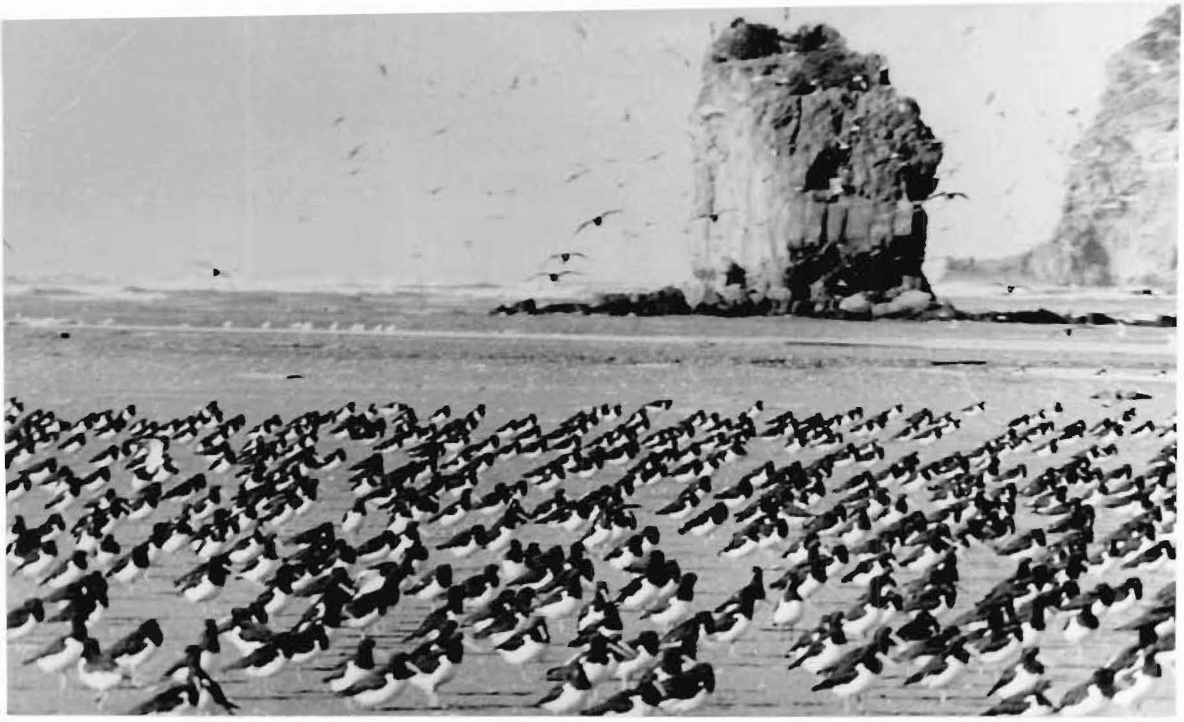


Plate 3.5

Oystercatchers congregated on high water roosts.

Upper - South Island Pied Oystercatchers at the
Heathcote-Avon estuary (June, 1966).
Centre - South Island Pied Oystercatchers at Manakau
Harbour (November, 1967).
Lower - High water roost at Jackson Bay where Black
and Variable Oystercatchers roost (July, 1967).

of birds, particularly South Island Pied Oystercatchers, consist of dense aggregations restricted to small roosting areas. Under these conditions birds are compelled to form tight flocks, neighbouring birds roosting well within the normal "fight-eliciting" distance (Lorenz, 1967). Fighting is however largely prevented by the adoption of the true sleeping posture. This posture is characterised by the insertion of the bill beneath the scapulars after the head has been rotated through 180° (see Plate 3.6). Whenever a bird ceases to maintain the sleeping posture, fighting occurs between it and neighbouring birds.

The high water roost is also extensively used by other charadriiform birds, resulting in the formation of dense multispecific flocks. Interspecific interactions between oystercatchers and other waders are minimised by species segregation within the roost (see Plate 3.7).

As the tide ebbs, movement to the feeding grounds begins. The oystercatchers gradually spread out over the feeding habitat as low water is approached, and so the cycle of behaviour is completed. A noticeable feature of the movement to the feeding localities is the occurrence of massed flights. Initially the birds disperse from the roost in small groups, but any time after high water the entire flock may simultaneously take to flight.

The cycle of behaviour described above is continuous throughout the periods of day and night, the latter based on nocturnal feeding observations and the night-time accumulation of faeces. Dewar (1915) noted that oystercatchers were "slavish followers of the tide" and that "the search for food continued after dark and was evidently carried on much as in daylight". He also claimed that darkness limited the range of the birds, the more distant feeding grounds being visited only on moonlight nights. No evidence of any such limitation is available from the present study or from the studies of Drinnan (1957) and Davidson (1967).

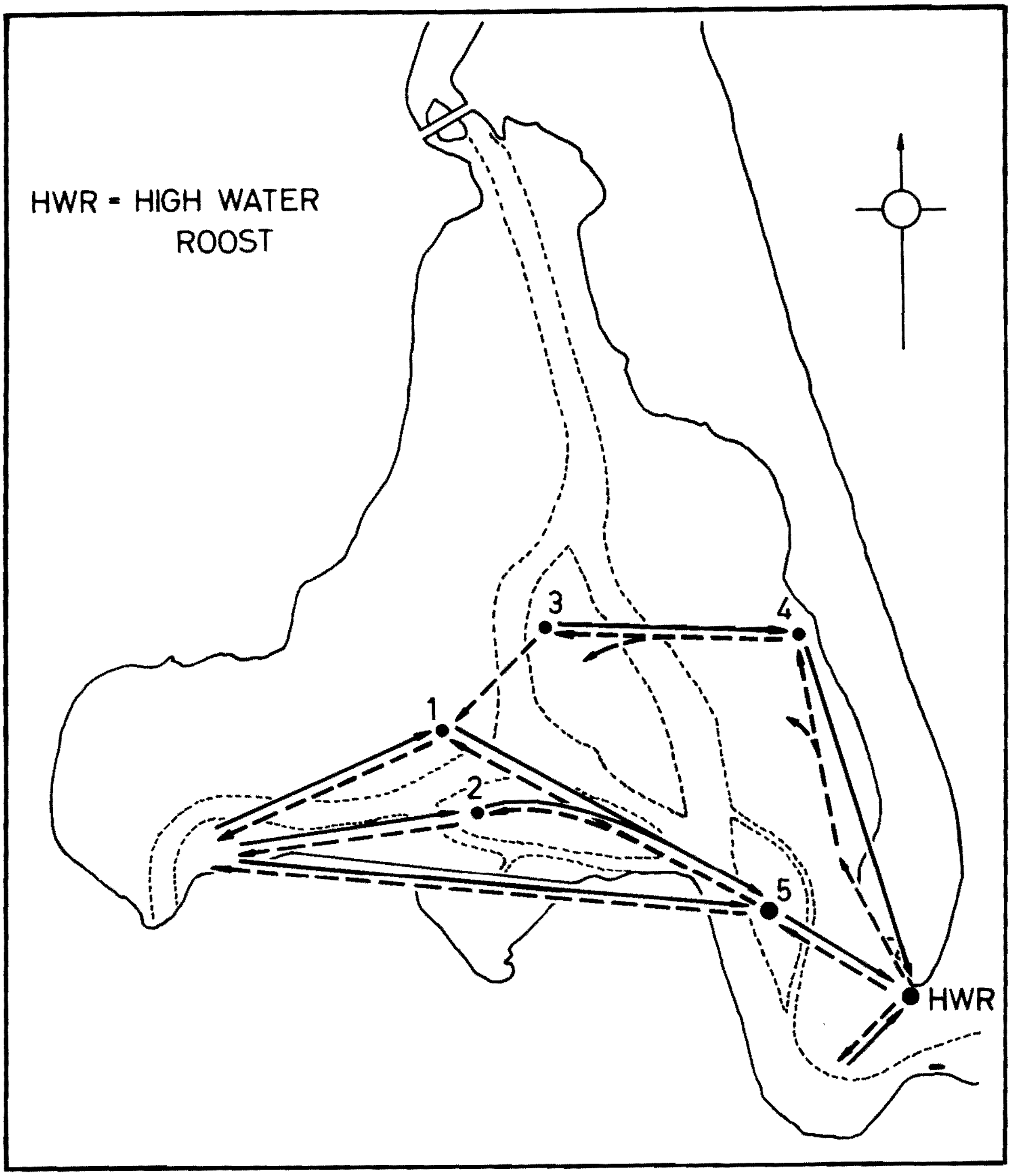
The formation of high water flocks at the Heathcote-Avon estuary follows a set pattern. Five intermediate sandflocks are

Plate 3.6

True sleeping posture of the South Island Pied Oystercatcher. Note that sleeping birds have their eyes closed and commonly stand on one leg.

Plate 3.7

Interspecific segregation of waders at the Heathcote-Avon high water roost. South Island Pied Oystercatchers roost away from the water's edge, whereas Eastern Bar-tailed Godwits (*Limosa lapponica*) and Eastern Knots (*Calidris canutus*) roost nearer to the water.


HWR = HIGH WATER ROOST
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HWR

Figure 3.6

Pattern of movements to and from the high water roost. Movements from the roost to the feeding grounds are depicted with solid arrows, and movements back to the roost from the feeding grounds are shown in broken arrows. Each sandflock is distinguished by an appropriate number.

formed at discrete feeding grounds, and once formed there is only a small degree of movement between them (see Fig 3.6). This flocking behaviour is so regular that it can be used to census the estuarine population of oystercatchers. As the tide rises the intermediate sand flocks fly to the high water roost, or form a huge pre-roosting flock on an elevated sand bar in Monck's Bay (Plate 3.8). The formation of this pre-roosting flock appears to be due to human disturbance of the high water flock. On week days, when the shore is relatively free of human intrusion, the pre-roosting flock is either very small or is not formed at all. Eventually the sea drives the birds from the sand bar onto the high water roost. During large spring tides, or at times when high water coincides with river flooding, the high water roost is inundated and the birds roost on the oceanic beach or the fields at the western edge of the estuary.

The pattern of movement to the feeding grounds is the reverse to that of sandflock formation (see Fig 3.6). Movement away from the roost does not begin immediately after the tide begins to ebb. There is a noticeable time lag between the initial ebbing of the tide and movement to the feeding grounds. Large scale movements begin when the beds of molluscs in each feeding area are exposed by the receding tide. As these beds are not visible from the high water roost, this time lag represents an acquired form of behaviour. Drinnan (1957) found that a time lag as great as two hours was commonplace.

In the course of this study, Black and Variable Oystercatchers were never observed to form intermediate sandflocks, this flocking behaviour being absent where they existed in populations discrete from flocks of the South Island Pied Oystercatcher. A relatively large flock of Variable Oystercatchers (c. 100 birds) use the rocks at Bluff, Northland, as a high water roost, and during low water periods they disperse along Ninety Mile Beach to feed. As the tide rises they fly directly back to the rocks to roost. The absence of sand-flocking behaviour was also apparent in a mixed

Plate 3.8

Part of the pre-roosting flock of South Island Pied Oystercatchers on an elevated sand bar in Monck's Bay, Heathcote-Avon estuary. Human disturbance of the high water roost causes the formation of this flock as the birds are reluctant to come ashore.

flock of Black and Variable Oystercatchers (c. 50 birds) at Jackson Bay, Westland. Where, however, small numbers of these oystercatchers occur with large flocks of South Island Pied Oystercatchers, they adopt sand-flocking behaviour and associate themselves with specific sand flocks.

The tidal cycle of behaviour is not continued in the summer inland breeding areas of the South Island Pied Oystercatcher, which conforms with the behaviour of its European conspecifer (Dewar, 1915). Where the latter breeds in coastal habitats however, a tidal cycle of behaviour is readily apparent, with maximum feeding of the young occurring at the time of low water (Tinbergen and Norton-Griffiths, 1964). The coastal breeding Black and Variable Oystercatchers of New Zealand also maintain this tidal cycle of behaviour during the summer breeding season, no doubt from necessity, as food is available only when the littoral region of the shore is exposed.

A fortnightly rhythm of behaviour correlated with the alteration between spring and neap tides was described by Dewar (1915). This was shown by an anticipation of the increasing height of the spring tides in the settlement on the high water roost. Dewar's view was refuted by Drinnan (1957) who noted that birds were loath to move higher than necessary up the shore, remaining on the lower regions until lifted off their feet by incoming water. The probable reconciliation of these two divergent views lies in the location of the high water roosts. The roosts described by Dewar were all at least 150 m from the shore, while the roosts in Drinnan's study were salt water marshes in close proximity to concealing vegetation.

At the Heathcote-Avon estuary, oystercatchers show this approximate fortnightly rhythm of behaviour provided they are not molested while roosting on the shore. The anticipation of higher spring tide levels at weekends is obscured by human activity on the beach in the region of the high water roost. Under these circumstances the birds are naturally reluctant to roost higher on the beach than is absolutely necessary. All New Zealand mainland species of oystercatcher show this rhythm of behaviour. Very little is known about the general behaviour of the Chatham Island Pied Oystercatcher except that it shows no tendency to form flocks, but rather exists as isolated pairs with territories which are defended throughout the year (Fleming, 1939). A mated pair of Variable Oystercatchers of intermediate plumage at Kaikoura Peninsula exhibit this territorial non-flocking behaviour as do other isolated pairs of Black and Variable Oystercatchers.

Wintering flocks of European Oystercatchers on the Firth of Forth were noted by Dewar (1915) to have "habitual feeding ranges or territories". In most cases, these feeding territories were clearly defined by intervening bands of shore with depauperate faunae unsuitable for feeding. Some flocks of birds which shared the same high water roost fed on different grounds. This view was supported by Drinnan (1957) who followed the daily movements of a bird which had the usual black parts coloured buff. Although these discrete feeding flocks could well be an incipient form of territorialism, the term territory in the above papers is misused. According to Odum (1959), a territory may be defined as a defended area, while a home range is a definite area to which activities are restricted. Clearly then, because oystercatchers in separate feeding flocks do not defend their feeding ground against other oystercatchers, they are occupying a home range and not a territory.

South Island Pied Oystercatchers at the Heathcote-Avon estuary possess distinctive home ranges. Colour-banded birds were always found feeding in set areas of the estuary. Moreover, each bird was found in the same sandflock from day to day (see Fig 3.8). The adherence of European Oystercatchers to particular sand flocks was noted by Davidson (1967) who found that it was not possible to set confidence limits on population estimates of colour-banded birds as "the distribution of the banded birds in the flocks appears to be non-random". This tenacity to a particular flock suggests that sand flocks are composed of birds with the same home range, and that the regular formation of flocks is necessary in maintaining the

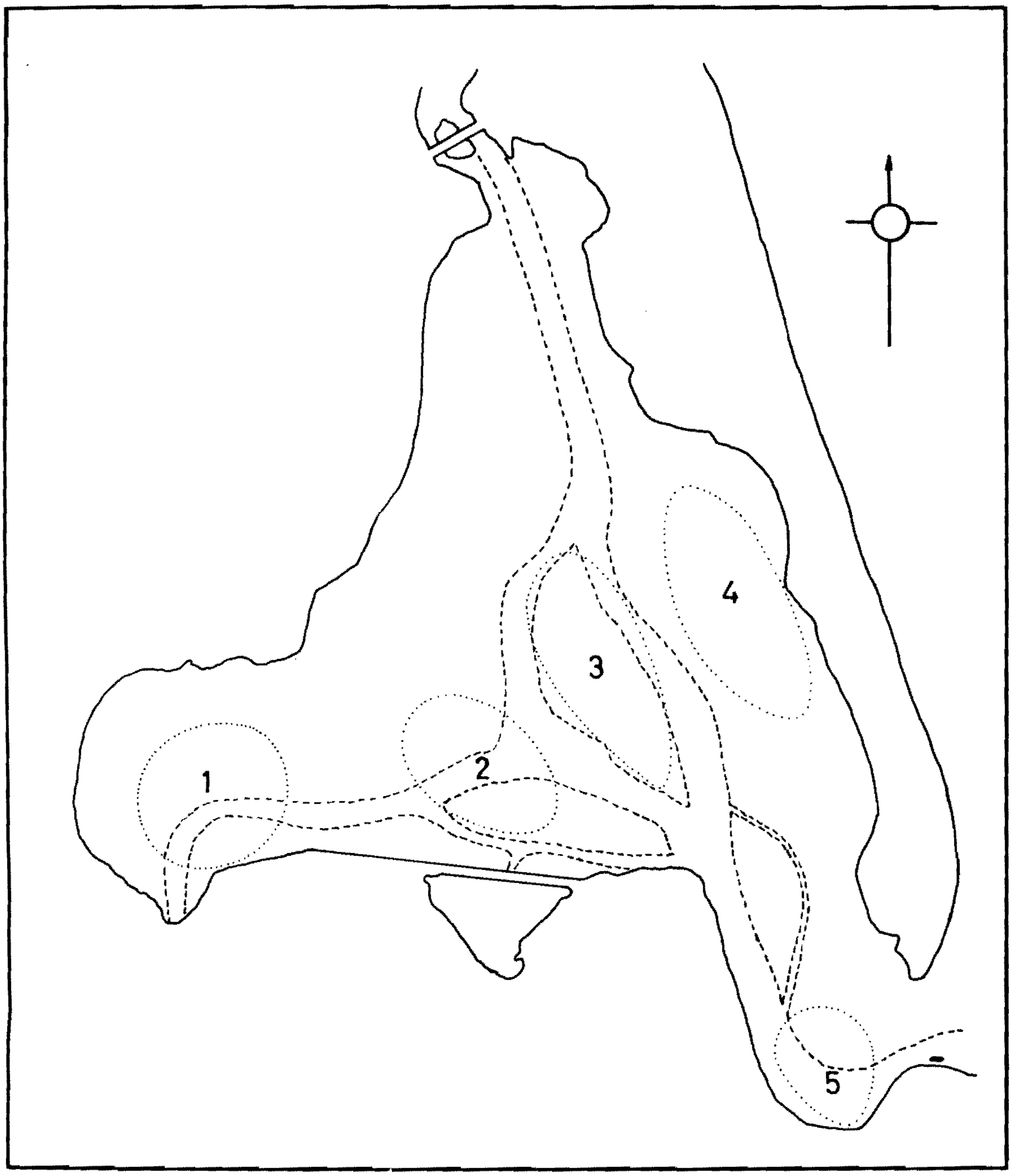
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Figure 3.7

Home ranges of South Island Pied and Black Oystercatchers at the Heathcote-Avon estuary as indicated by sight recoveries.

home-range system in the feeding area. Such a system would ensure that the available food supplies were utilised with maximum efficiency. Two immature Black Oystercatchers also maintained home ranges in the estuary (see Fig 3.8). Isolated mated pairs of Black, Variable and Chatham Oystercatchers actively maintain territories throughout the year, and vociferously attack any intruders. In these instances the breeding and feeding territories are usually identical although the former is often a contraction of the latter. The existence of a home range system at a feeding area seems to depend upon the number of birds inhabiting it; when flocks are present home ranges are occupied, and when isolated pairs are present territories are maintained. The result in either case is similar, food resources being utilised with maximum efficiency.

B. PREY - SPECIFIC FEEDING BEHAVIOUR

When feeding at low water periods on the various beds of molluscs which form their main prey, oystercatchers are not uniformly distributed, but are found concentrated in areas of high prey density where conditions favour a high feeding rate (see Plate 3.9). The effect of prey concentration on the distribution and feeding rate of South Island Pied Oystercatchers at the Heathcote-Avon estuary is shown in Table 3.1.

TABLE 3.1 THE EFFECT OF PREY CONCENTRATION ON THE DISTRIBUTION AND FEEDING RATE OF OYSTERCATCHERS (*Haematopus ostralegus*) AT THE HEATHCOTE-AVON ESTUARY

Mean number of birds/ study site	Mean cockle concentration /sq. metre	Mean feeding rate (Cockles / hr.)	Number of observations
22	78	96	10
16	54	60	14
10	42	48	12
5	33	24	14
1	20	24	11

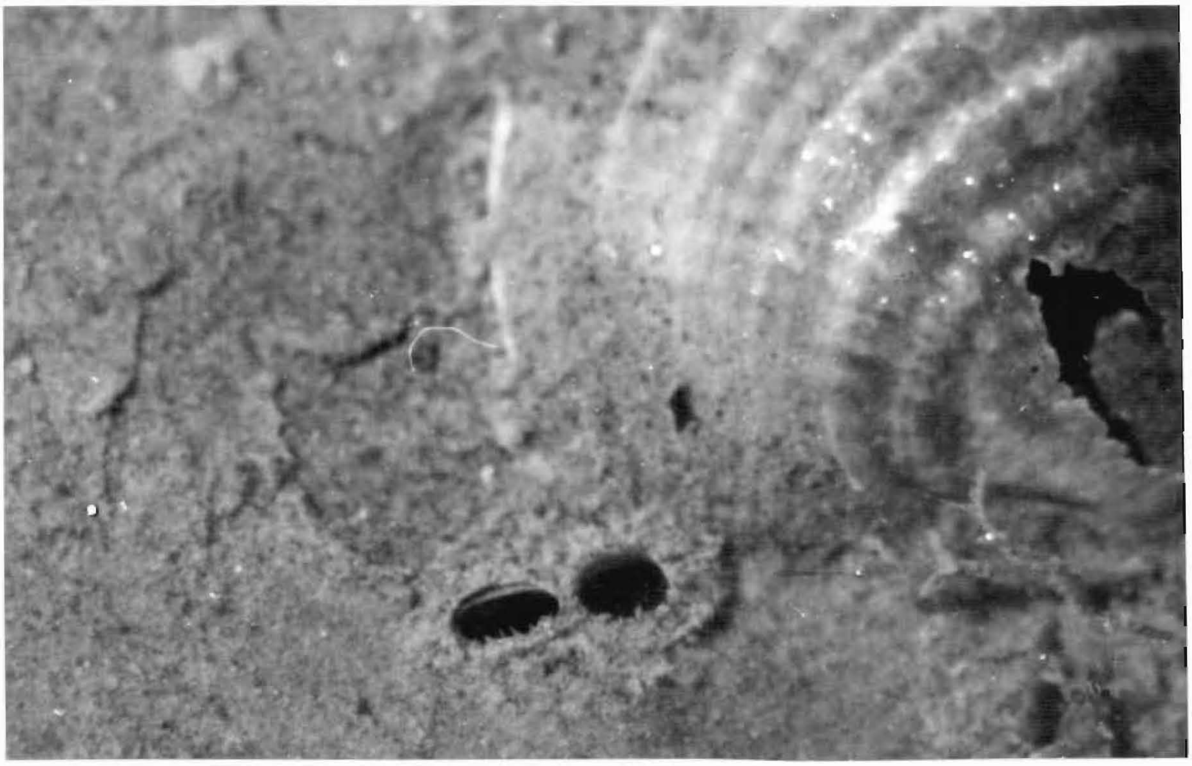

Plate 3.9

South Island Pied Oystercatchers feeding at the Heathcote-Avon estuary. The birds are not uniformly distributed, but tend to aggregate in areas of high prey concentration.

Plate 3.10

A gaping cockle as indicated by the presence of siphons at the surface of the substrate. Each siphon is approximately 4 mm across, their relative size being shown by the adjacent shell which is 51 mm long.

Feeding rates are optimal, judging from feeding rate data, when the beds are covered by 1 to 10 cm of water, and large numbers of birds follow this region of shallow water in and out with the tide. At low water, the littoral feeding grounds are completely exposed, forcing the birds to seek out their food in uncovered areas. For convenience, the location and taking of prey will be described under three headings:-

1. Location of Prey in Areas Covered by Shallow Water.

The invertebrates which form the prey of oystercatchers feed at the water/substrate interface when covered by water, and are therefore most vulnerable to predation at this time. Thus feeding conditions will be optimal for the birds when the tide is covering or uncovering a dense concentration of prey species.

As much of the benthos of the Heathcote-Avon estuary is composed of mud-dominated substrates, the molluscan infauna consists chiefly of the cockle Chione stutchburyi. The presence of feeding cockles is indicated by the occurrence of siphons (see Plate 3.10) or small depressions above the siphons, at the surface of the substrate. When seeking actively feeding cockles, the South Island Pied Oystercatcher wades slowly forward, head down and cocked slightly to one side, the body parallel to the water and the bill almost vertical (see Plate 3.11). Occasional random probing may occur, but location of the cockles seems to be by sight in most instances. Evidence for this is found in the occurrence of "semi-probes", the bird plunging at something which has attracted its attention, but halting the strike on or just below the water level. Occasionally a bird will turn through an angle as great as 180° to exploit a potential food source sighted in passing. The most conclusive evidence for the hypothesis that prey species are located by sight comes from a calculation of feeding success, which is taken to mean the percentage success with which food is obtained relative to the number of attempts (probes) made at food gathering. The feeding success of South Island Pied Oystercatchers at the

Plate 3.11

South Island Pied Oystercatchers feeding on a pipi bed at the Heathcote-Avon estuary. Note the birds at the centre of the plate which show the typical "searching-for-food" posture.

Heathcote-Avon estuary is shown in Table 3.2.

TABLE 3.2 FEEDING SUCCESS OF OYSTERCATCHERS (*Haematopus ostralegus*) IN RELATION TO ATTEMPTS MADE AT FOOD GATHERING IN THE HEATHCOTE-AVON ESTUARY.

Locality	Date	Mean No. of probes/ obs. period	Mean No. of cockles/ obs. period	Mean % feeding success
Mount Pleasant Yacht Club area	12/6/66	15.2	8.1	53.2
	30/6/67	10.4	6.2	57.3
	25/6/68	17.7	9.3	52.6
Mid-estuarine bars	21/6/66	19.5	11.7	60.2
	3/7/67	22.8	12.5	54.7
	27/6/68	16.6	8.4	51.6

Number of observations at each date = 20

Note: Data was collected only during peak feeding periods near the time of low water.

The figures given for feeding success in the above table are maximal because all observations were taken for birds which were feeding on a dense bed of cockles at a time when feeding success was known to be greatest (see section 3.6C) i.e. in the period an hour either side of low water. Under such optimal feeding conditions, South Island Pied Oystercatchers are successful in locating a cockle at every second attempt. This represents a much higher rate of success than would be expected due to random probing with no visual mechanism involved. In a check on the success rate of random probing in the mid-estuarine bars feeding area, 10 samples each of ten probes were made at random with an oystercatcher bill. The mean feeding success in these samples was 9%, compared with 51.6% for oystercatchers in June 1968. The difference between these two means was statistically significant (*$t_{28} = 15.9$, $p < 0.001$), and the disparity between these relative success rates becomes even more significant if only the cockles caught gaping are considered. During the observations the birds pierced gaping cockles with their bills in 85.8% of the successful probes, whilst the experimental trial did not locate any gaping cockles at all.

In order to test the hypothesis that the maximum feeding success of oystercatchers is solely attributable to the location of gaping cockles, 10 samples each of ten probes with an oystercatcher bill were made at gaping cockles as indicated by the presence of siphons at the surface of the substrate. When conditions were ideal for sighting cockle siphons i.e. bright sunshine, no wind, cockles covered by .1 to 10 cm of water, the mean percentage of successful piercing probes was 46%. The difference in the means for the birds and the experimental trial was not significant (*$t_{28} = 1.87$, $0.1 > p > 0.05$). The higher recorded success rate of the birds was probably due to a more co-ordinated and better directed piercing probe than was possible to attain with the oystercatcher bill.

The best explanation of the data presented in this section is that when feeding conditions are optimal, oystercatchers locate cockles by the presence of siphons at the surface of the substrate. The success of feeding attempts under these conditions is directly attributable to the sight location and piercing of gaping cockles.

All three New Zealand mainland races of oystercatcher appear to sight their prey when the latter is open and feeding, judging from the comparative feeding success calculations taken at peak feeding periods near low water (see Table 3.3). The difference between the mean percentage feeding success for the South Island Pied Oystercatcher and the Black Oystercatcher was not significant ($t_{38} = 0.61$, $0.6 > p > 0.5$), as also was the difference between the means for the South Island Pied Oystercatcher and the Variable Oystercatcher ($t_{33} = 1.75$, $0.1 > p > 0.05$). Thus all three races of oystercatcher seem to possess equal ability at locating gaping cockles.

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* t_{28} = t value with 28 degrees of freedom

TABLE 3.3 COMPARISON OF FEEDING SUCCESS OF NEW ZEALAND RACES OF OYSTERCATCHER AT WESTHAVEN INLET

Race	No. of obs.	Mean No. probes/ 5 min.	Mean No. cockles/ 5 min.	Mean % Feeding success
South Island Pied Oystercatcher	16	18.4	8.6	46.6
Black Oystercatcher	24	14.9	7.1	47.7
Variable Oystercatcher	19	16.7	7.3	43.7

The location of other bivalves which form part of the diet of oystercatchers is also probably by sight. The pipi (Amphidesma australe), the tua-tua (A. subtriangulatum), the large wedge shell (Macomona liliana), the ribbed venus shell (Protcthaca crassicosta) and the dosinias (Dosinia anus and D. subrosea), all possess siphons for filter feeding at the substrate/water interface. The large wedge shell (Macomona liliana) frequently occurs at a depth of 3 to 10 cm in the substrate of the Heathcote-Avon estuary, and the only indication of its presence is provided by the siphons at the surface. Oystercatchers which take these bivalves are frequently seen with their bills completely buried in the substrate, indicating they have followed the siphon canals to the buried shell. The occurrence of bird footmarks and probes can often be used to detect concentrations of wedge shells (Morton & Miller, 1968).

The location of mussels on hard substrates which are covered by a shallow sheet of water is by sight. In the case of mussels only those shells which are gaping are attacked, showing that the oystercatchers distinguish suitable mussels by the presence of a gape. Not only are the birds able to see the gape, but their piercing probes are almost always orientated down the longitudinal axis of the gape (Dewar, 1908; Drinnan, 1958a; Norton-Griffiths, 1967). Fresh water mussels (Hyridella menziesi) in Lake Tuakitoto, Kaitangata, are also attacked when gaping (McKenzie, 1963).

Fast-moving preys such as amphipods (Talorchestia spp.), marine shrimps (Palaemon affinis), small flounders (Rhombosolea plebeia) and mud crabs (Helice crassa) are located by their movement, as they are only taken when moving (pers. obs.).

2. Location of Prey in Areas Exposed by the Tide.

On uncovered substrates the posture of oystercatchers in seeking food is very similar to that described previously, but location of the prey appears to be almost solely by touch. When the feeding grounds are completely exposed, the birds explore any depression in the surface of the substrate. In soft substrates oystercatchers move slowly forward making a series of short vertical probes with the bill slightly open and beneath the surface. The regularity of this probing is occasionally interrupted by a lifting of the bill out of the substrate, but the process is almost immediately repeated in another area. The high frequency and low amplitude of this probing is characteristic of this method of locating prey.

In dense beds of brood cockles (those in their first winter and usually measuring between 5 and 15 mm) in the Burry Inlet, South Wales, both Hancock (1963) and Davidson (1967) observed bill probe marks. As the birds walked forward the mandibles were seen to be held slightly open and rapid pecking movements were made. Larger second winter cockles located by this method were selectively removed. The searching probe with the mandibles open was also reported by Hulscher (1964), who calculated that the success rate of the oystercatchers' search for cockles was greater than would be achieved by chance. His calculations were based on the relative surface area of cockle and bill tip, and the proportion of sand occupied by the shellfish.

Unusual feeding behaviour on an exposed sandy flat was noted by Davidson (1967). The expected random probing/search behaviour was not in evidence as birds were finding cockles at every second

Plate 3.12

Dense concentrations of opened cockle shells at the Mt. Pleasant Yacht Club study area, Heathcote-Avon estuary. Such a mass of shells makes the location of inhabited cockles a difficult task for feeding oystercatchers.

or third probe. An experimental check on random probing with a wide-bladed sheath knife located 10 cockles from 300 probes, yet from observations of the birds feeding it had been established that it would have taken them only 20 to 30 probes to find this number of shellfish. On careful scrutiny of the sand surface there was no superficial evidence of the presence of buried cockles; the actual means employed by the birds was not clear, but according to Davidson some visual or auditory mechanism must have been involved.

When the surface of the substrate is littered with dense concentrations of old opened shells, the location of prey becomes extremely difficult (see Plate 3.12). Although some of the younger birds painstakingly investigate each shell, the majority of birds use a much faster method of differentiating between occupied and empty shells. Two or three short sharp blows are delivered to the shell with the bill held in a vertical position. If the shell is uninhabited the valves are flexible beneath the applied pressure, but if inhabited the valves are rigid and immoveable. A possible explanation for this behaviour is that the birds are able to detect flexibility differences in response to their hammering, and utilise it to locate live prey. All three mainland races of oystercatcher show this type of prey location when mollusc beds are exposed by the tide.

The acute eyesight of oystercatchers is well illustrated by a method of prey location at Jackson Bay, where all three races are represented. Quite extensive beds of tua-tuas occur in the littoral zone of sandy beaches there, and form an important part of the birds' diet. Like most other exposed west coast beaches, wave action is usually considerable and with it is associated a strong undertow which keeps the sand constantly in motion. The movement of the sand often results in the uncovering of tua-tuas, especially so in the undertow following each wave. Oystercatchers which are following the waves in and out frequently sight these exposed tua-tuas, and rush to pick them up before another wave covers the prey.

The role of learning in prey location is graphically illustrated

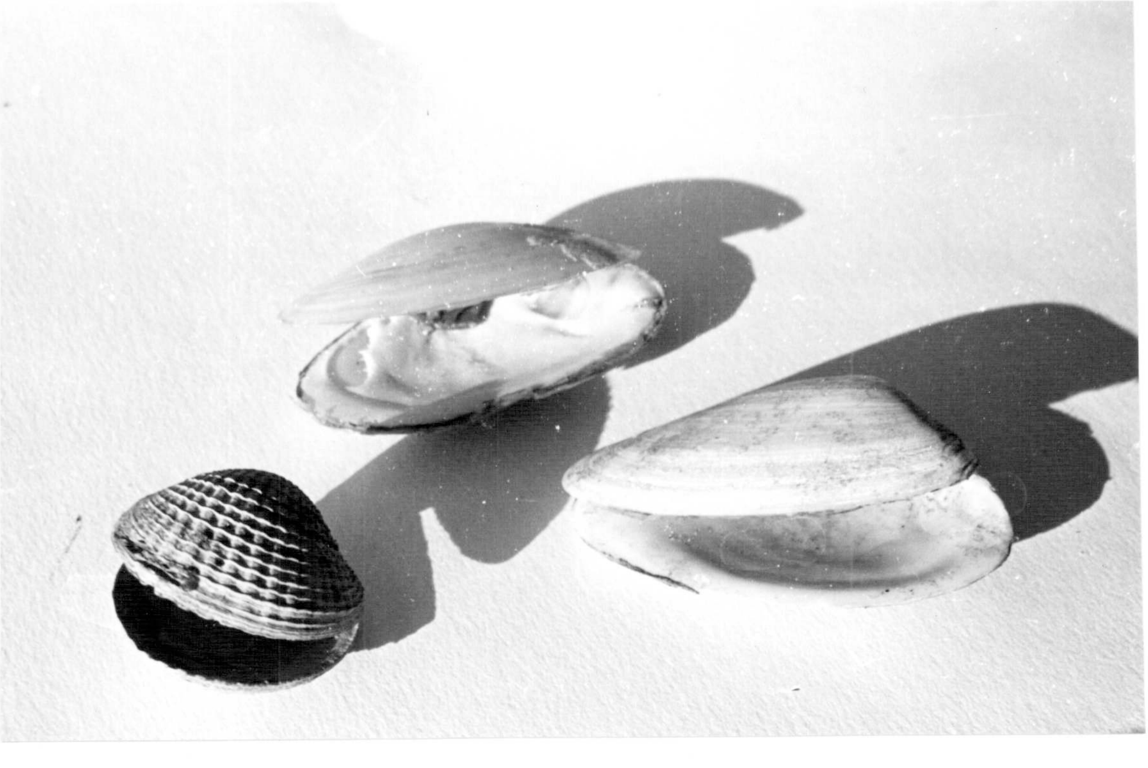


Plate 3.13

Shells of the pipi (*Amphidesma australe*), the tua-tua (*A. subtriangulatum*) and the cockle (*Chione stutchburyi*) which have been pierced. Note the complete absence of damage to the ventral margin of the shells.

by South Island Pied Oystercatchers which feed on Brighton beach. The bivalves *Dosinia anus* and *D. subrosea* occur abundantly in the sand, but are not visible at the surface. When the tide has exposed the beds, the presence of bivalves is indicated by a jet of water which is squirted from the siphons to a height of approximately 1 m above the sand. Nearby birds which see the jet of water rush to the site and probe vigorously for the gaping shell, often with success. Not all of the birds utilise this method of prey location; only those birds which have learned to associate the jet of water with the presence of a bivalve consistently show this behaviour.

The location of amphineuran and gastropod molluscs on hard substrates, and of the mud-snail (*Amphibola crenata*) in estuaries, is solely by sight, as these preys occur abundantly at the surface. The problem facing oystercatchers feeding on rocky shores is not one of prey location, but rather one of removing prey which are firmly affixed to the rocks.

Polychaetes are sometimes taken in the course of feeding on mollusc beds. Whether or not the bed is covered with water, location of the worms appears to be by touch. The typical feeding behaviour associated with the taking of polychaetes is that of random probing, and for this reason it would seem that oystercatchers rarely sight this prey.

3. Methods of Taking Prey

The methods by which oystercatchers extract bivalve molluscs from their shells are basically similar for each bivalve, with small differences associated with the mode of location. When a bivalve is sighted, the bird makes an initial sharp vertical probe at it. If the bill penetrates between the two valves of the mollusc, opening of the shell is often attempted in situ, provided the mollusc is near the surface of the substrate. Should the bivalve be pierced at some depth below the surface, the bill is wedged between the valves and the animal is removed from the substrate and opened at the surface, or it is carried onto the exposed firmer shore and the task completed there. These observations are readily

Plate 3.14

Initial piercing probe of the bill of a South Island Pied Oystercatcher down the long axis of the gape of a cockle.

Plate 3.15

Rotation of the bill through 90° to prize the valves apart. Prizing movements follow the initial piercing probe in Plate 3.14.

confirmed by chasing the birds away from freshly captured cockles.

The method of opening bivalves which have been pierced by the initial location probe is characteristic. The valves are parted by repeated pressure thrusts towards the centre of the animal, and in many cases deep footprints are left around an empty shell. If the piercing probe severs one or both of the adductor muscles, opening and stripping of the shell is completed in as little as five seconds (see Plate 3.13). When the adductors are still intact after the piercing probe, the bill is driven more deeply between the valves by pressure thrusts against the substrate. In the course of the piercing probe the bill is orientated to enter the shell down the long axis of the gape (see Plate 3.14). The valves of the shell are therefore initially parted by the minimum dimension of the bill, bill width, which at the tip of the bill is often less than 1 mm wide. Deeper thrusts into the shell allow entrance of a wider part of the bill, causing valve separation of approximately 3 mm. When this has been achieved the bird then turns its bill through 90° so the 9 to 12 mm height of the bill forces the valves wider apart (see Plate 3.15).

The prizing movement described above was noted by Tinbergen & Norton-Griffiths (1964) when breeding birds were seen preparing mussels for their young. The rotation of the body to effect prizing of the valves apart was described for the European Oystercatcher (_Haematopus ostralegus_) by Dewar (1908), who found that the rotation was always to the bird's left hand side. This view was supported by Webster (1941) who observed the same behaviour for the North American Black Oystercatcher (_H. bachmani_). The direction of rotation of the New Zealand oystercatchers is also largely to the left, but not invariably so, as shown in Table 3.4.

According to Stresemann (1929) the constant left hand rotation in the prizing movement results in asymmetry in the maxillary and lacrimal regions of the adult skull. No such skull asymmetry occurs in New Zealand oystercatchers (see Plate 3.16).

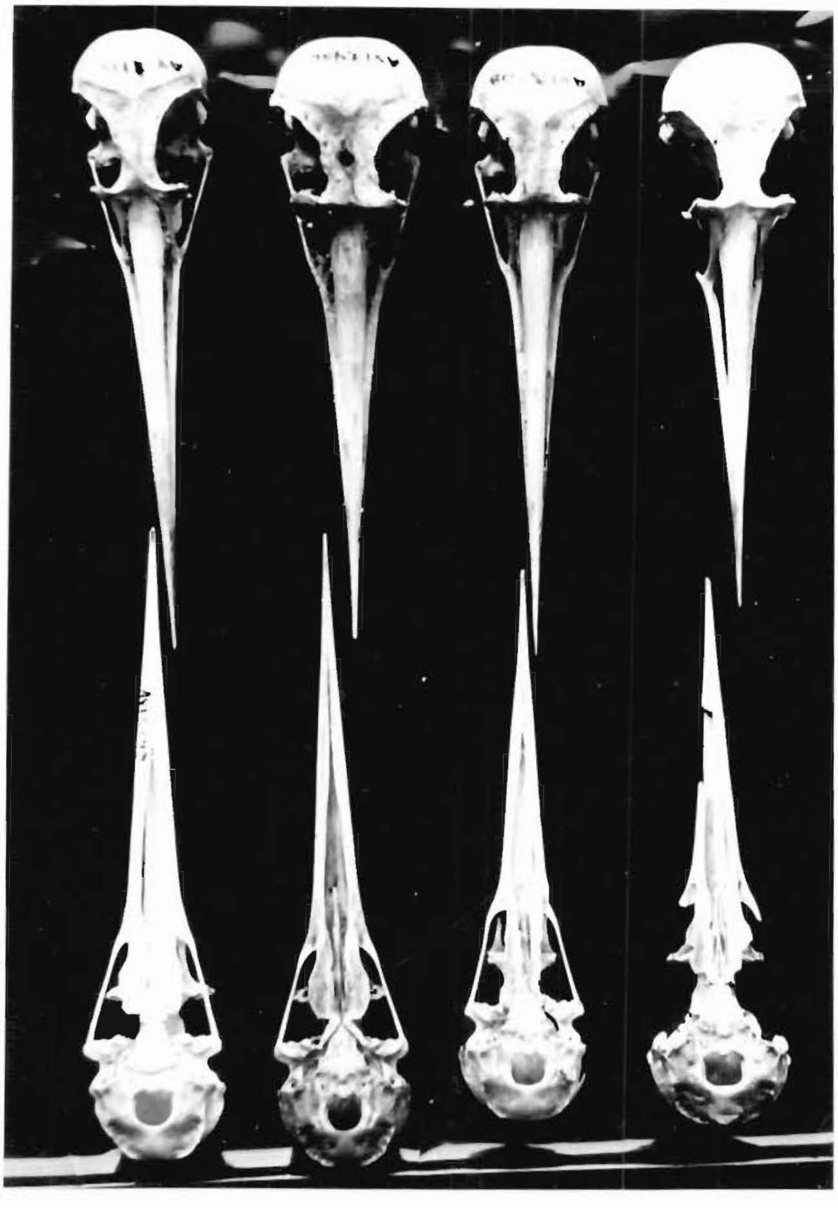


Plate 3.16

Skulls of New Zealand oystercatchers photographed from their dorsal aspect (above) and ventral aspect (below). Note their symmetry especially in the maxillary and lacrimal regions.

Key to skulls (left to right): South Island Pied Oystercatcher, Black Oystercatcher, Variable Oystercatcher, Chatham Island Oystercatcher.

TABLE 3.4 DIRECTION OF ROTATION BY NEW ZEALAND OYSTERCATCHERS WHEN PRIZING OPEN BIVALVE SHELLS

Race	No. of obs.	Prey Species	Direction of Rotation	
			To the Left	To the Right
South Island Pied Oystercatcher	17	_Chione stutchburyi_	94.1%	5.9%
Black Oystercatcher	14		100%	0%
Black Oystercatcher	22	_Amphidesma subtriangulatum_	90.9%	9.1%
Variable Oystercatcher	14		100%	0%
Black Oystercatcher	20	_Mytilus edulis_	95%	5%

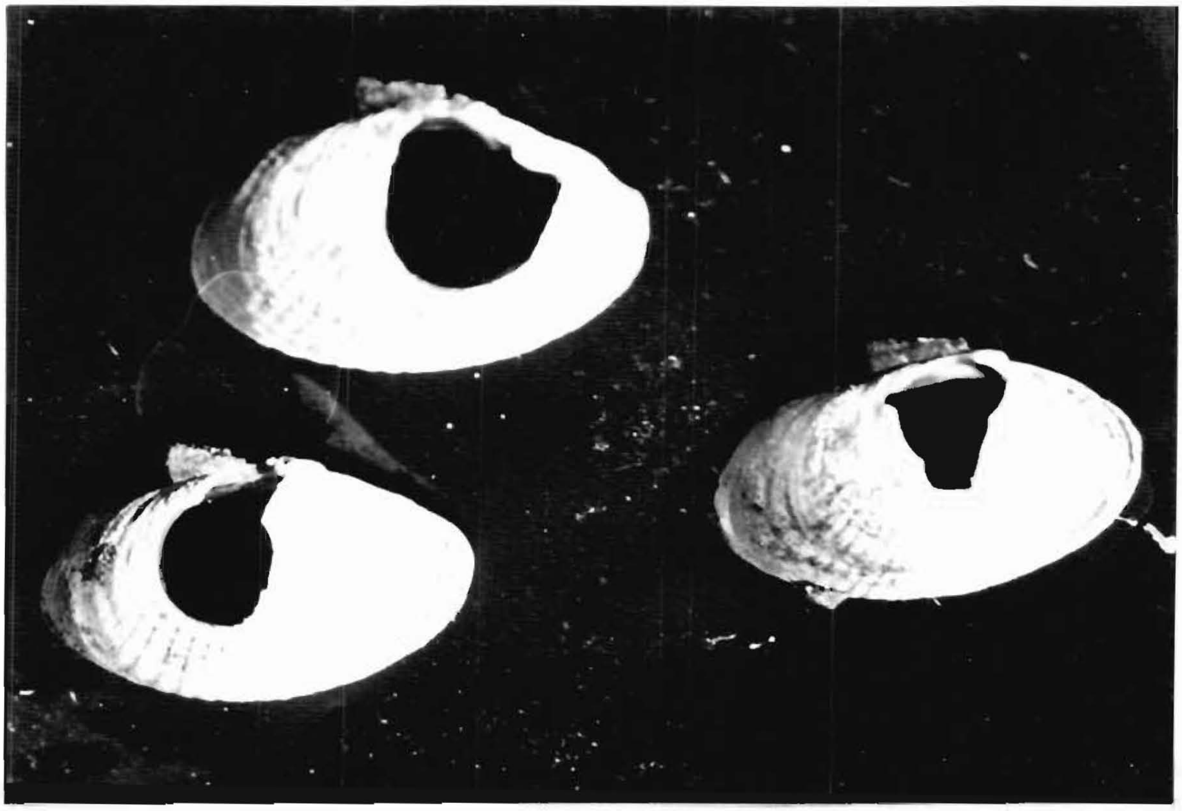
After the valves are separated sufficiently to allow easy entrance to the bill, the body of the bivalve is removed in two or three mouthfuls and swallowed, leaving only minute remnants of the mantle margin and adductor muscles in the shell.

The location of bivalves which are gaping is not always followed by a successful piercing probe. Occasionally bivalves escape the piercing probe by firmly drawing their valves together. These closed shells are removed from the substrate by inserting the bill beneath the animal and levering against the substrate, or by seizing the animal between the mandibles and pulling strongly upwards. Norton-Griffiths (1967) has shown that the taking of closed mussels (_Mytilus edulis_) from hard substrates depends upon the birds' strength in overcoming byssal attachment. Unless the mussels can be removed from the substrate they cannot be opened as the major point of access to the shell, the byssal cleft, is obscured.

Firmly closed bivalves which have been dug up are dealt with in one of two methods. Usually admittance is gained to the interior of the shell by hammering the valves with the point of the bill. The body of the bird is drawn erect and the bill reflexed into a vertical position. From this attitude the shell is hammered vigorously, the amplitude of the blows often being as great as 3 cm. Because of the erect position from which the shells are hammered, the bird is able to generate considerable power in each hammering probe.

At the Heathcote-Avon estuary, shells of both the cockle (Chione stutchburyi) and the pipi (Amphidesma australe) are hammered. Hammering is continued until a hole is made in the shell, and this initial hole is enlarged until the body of the animal can be removed through it. The position at which the shell is hammered differs for cockles and pipis. The valves of the cockles are hammered in the region of the umbo which is the thinnest region of the shell, mainly because shell deposition occurs at the mantle margin (see Plate 3.17). Where the valves have been bored by the marine boring worm (Polydora ciliata), oystercatchers hammer at this region of weakness in preference to the umbo (see Plate 3.18). Of a sample of 100 opened shells weakened by borers, 92 were hammered at borer sites.

Hammering of cockles at the Heathcote-Avon estuary contrasts sharply with the methods of taking the same prey at Collingwood beach in Golden Bay, Nelson. At this oceanic beach hammered shells are completely absent, as all shells are opened by piercing between the valves. The explanation of this lack of hammering behaviour lies in the relative structure of the cockle shells under estuarine and oceanic conditions. The major element in the shells of marine shellfish is calcium, which is extracted from the surrounding water and laid down in the shell (Orton, 1925; Fox and Coe, 1943; Robertson, 1941; Bevelander, 1948; Wilbur and Jodrey, 1952; Rao and Goldberg, 1954). Thus the rate of deposition of calcium in a



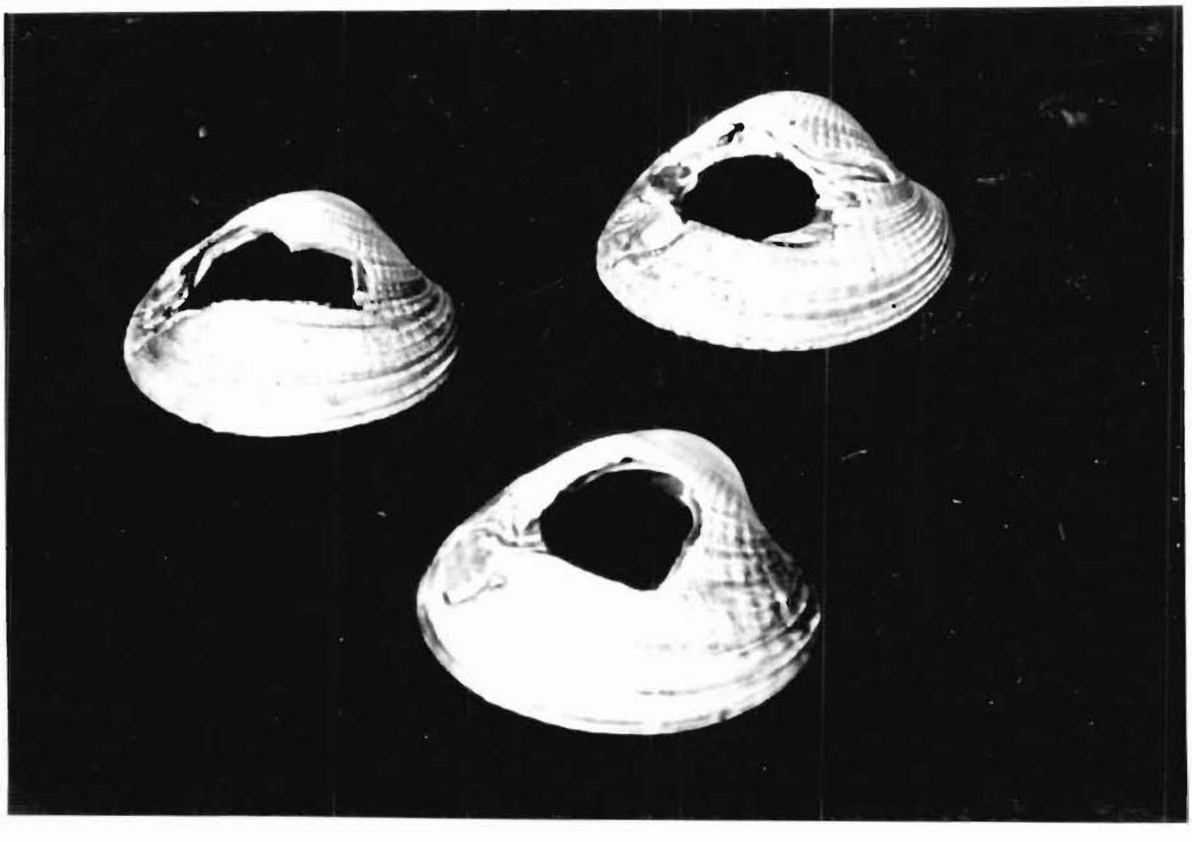


Plate 3.17

Shells of cockles which have been hammered. Note the characteristic damage to the umbo region of the shell.

Plate 3.18

Shells of cockles which have been hammered at areas weakened by marine boring organisms.

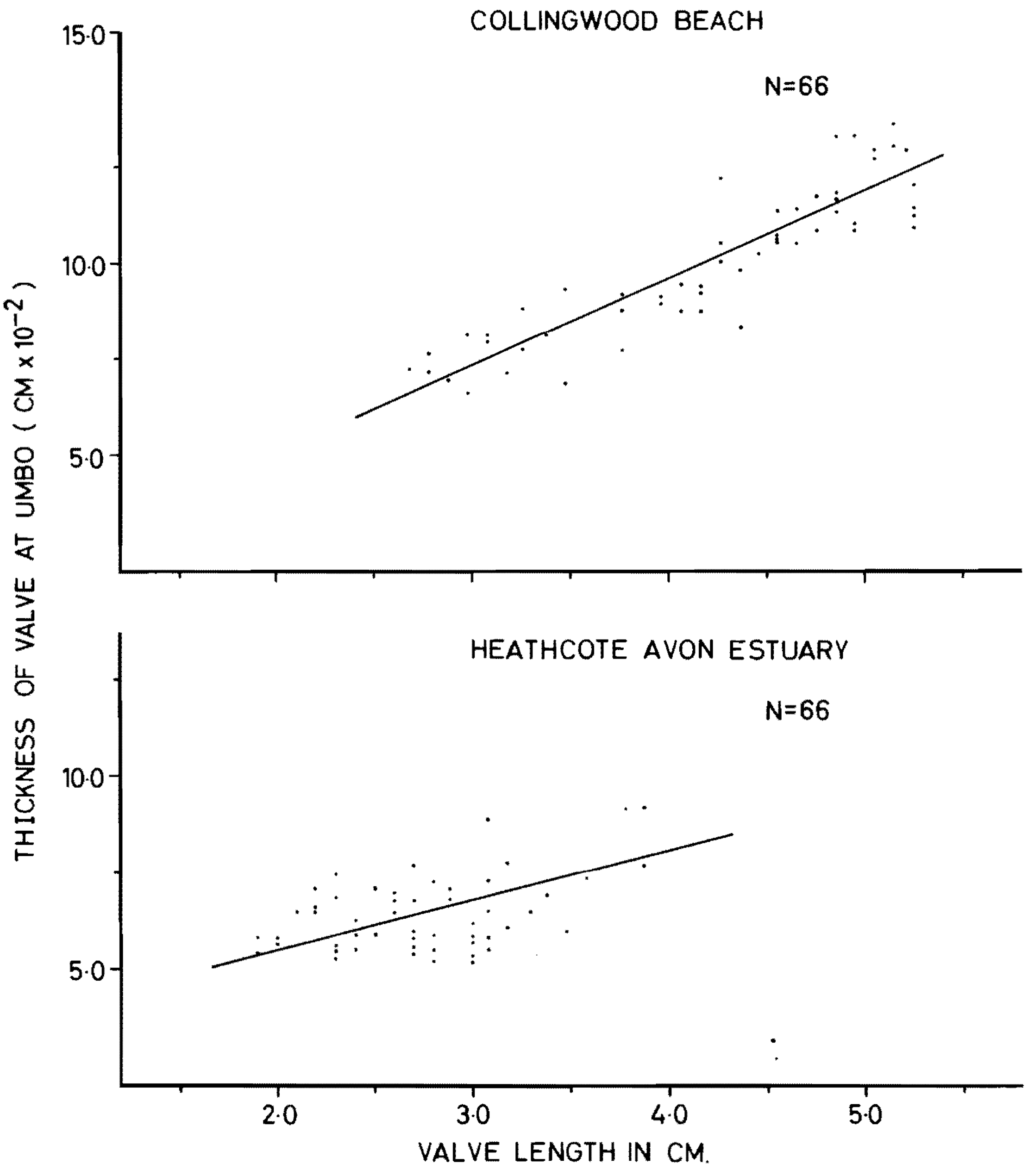

COLLINGWOOD BEACH
N=66
15·0
10·0
5·0
HEATHCOTE AVON ESTUARY
N=66
10·0
5·0
THICKNESS OF VALVE AT UMBO (CM x 10^{-2})
2·0
3·0
4·0
5·0
VALVE LENGTH IN CM.

Figure 3.8

Comparison of shell thickness at the umbo for cockle shells from an oceanic beach (Collingwood) and an estuary (Heathcote-Avon). The steeper slope of the upper graph shows clearly that cockle shells are much thicker at the oceanic location than the estuarine one.

shell, and shell thickness, will therefore depend upon the salinity of the water in which the mollusc lives. Near the Heathcote bridge, where most of the hammered shells occurred, the salinity of the water was found to be only 1.5‰ compared with 33.5‰ at the seaward end of the estuary (Linzey, 1944). It would be expected in comparing the thickness of the cockle shells at the umbo that estuarine shells would be considerably thinner than their counterparts from an oceanic beach, and the results of this comparison are shown in Fig 3.8. The shells from the oceanic beach at Collingwood are, as expected, significantly thicker in the umbo region than the shells from the Heathcote-Avon estuary ($t_{132} = 2.17$, $0.05 > p > 0.02$). The absence of hammered shells at Collingwood is thus directly attributable to the greater thickness of the shells in the umbo region.

Another method of opening closed cockle shells which have escaped the initial piercing probe is evident at Collingwood. When the valves are tightly closed on one another, a very slight persistent gape is obvious where the siphons protrude during feeding. Oystercatchers attempting to open closed cockles first orientate themselves so that the point of the bill comes into contact with the gape of the cockle down its long axis. Pressure thrusts are then made against the gape until the valves are forced apart. The percentage of "failures" at opening closed shells is very much higher for this method of shell-opening (23%) than it is for hammering (7%).

In contrast to cockles, the valves of pipis are hammered near the mantle margin, probably because the shell is extremely thin there, often being drawn out into thin sheets of periostracum at its extremities. Invariably, hammering results in the fracture of a valve at its ventral border (see Plate 3.19). The bird's bill is inserted through the chipped region of the shell and the body of the pipi extracted.

The proportion of shells hammered to those pierced by South Island Pied Oystercatchers at the Heathcote-Avon estuary, differ for the species of prey concerned (see Fig 3.9). Whereas hammering is

Plate 3.19

Shells of the pipi which have been hammered. Note the uniformity of the damage to the ventral border of the valves.

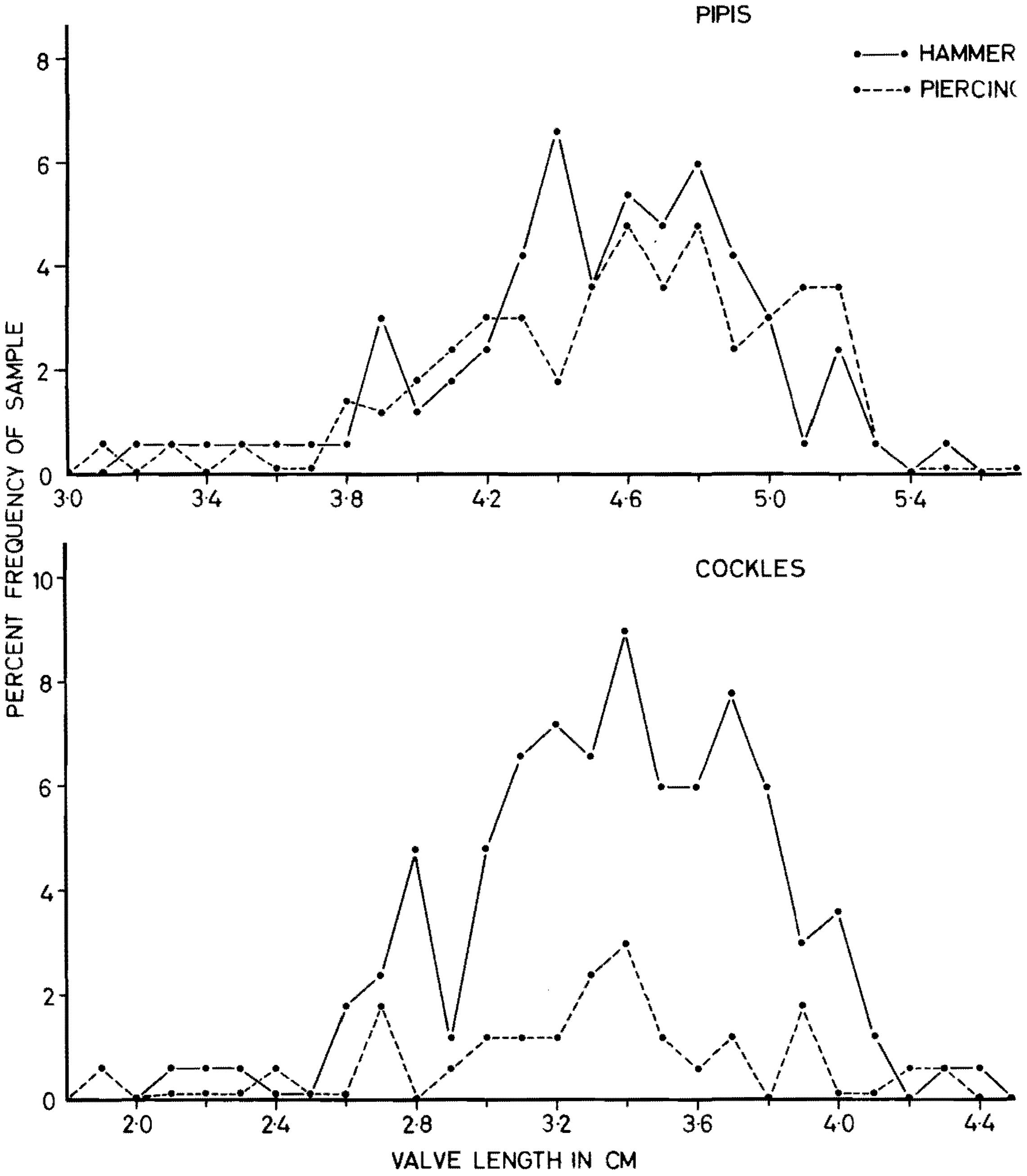

PIPIS
HAMMER
PIERCIN
8
6
4
2
0
3·0
3·4
3·8
4·2
4·6
5·0
5·4
PERCENT FREQUENCY OF SAMPLE
COCKLES
10
8
6
4
2
0
2·0
2·4
2·8
3·2
3·6
4·0
4·4
VALVE LENGTH IN CM

Figure 3.9

Comparative ratios of shells hammered to those pierced for both cockles and pipis.

approximately three times as prevalent as piercing for cockles, pipi opening is performed almost equally by both methods. This indicates that either pipis are more easily sighted when gaping than cockles are, or, pipis are easier to open by pressure thrusting against the persistent gape.

Methods used by Black and Variable Oystercatchers for opening the blue mussel (Mytilus edulis) and the small mussel (Modiolus neozelanicus) are identical to those described by Norton-Griffiths (1967) for the European Oystercatcher. When gaping under water, the mussels are pierced between the valves, detached from the substrate, and prized open. Mussels exposed to the air have tightly closed valves, and entrance to the shell can only be attained by hammering a hole through one of the valves. Smaller mussels are removed from the substrate and orientated with their flatter vertical side upwards, but large mussels in excess of 6 cm are hammered in situ, with both the ventral and dorsal borders being hammered (see Plate 3.20) depending on which aspect is presented uppermost. Dense concentrations of the small mussel (Modiolus neozelanicus) which are less than 2 cm in length are dealt with simply by tearing shells from the substrate and swallowing them whole. Birds feeding in this manner shed faeces which are full of crushed shell fragments. South Island Pied Oystercatchers were never observed feeding on mussels, but Jackson (1964) recorded birds levering them open in Manakau Harbour.

On rocky shores, limpets and chitons form the major prey of oystercatchers. The large shore limpet (Cellana denticulata) is consistently taken by the Black and Variable Oystercatchers at Kaikoura Peninsula. When limpets are first exposed by the tide, their shells are not drawn tightly down over the foot, and a small gap exists between the substrate and the shell. The birds inspect each limpet in turn and only attack the animals that display this gap. When a suitable limpet is located, the bird lowers its head, points its bill toward the ground at a low angle, and delivers a sharp chipping stroke on the edge of the shell. Smaller limpets

Plate 3.20

Shells of the blue mussel which have been hammered in both dorsal and ventral margins.

are usually toppled over by the first blow. With larger shells this preliminary stroke which has weakened the limpet's grip and, perhaps, chipped the shell (see Plate 3.21), is followed by firm and laborious pushing, assisted by lateral bill swaying, or a to-and-fro rotation of the bill. If this does not complete detachment, the bill is forced under the shell, which is levered up until the shell topples over. The limpet is then seized and carried to a niche or crevice in the rock, where it is neatly detached from the shell by scissor-like movements of the bill at the mantle margins. Detachment is often completed by the bird shaking its bill and flicking the shell off the body of the limpet. Identical behaviour was noted for the European Oystercatcher by Dewar (1913), and for the North American Black Oystercatcher by Webster (1941). Audubon (1840) noted that American Pied Oystercatchers knocked limpets off rocks by chiselling between them and the rocks, but he apparently missed the preliminary sharp blow delivered to the shell.

New Zealand mainland races of oystercatcher all take chitons from rocky shores. In attacking chitons, the first stroke is delivered as on a limpet, but unless the chiton is toppled over at once further movements are quickly made. One area of the leathery shell is detached by lateral pressure delivered with the tip of the bill, thus breaking the vacuum set up by the muscular foot of the mollusc. The bill is then slipped under the chiton, flat side against the rock, and the animal is cut from the rock by scissor-like movements of the bill. Removal of the animal from the shell is a laborious process, which sometimes takes as much as three or four minutes when a tight-fitting niche cannot be found to hold the animal firmly. Extraction of the flesh of the chiton is achieved so that it remains in one piece, and the shell is left almost totally empty (see Plate 3.22). Both the snakeskin chiton (Sypharochiton pelliserpentis) and the green chiton (Amaurochiton glaucus) are dealt with in this way.

Gastropods such as the mudsnail (Amphibola crenata) and the common topshell (Melagraphia aethiops) are taken in a similar manner

Plate 3.21

A shell of the large shore limpet (*Cellana denticulata*) which has been gouged by the force of a chipping stroke delivered by a Variable Oystercatcher.

Plate 3.22

Ventral view of the shell of the green chiton (*Amaurochiton glaucus*) which has been stripped of its flesh content. Note the efficiency with which the shell has been cleaned.

to that described by Dewar (1910) for the purple shell (Purpura lapillus). The bill is inserted into the aperture and pressure applied against the wall of the outside whorl, resulting in a small circular hole chipped through the shell opposite to the operculum (see Plate 3.23). The shell is then rotated until the chipped hole is presented uppermost. In this position the bill is inserted into the hole and leverage is applied towards the apex of the shell using the outside whorl as a fulcrum. Under this pressure the dorsal aspect of the shell is fractured and the exposed soft-parts removed (see Plate 3.23). Of a sample of 150 shells of the mudsnail from the Heathcote-Avon estuary, 128 showed no signs of damage, 14 had holes in the outside whorl, and only 8 were broken open. The effort involved in taking these gastropods apparently makes them a relatively unutilised prey. During the course of this study only South Island Pied Oystercatchers were seen to take mudsnails, and this species alone possessed opercula in the gut samples.

Crabs are demolished very efficiently by all three mainland races of oystercatcher. Captured prey are placed on their backs, a blow is aimed at the region of the supraoesophageal ganglia, and then the flesh is rapidly removed from the carapace. Identical prey-specific behaviour was noted for the European Oystercatcher when feeding on the shore crab (Carcinus maenas) (Tinbergen & Norton-Griffiths, 1964).

In summary, oystercatchers possess a wide range of prey-specific feeding behaviour patterns to cope with the various sizes and species of prey found under the widely fluctuating environmental conditions of the sea shore. Each behaviour pattern is neatly adapted to the structure and habits of the prey. All New Zealand mainland races of oystercatcher possess the same range of prey-specific feeding behaviour patterns, but their development within any one race is subject to variation. South Island Pied Oystercatchers show strongly developed behaviour patterns for preying on estuarine cockles and pipis, whereas Black and Variable Oystercatchers are behaviourally orientated to take mussels and limpets

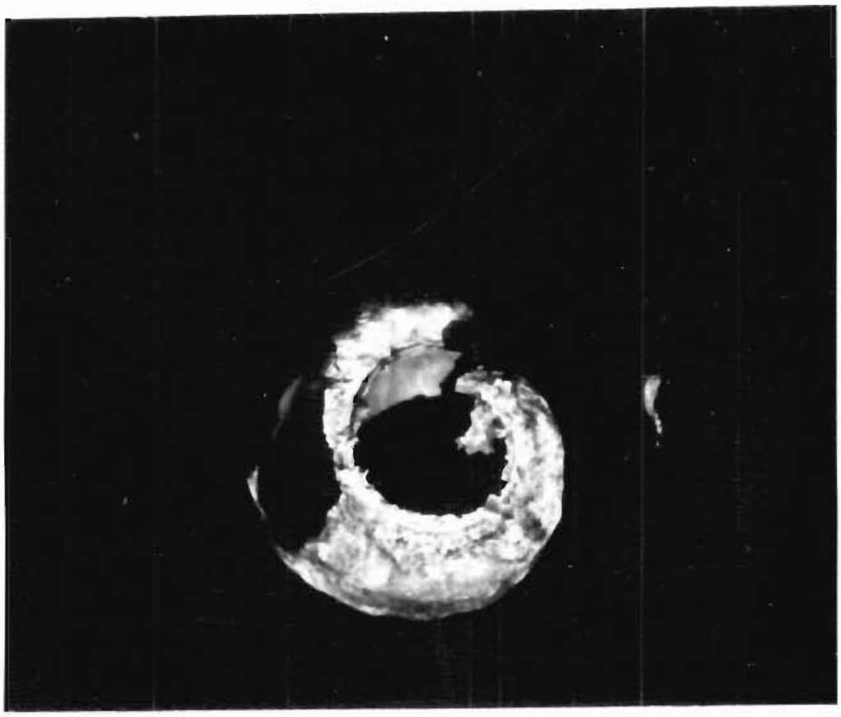


Plate 3.23

Stages in the opening of the shell of the mudsnail (*Amphibola crenata*)

Upper - initial stage with a small hole in the outermost whorl.

Lower - final stage with the top of the spire removed.

from rocky shores. The relative expression of these prey-specific patterns in each race no doubt contributes towards their partial habitat segregation, and mitigates the effects of competition where they co-exist.

C. FACTORS AFFECTING FEEDING BEHAVIOUR

1. Climatic Factors

Although a wide range of weather conditions was encountered during the course of this study, oystercatchers were found to feed at all low water periods except during gale-force winds, in which case they took shelter in unexposed areas. The greatest modifying factor was found to be wind. On windy days piercing of bivalves was rarely observed, and the prey was located mainly by random probing. The switch from visual to touch location is probably due to the wind producing ripples on the surface of the water, making it impossible for the birds to sight their prey. The same behaviour was noted during periods of heavy rain, presumably for the same reason. South Island Pied Oystercatchers feeding on early morning tides in winter are sometimes prevented from taking prey when the exposed beach is frozen by a heavy frost.

2. Physical Factors

The water content of the substrate is directly responsible in determining whether bivalves are opened in situ or carried ashore for opening on a firmer area. As Drinnan (1957) commented, "the water content of the sand, and therefore its resistance to pressure, appears to be important in opening shells." Chapman (1949) has shown that an increase in sand height by a few centimetres with the resultant loss of water by drainage increases the resistance to penetration, as measured by the burrowing rate of *Arenicola* and by a penetrometer.

The carrying of shells at the Heathcote-Avon estuary is most evident at the Monck's Bay pipi bed where the substrate is composed almost entirely of sand. Although some pipis are opened at the site of their capture, the majority are pierced and carried up onto the beach. There are two ways in which the birds locate an area of sand resistant enough to allow the shells to be opened on it:

(a) by random wandering, opening being attempted at intervals of a few metres until a suitable area is located. Occasionally shells are opened close to the waterline, but persistent application of pressure on the shells in soft sand may lead to burying of the mollusc (see Plate 3.24); and,

(b) by flying up to supralittoral regions of the beach where the sand is firm enough to support opening attempts (see Plate 3.25). The carrying of cockles at the Heathcote-Avon estuary is on a much reduced scale to that of pipis. At the feeding grounds near the upper end of the estuary, cockles are carried only short distances from the water, probably because the drainage of the mud is so poor that there are no significant differences in surface resistance over the shore.

The carrying of bivalves ashore for opening purposes appears to be associated with sandy habitats, and the three mainland races of oystercatcher all perform this type of behaviour when feeding at such areas. A specialised type of carrying behaviour was noted for the European Oystercatcher by Davidson (1967), who found that the birds carried cockles to distinct areas of the sand to form 'feeding piles'. He suggested that the formation of these piles was to provide a firmer surface on which to open shells. Bivalves were scattered over the surface of the present study area and aggregations of predated shells were not present (see Plate 3.26).

3. Competition

Both interspecific and intraspecific competition influence feeding behaviour. Interspecific competition for food is provided by three species: the Red-billed Gull (Larus novaehollandiae), the Black-backed Gull (L. dominicanus) and the Eastern Bar-tailed Godwit (Limosa lapponica). The two species of gull are "parasitic" on the oystercatchers, stealing food which the latter have located. Oystercatchers feeding in shallow water are constantly followed by both types of gull, and when the bird locates and pierces a bivalve,

Plate 3.24

A pipi which has been opened near the waterline. The water content of the sand in this region of the shore is too high, and the sand is therefore not firm enough to support the shell against the opening attempt.

Plate 3.25

South Island Pied Oystercatchers opening cockles on the supralittoral region of the beach where the sand is firm enough to prevent the shell from being buried by opening pressures exerted by the bird.

Plate 3.26

General view of the Mt. Pleasant Yacht Club study site at the Heathcote-Avon estuary. Note the scattered nature of the bivalves on the surface; aggregations of predated shells were not present.

it is frequently harassed by two or three gulls until the bivalve is dropped or eaten. When the tide begins to expose the feeding grounds, harassment is often acute because feeding flocks are confined to small emergent areas. Oystercatchers feeding in the Monck's Bay pipi beds of the Heathcote-Avon estuary near high water frequently are "robbed" of their prey. However, as the gull population is small (c. 200 birds) in comparison to that of oystercatchers (c. 4000 birds), competition from this source is not serious, especially at low water periods when large feeding grounds are exposed.

When harassment from gulls is temporarily severe, oystercatchers modify their feeding behaviour to reduce competitive interactions. Pierced bivalves which would normally have been carried ashore for opening are opened where they are located. In this manner, the prey can be opened and devoured before gulls are able to effectively harass the feeding bird. Localised opening of prey can, however, result in a higher incidence of failures at shell opening as the substrate is often too soft to support the pressure of the opening attempts.

Competitive interactions are greatest between juvenile Red-billed Gulls and South Island Pied Oystercatchers. Tinbergen & Norton-Griffiths (1964) noted the same effect for European Oystercatchers and the juvenile Black-headed Gulls (Larus ridibundus); they attributed this behaviour to the fact that the young gulls had not yet learnt to fear the oystercatchers' bills. Black and Variable Oystercatchers are rarely menaced by "parasitic" gulls, their larger body size apparently inhibiting attacks.

Godwits provide direct, but passive competition, as they prey on the same food species as oystercatchers. During this study interspecific interactions with godwits were never noted even when they were feeding amongst oystercatcher flocks. At Farewell Spit and the Heathcote-Avon estuary the effects of competition from godwits are minimised as species segregation occurs within the feeding habitat.

Intraspecific competition is relatively rare, probably because food is abundant at the major wintering haunts. Densities of birds during periods of maximum feeding intensity are as high as one bird/m^2 before competitive interactions become apparent (see Plate 3.27). Interactions almost always take the form of threat postures which frequently culminate in a piping display. Although Makkink (1942) has shown that the piping display has both sexual and aggressive elements, during competitive interactions the display appears to be wholly aggressive and may be followed by fighting. The display, which is similar in all New Zealand races, is characterised by a specific posture. The head is held stiffly forward inclined at an angle to the horizontal, the hackles raised, the half-open vibrant mandibles pointed vertically toward the ground, the wings raised upwards and away from the body, and the tail depressed (see Plate 3.28). Piping is always accompanied by a ringing call which begins as sharp "pic" notes and quickly gathers into a prolonged chorus "kervee - kervee - kervee - kervee - kervee" etc., finally ending in a high pitched trilling note. Usually the display results in the intruding bird being driven off, but where two birds continue to pipe aggressively to one another a fight may ensue. This aggressive piping is different from "social piping" (see Ch. 4.7) as its function is to maintain dispersion within the feeding habitat rather than to effect pair formation. Piping displays and fighting are most apparent at the beginning of each new feeding period as the birds are hungriest at this time and are confined in high densities to small exposed areas of the feeding grounds.

3.6 FOOD INTAKE

The accurate assessment of the daily food intake of oystercatchers depends upon evaluation of means of the following factors:

A. the numbers of birds feeding over each tidal cycle;

B. the length of the daily feeding period; and

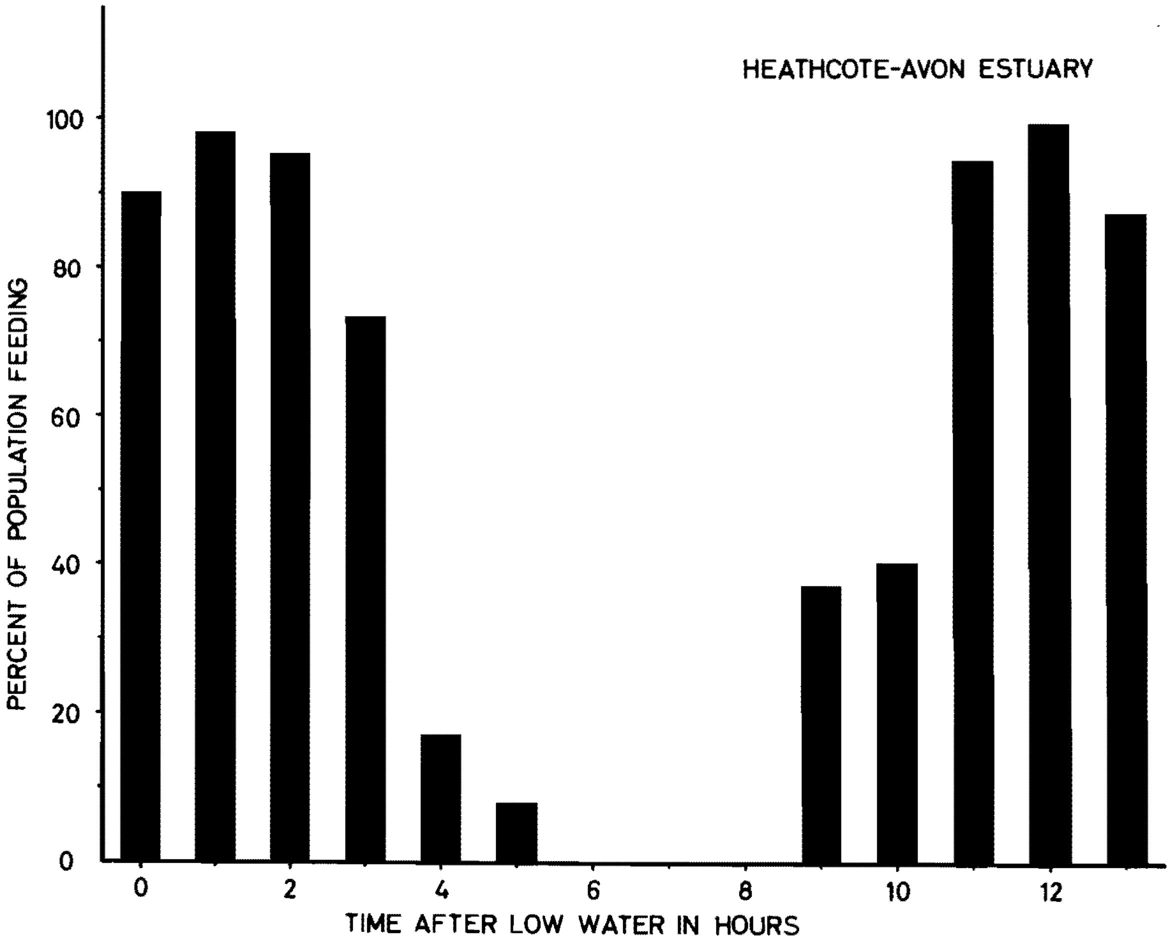
C. the rate at which food is taken i.e. the feeding rate.

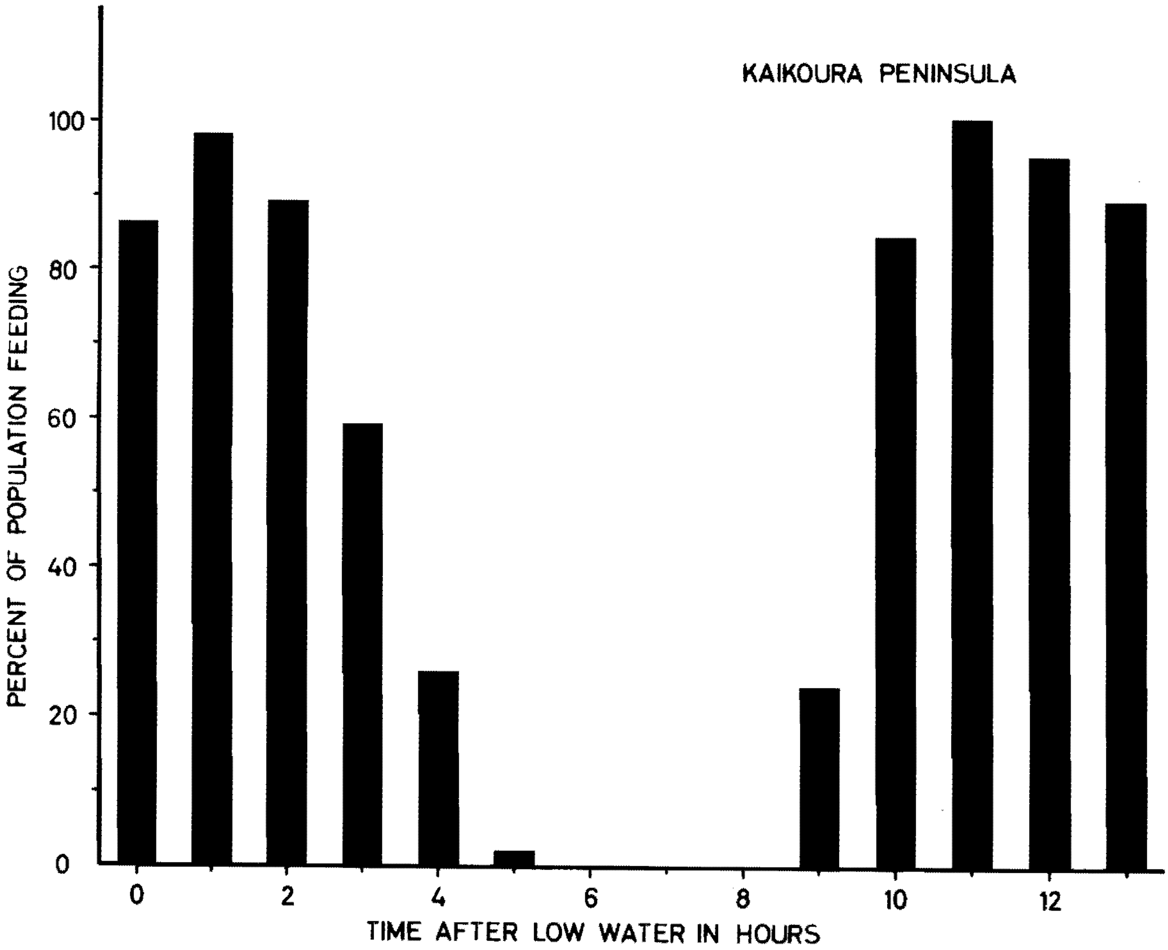
Plate 3.27

South Island Pied Oystercatchers feeding in a dense flock at the Monck's Bay study site, Heathcote-Avon estuary. Even at these densities intraspecific competition is not apparent.

Plate 3.28

Aggressive piping display of the South Island Pied Oystercatcher. Note that the tail is depressed, the wings raised upwards and away from the body at the carpal flexure, the neck extended forward and the mandibles pointed downward. Further evidence of the aggressive nature of this posture is provided by the bird on the left which has its neck hackles raised preparatory to an aggressive response.


HEATHCOTE-AVON ESTUARY
PERCENT OF POPULATION FEEDING
100
80
60
40
20
0
0
2
4
6
8
10
12
TIME AFTER LOW WATER IN HOURS


KAIKOURA PENINSULA
PERCENT OF POPULATION FEEDING
100
80
60
40
20
0
0
2
4
6
8
10
12
TIME AFTER LOW WATER IN HOURS

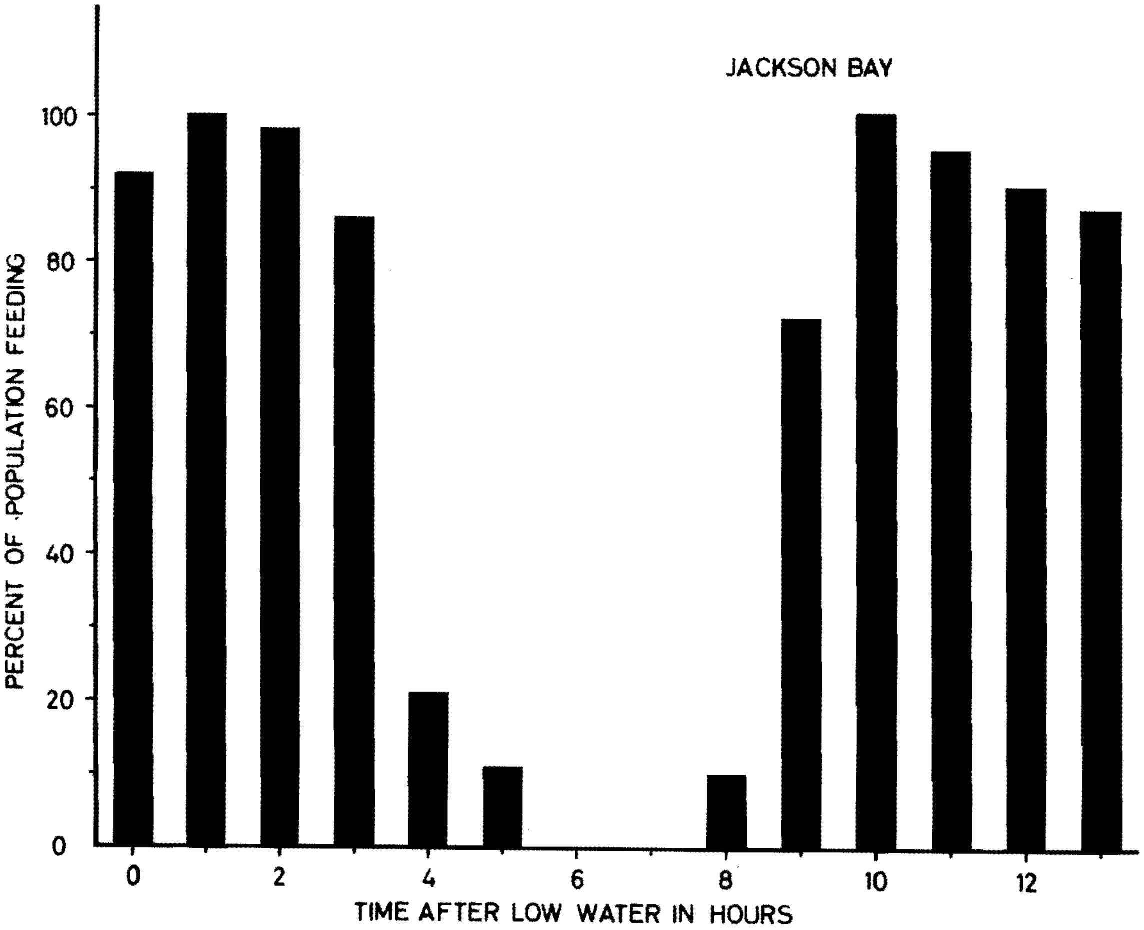

JACKSON BAY
PERCENT OF POPULATION FEEDING
0
20
40
60
80
100
0
2
4
6
8
10
12
TIME AFTER LOW WATER IN HOURS

Figure 3.10

The number of birds feeding during a tidal cycle at the Heathcote-Avon estuary, Kaikoura Peninsula and Jackson Bay.

A. Numbers of Birds Feeding Per Tidal Cycle

The numbers of birds feeding at any one time depends ultimately upon the state of the tide. At high water there are no birds feeding while at low water the entire population is on the feeding grounds. Although feeding is continuous on a flock basis, individual birds show an alternation of feeding and rest periods at approximately two-hourly intervals. The duration of the rest period is usually in the order of 10 minutes, but may vary considerably from this. The function of these rest periods is presumably either to allow digestion to catch up with food intake or to prevent or recover from feeding fatigue.

The relationship between tidal levels and the number of birds feeding is shown in Fig 3.10 for New Zealand mainland races of oystercatcher. Irrespective of race or locality the feeding of oystercatchers in marine littoral habitats is controlled by the state of the tide. Following high water periods there is a noticeable time lag between the ebbing of the tide and the movement of the birds to the feeding grounds. Movement from the high water roost begins only when the tide has ebbed sufficiently to expose molluscan prey beds for feeding (see Ch. 3.5A). A feature of the graphs in Fig 3.10 is the abrupt increases in the numbers of birds feeding as the tide ebbs, mainly because of the occurrence of mass flights, whereas the cessation of feeding is a more drawn-out process due to the formation of sandflocks at the feeding grounds.

If the alternation between feeding and rest periods is disregarded, then the number of birds feeding per tidal cycle is equivalent to the total population at the study area. Population counts taken during 1967 at the Heathcote-Avon estuary, Kaikoura Peninsula and Jackson Bay are summarised in Table 3.5. (The mean number of birds feeding at each study area during the year was determined by summing the counts and dividing by the number of counts.)

The figures for the mean numbers of birds feeding in the areas are actually lower than the population peaks recorded in mid-winter because they include summering populations of non-breeding birds which remain at the wintering haunts throughout the year. From these figures yearly predation and food intake estimates can be made.

TABLE 3.5 MEAN NUMBERS OF OYSTERCATCHERS FEEDING IN STUDY AREAS DURING 1967

Race	Locality	Mean No. of birds feeding in area	No. of observations
South Island Pied Oystercatcher	Heathcote-Avon estuary	2,838	12
	Kaikoura	15	7
	Jackson Bay	13	5
Black Oystercatcher	Heathcote-Avon estuary	2	12
	Kaikoura	2	7
	Jackson Bay	53	5
Variable Oystercatcher	Heathcote-Avon estuary	0	12
	Kaikoura	2	7
	Jackson Bay	3	5

B. Length of Daily Feeding Period

The duration of the tidal cycle is in the vicinity of 13 hrs. As oystercatchers do not feed approximately 2 hr either side of high water, they therefore have a maximum feeding period of 9 hr per tidal cycle. Each individual bird feeds for a different length of time, so that the population as a whole can only be represented by a mean value for the length of the daily feeding period. For this study, the mean period was defined as the time during which half or more of the birds were actively feeding. By fitting a horizontal line through the 50% population value, the mean length of the feeding period can be read off from the graph of the number of birds per tidal cycle (see Fig 3.11). On an average, then, oystercatchers feed for 6 hr per tidal cycle at the Heathcote-Avon estuary, 6½ hr at Kaikoura Peninsula, and for 7 hr at Jackson Bay. The corresponding daily rates (assuming two tidal cycles/day) are 12 hr, 13 hr and 14 hr respectively.

C. Feeding Rate

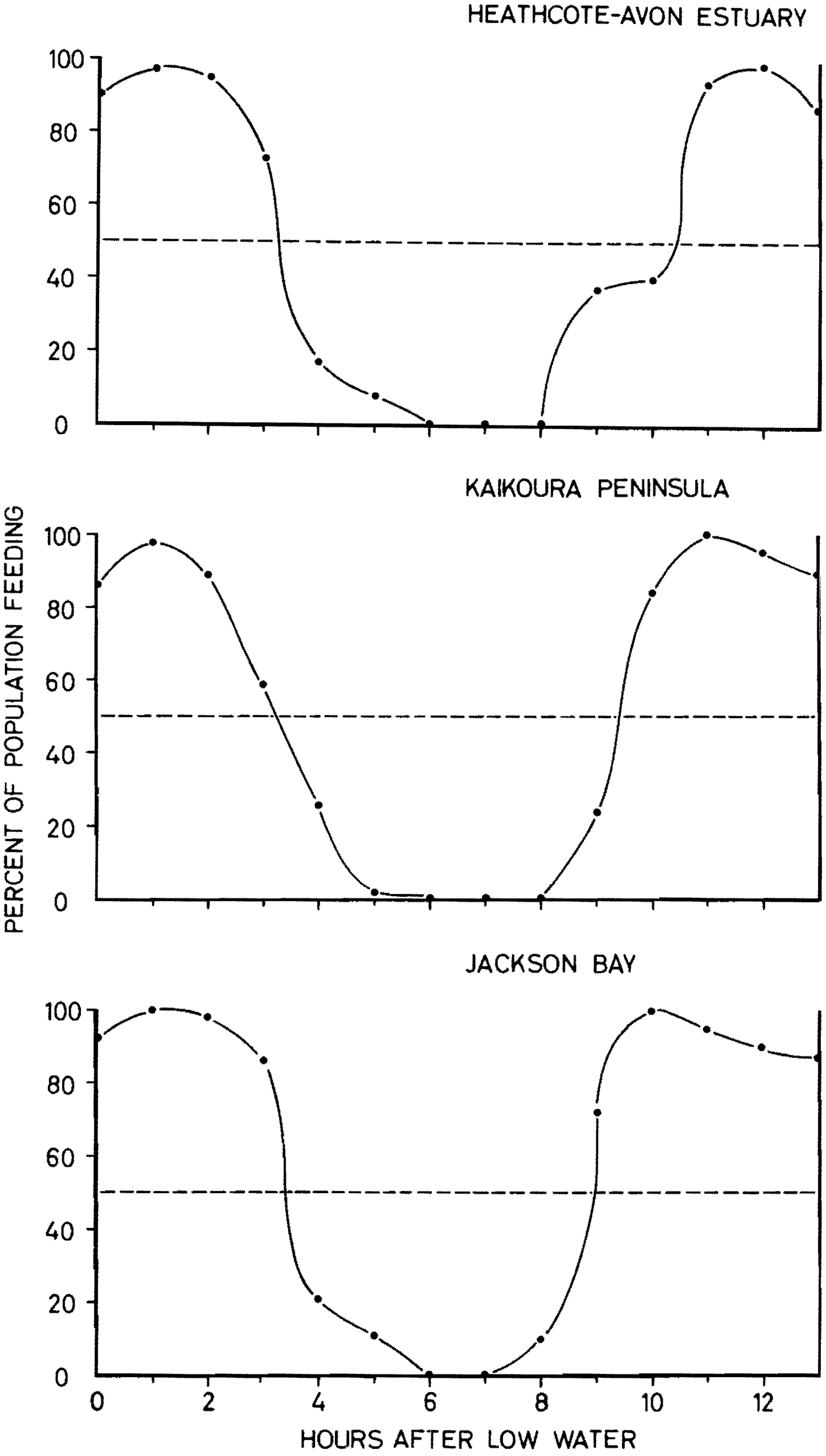
The rate at which oystercatchers feed is dependent upon seven main factors:

I. the state of the tide;
II. the environmental conditions;
III. the season (and thus ambient temperature);
IV. food availability;
V. the size of the prey species;
VI. the age of the feeding birds; and,
VII. the rate at which food is searched for.

Each of the above factors interact with one another so that the observed feeding rate at any one time is a product of their interaction. A general discussion of the rate at which oystercatchers feed would require an integration of the assessments of the relative importance of each factor. This in turn would require the use of controlled conditions, which were not possible to achieve in the study. Accordingly, the effect of each factor on the rate of feeding is discussed separately below and no attempt is made to assess its relative importance.

I. The Effect of Tidal Levels on Feeding Rates

The rate at which oystercatchers feed varies with the level of the tide. Feeding rates are highest when the tide is retreating or advancing over the feeding grounds, and lowest when the beds of molluscs are completely exposed. These rates are a reflection of the availability of food (see section 3.6 C.IV). High feeding



HEATHCOTE-AVON ESTUARY
KAIKOURA PENINSULA
JACKSON BAY
PERCENT OF POPULATION FEEDING
100
80
60
40
20
0
0
2
4
6
8
10
12
HOURS AFTER LOW WATER

Figure 3.11

Graphs for calculating the mean length of feeding periods at the Heathcote-Avon estuary, Kaikoura Peninsula and Jackson Bay. The dotted line represents the 50% population limit, so that the lengths of the mean feeding periods can be read off directly below the points at which the dotted lines cut the curves.

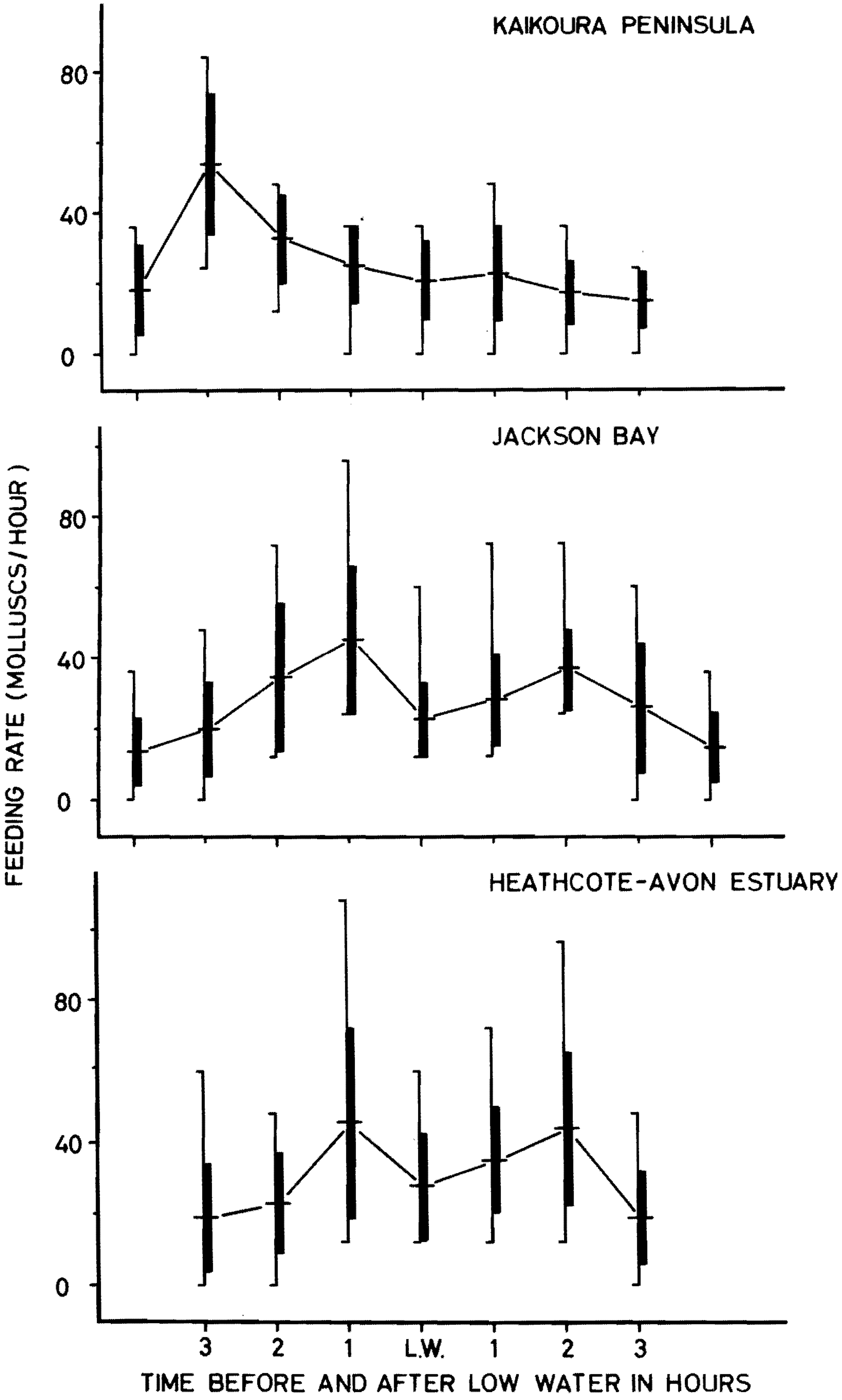

KAIKOURA PENINSULA
JACKSON BAY
HEATHCOTE-AVON ESTUARY
FEEDING RATE (MOLLUSCS/HOUR)
80
40
0
3
2
1
L.W.
1
2
3
TIME BEFORE AND AFTER LOW WATER IN HOURS

Figure 3.12

Feeding rates during a tidal cycle at the Heathcote-Avon estuary, Kaikoura Peninsula, and Jackson Bay. The vertical line extensions indicate the range, the blacked-out portions one standard deviation either side of the mean, and the horizontal line the mean. Data were collected for all three races at Jackson Bay, for Black and Variable Oystercatchers at Kaikoura, and only for South Island Pied Oystercatchers at the Heathcote-Avon estuary.

rates are attributable to sight location of gaping bivalves in areas of dense prey concentration whereas low feeding rates are due to random probing/search behaviour. The effect of tidal levels on the rate of feeding is shown in Fig 3.12. At the Heathcote-Avon estuary and Jackson Bay, where the birds are feeding at or near the waterline, two peaks of feeding occur. One main peak of feeding occurs approximately 1 hr before low water and a second smaller peak occurs approximately 2 hr after low water. The first peak is associated with optimal feeding conditions i.e. the major beds of molluscs are covered by 2 - 10 cm of water allowing good sight location of prey, and the second peak is a direct result of an enhanced probe rate (see section 3.6 C.VII).

At Kaikoura Peninsula there is a large peak of feeding immediately following the exposure of limpets (Cellana denticulata and C. ornata) as it is at this time that these molluscs are most vulnerable to predation. A second peak of feeding does not occur here because the limpets become harder and harder to knock off the rocks with increasing time of emergence, due to their habit of drawing the shell firmly down onto the substrate to prevent desiccation. At Jackson Bay all three races of oystercatcher were present and feeding on the same food; examination of their comparative feeding rates (Fig 3.13) does not indicate any interracial differences in feeding rate during a tidal cycle.

II. The Effect of Environmental Conditions on Feeding Rates

The major environmental conditions affecting the rate of feeding are climatic. Adverse weather conditions, such as strong wind and/or rain, cause changes in the methods of prey location (see section 3.5 C.1). The increased difficulty in sight location of gaping bivalves causes feeding birds to change to random probing of the substrate. As a result of this random prey location, feeding rates drop considerably when compared with rates during good weather conditions (see Fig 3.14). Oystercatchers feeding on hard substrates are not subject to a comparable drop in feeding rate as the location of prey is a much simpler task. Feeding completely ceases

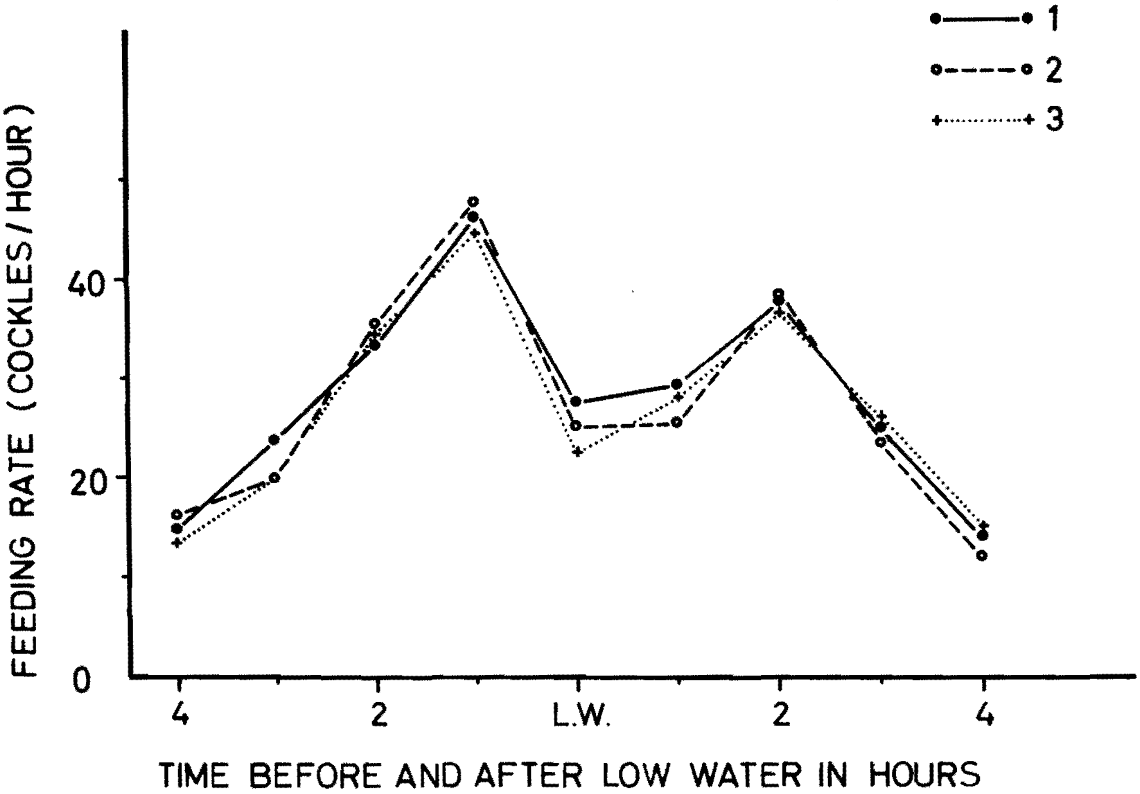

1
2
3
FEEDING RATE (COCKLES / HOUR)
40
20
0
4
2
L.W.
2
4
TIME BEFORE AND AFTER LOW WATER IN HOURS

Figure 3.13

Comparative feeding rates of the New Zealand races of oystercatcher feeding on tua-tuas at Jackson Bay.

Key to numbers:

1. Variable Oystercatcher
2. South Island Pied Oystercatcher
3. Black Oystercatcher.

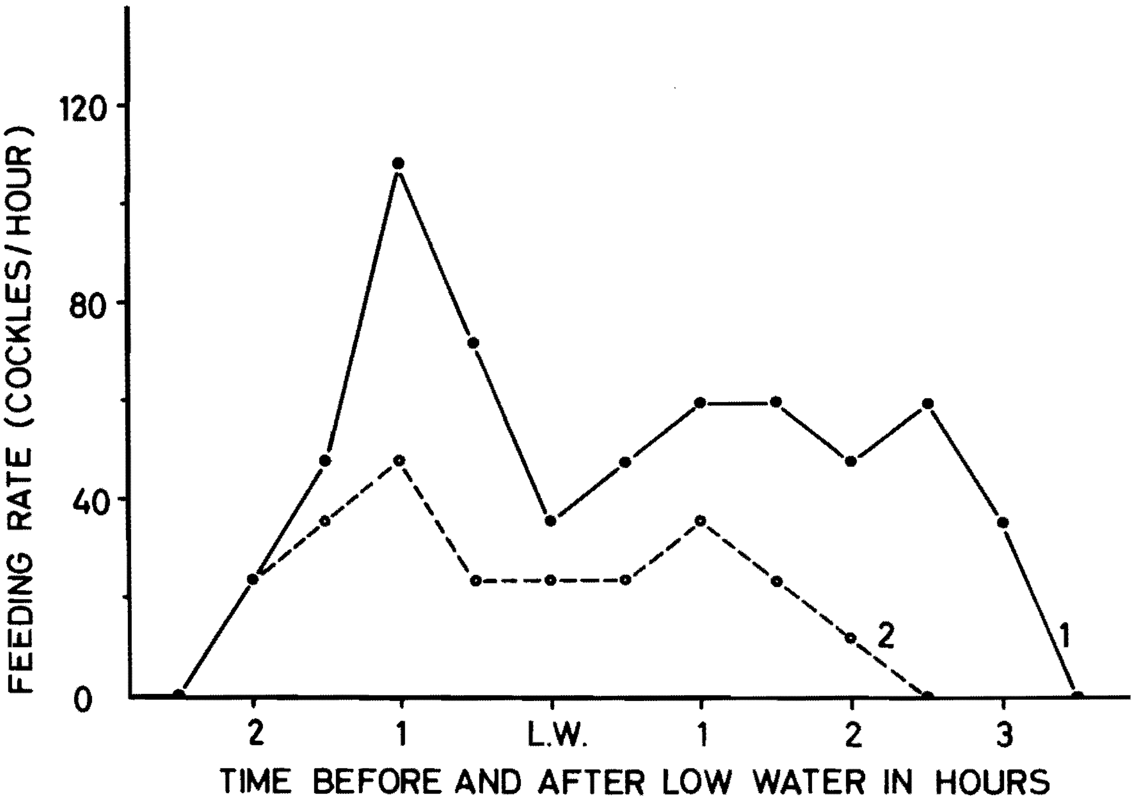

FEEDING RATE (COCKLES/HOUR)
120
80
40
0
2
1
L.W.
1
2
3
TIME BEFORE AND AFTER LOW WATER IN HOURS
2
1

Figure 3.14

Comparative feeding rates of South Island Pied Oystercatchers during a tidal cycle at the Heathcote-Avon estuary.

Key to numbers:

1. Favourable weather conditions for feeding
2. Adverse weather conditions for feeding.

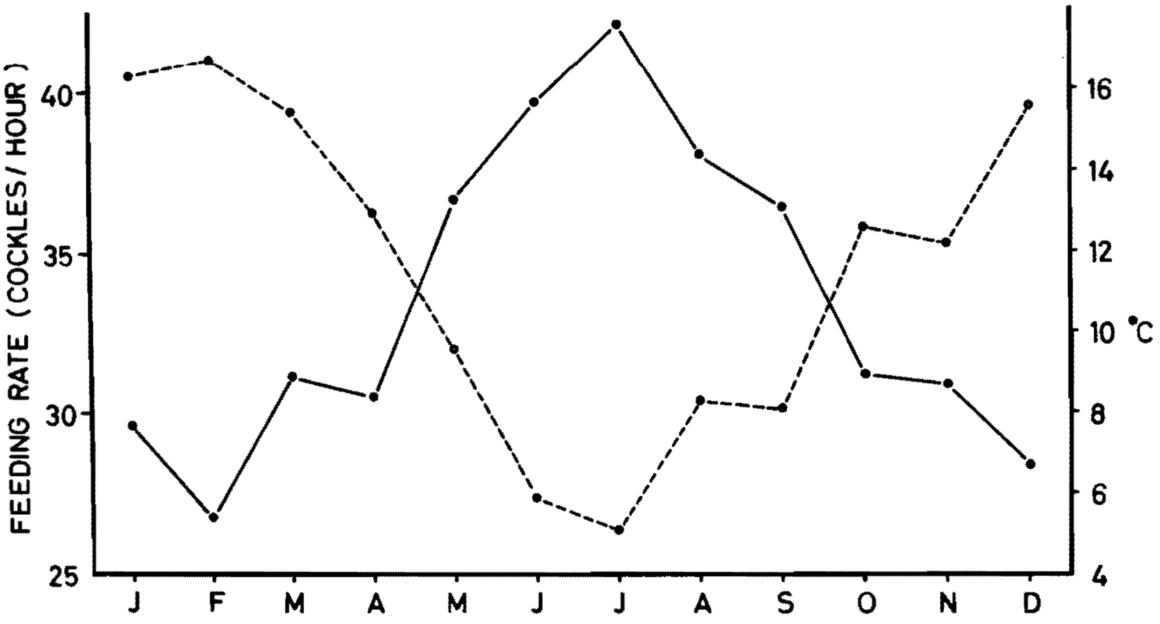

FEEDING RATE (COCKLES / HOUR)
40
35
30
25
16
14
12
10 °C
8
6
4
J
F
M
A
M
J
J
A
S
O
N
D

Figure 3.15

Inverse relationship between feeding rates of South Island Pied Oystercatchers and the mean monthly air temperatures at the Heathcote-Avon estuary. The solid line indicates feeding rates and the dotted line temperature.

in these areas when torrential rain and/or gale-force winds coupled with severe wave-action occur.

III. The Effect of Season on Feeding Rates

The rate at which oystercatchers feed varies with the season and thus the ambient temperature. Seasonal variation in feeding rate is shown in Fig 3.15 for South Island Pied Oystercatchers feeding at the Heathcote-Avon estuary. During 1967 mean monthly feeding rates were highest in the mid-summer months of January, February and December, and lowest in the mid-winter months of June and July. The seasonal trend in feeding rates is therefore a direct reflection of the mean temperatures existing through the seasons. The inverse relationship between ambient temperature and the rate of feeding is a function of the gradient between ambient temperature and body temperature. Kendeigh (1949) has shown that energy requirements and food intake of the House Sparrow (*Passer domesticus*) increase steeply as the ambient temperatures decrease. In winter, then, oystercatchers combat the relatively large temperature gradient by feeding at a faster rate and converting some of the extra food into heat energy. During mid-summer the temperature gradient is much smaller, and the birds feed at a slower rate as very little food is diverted into heat production. Comparative studies were not made for Black and Variable Oystercatchers, but it seems reasonable to assume that all these races vary their rate of feeding inversely with ambient temperature as they encounter similar temperature regimes. Similar seasonal variations in feeding rate were noted for the European Oystercatcher by Drinnan (1957, 1958a), Hulscher (1964), and Davidson (1967).

IV. The Effect of Food Availability on Feeding Rates

One of the most important factors affecting the rate at which oystercatchers feed is food availability. When birds are feeding on substrates containing beds of bivalve molluscs, food is most "available" when the area is covered by 2 - 10 cm of water during good weather conditions. Thus tidal levels and food availability are very closely linked, but food availability in terms of actual numbers of prey present has a more direct effect on feeding rate than does the tidal level. The correlation between food availability and the rate of feeding of South Island Pied Oystercatchers at the Heathcote-Avon estuary is shown in Fig 3.16. Feeding rates are high where dense prey concentrations occur, and low where prey occurs sparsely. Feeding peaks are enhanced where the tide is receding or advancing over an area of dense prey concentration. Since it has been shown in Fig 3.13 that South Island Pied, Black and Variable Oystercatchers feed at approximately the same rate, it follows that the feeding rate of each race will be equally affected by food availability.

V. The Effect of Prey Size on Feeding Rates

Prey size has a direct effect on the rate at which oystercatchers feed. This relationship is expressed in Table 3.6 for study sites within the Heathcote-Avon estuary. All data were recorded one hour before low water so that results would be strictly comparable.

TABLE 3.6 RELATIONSHIP BETWEEN FEEDING RATES OF SOUTH ISLAND PIED OYSTERCATCHERS AND SIZE OF PREDATED COCKLES

Study Site	Feeding Rate (Cockles/hr)	Modal size (cm) of cockles eaten	Flesh volume (ml) of modal size
Off Redcliffs	108	3.1	1.9
Mid-estuary	84	4.0	2.7
Monck's Bay	48	4.6	4.8
Off Scott Park	24	5.3	6.0
	N = 40	N = 30	N = 10

Note: N, the sample size, applies to figures for each study site

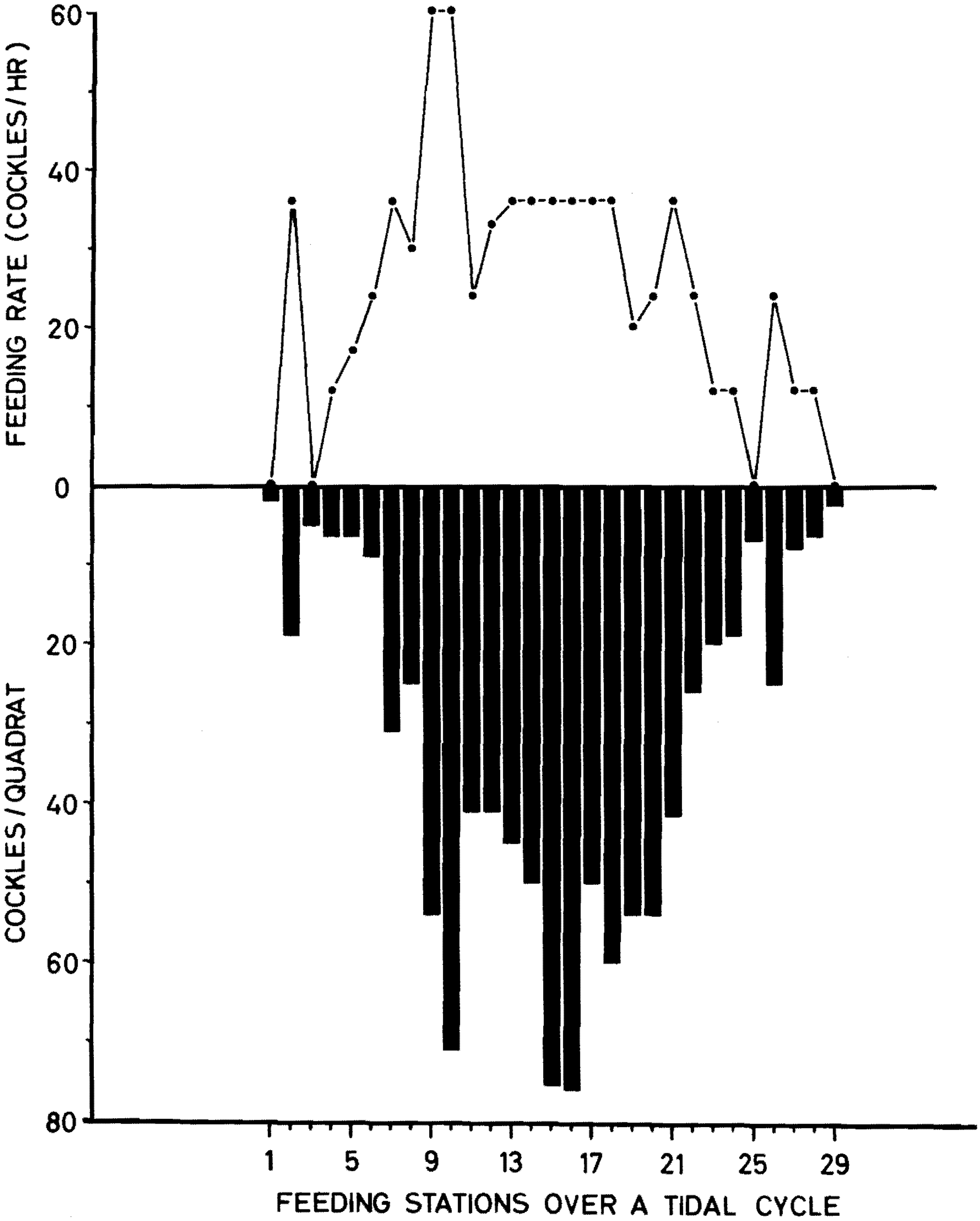

FEEDING RATE (COCKLES/HR)
60
40
20
0
20
40
60
80
COCKLES/QUADRAT
1
5
9
13
17
21
25
29
FEEDING STATIONS OVER A TIDAL CYCLE

Figure 3.16

Correlation between feeding rates of South Island Pied Oystercatchers and food availability at the Heathcote-Avon estuary. The feeding stations are taken over a tidal cycle so that food is more "available" approximately 1 hr before and 2 hr after low water, hence the peaks at these times.

At any one time, South Island Pied Oystercatchers at various sites in the estuary feed at a rate which is proportional to the size of the cockles they are taking. Since the size of a cockle is related to its flesh volume, then the feeding rate of oystercatchers is dependent upon the volume of cockle flesh ingested per unit time. A similar relationship was found for the European Oystercatcher (Davidson, 1967). This relationship would not be valid if oystercatchers showed a distinct size selection of their prey as suggested by Dewar (1908) as all birds should feed on approximately the same size prey at approximately the same rate. A comparison of the size of predated and live bivalves is shown in Fig 3.17 for three different study areas. All three mainland races of oystercatcher show no size selection whatsoever, but rather take any size prey that is available to them. This finding agrees with that of Davidson (1967) working with the European Oystercatcher.

VI. The Effect of Age on Feeding Rates

Oystercatchers belonging to the age classes of either first year or older birds (see Ch. 4.5) feed at different rates. Tinbergen & Norton-Griffiths (1964) noted that young oystercatcher chicks were only capable of simple feeding movements which were far removed from the complex feeding behaviour patterns of their parents. It would be expected from this that juvenile first-year birds would lack feeding experience and thus feed at a slower rate than older birds. Norton-Griffiths (1967) suggested that young European Oystercatchers were taught to feed by their parents in either the hammering or piercing technique, but not both, and he also suggested that the technique taught to the young was the one exclusively used by the parent. His observations were confined to coastal breeding birds where the young followed their parents for several months. In New Zealand, however, South Island Pied Oystercatchers breed far away from the wintering areas. Juveniles tend to migrate to northern harbours and estuaries whilst adults remain tenacious to southern winter haunts. It seems unlikely, therefore, that the parents teach their young prey-specific feeding behaviour.

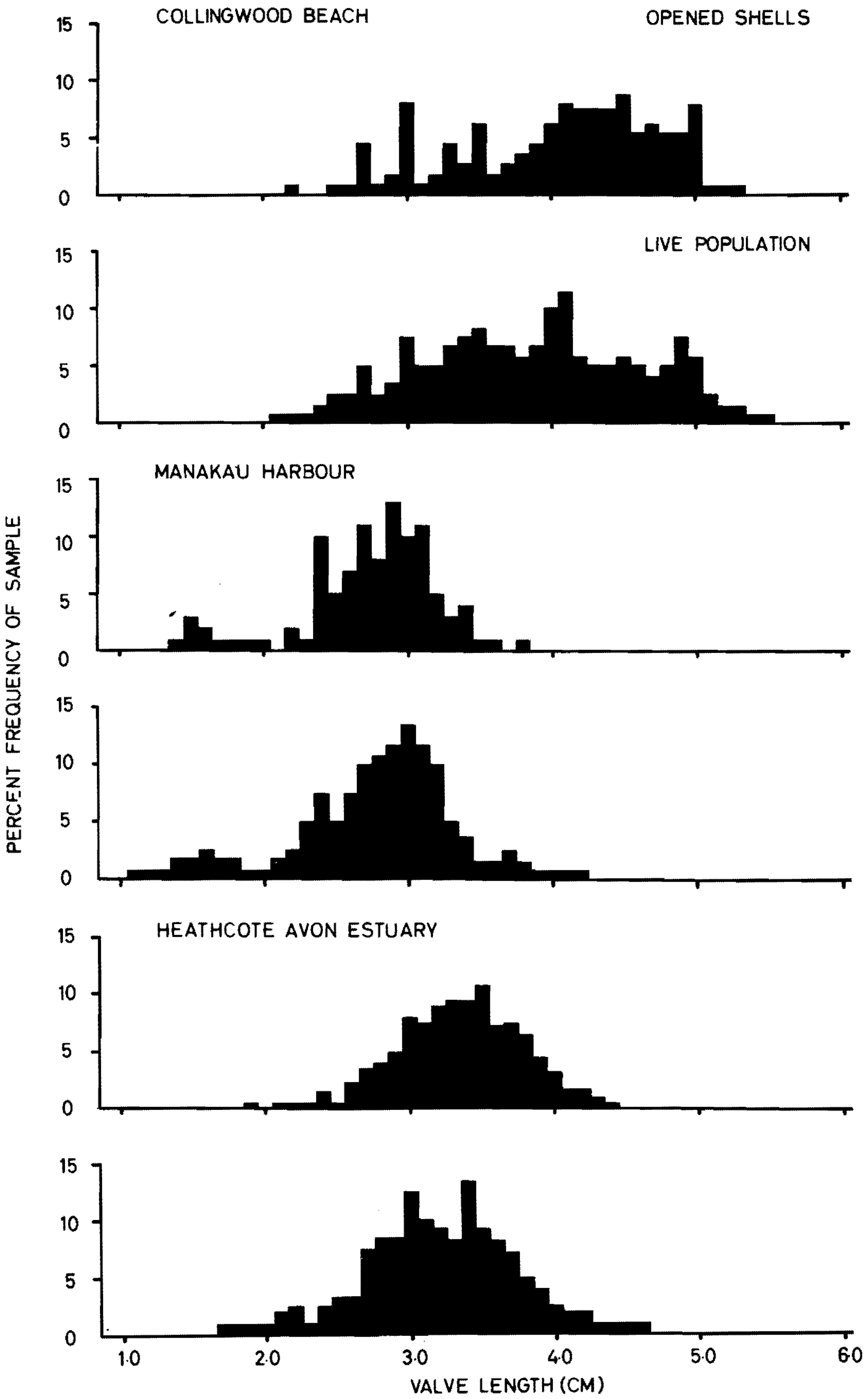

COLLINGWOOD BEACH
OPENED SHELLS
LIVE POPULATION
MANAKAU HARBOUR
HEATHCOTE AVON ESTUARY
PERCENT FREQUENCY OF SAMPLE
0
5
10
15
1·0
2·0
3·0
4·0
5·0
6·0
VALVE LENGTH (CM)

Figure 3.17

Comparison of the size distributions of predated and live populations of bivalve preys at the Heathcote-Avon estuary, Kaikoura Peninsula and Jackson Bay. Note the absence of size selection of prey by oystercatchers.

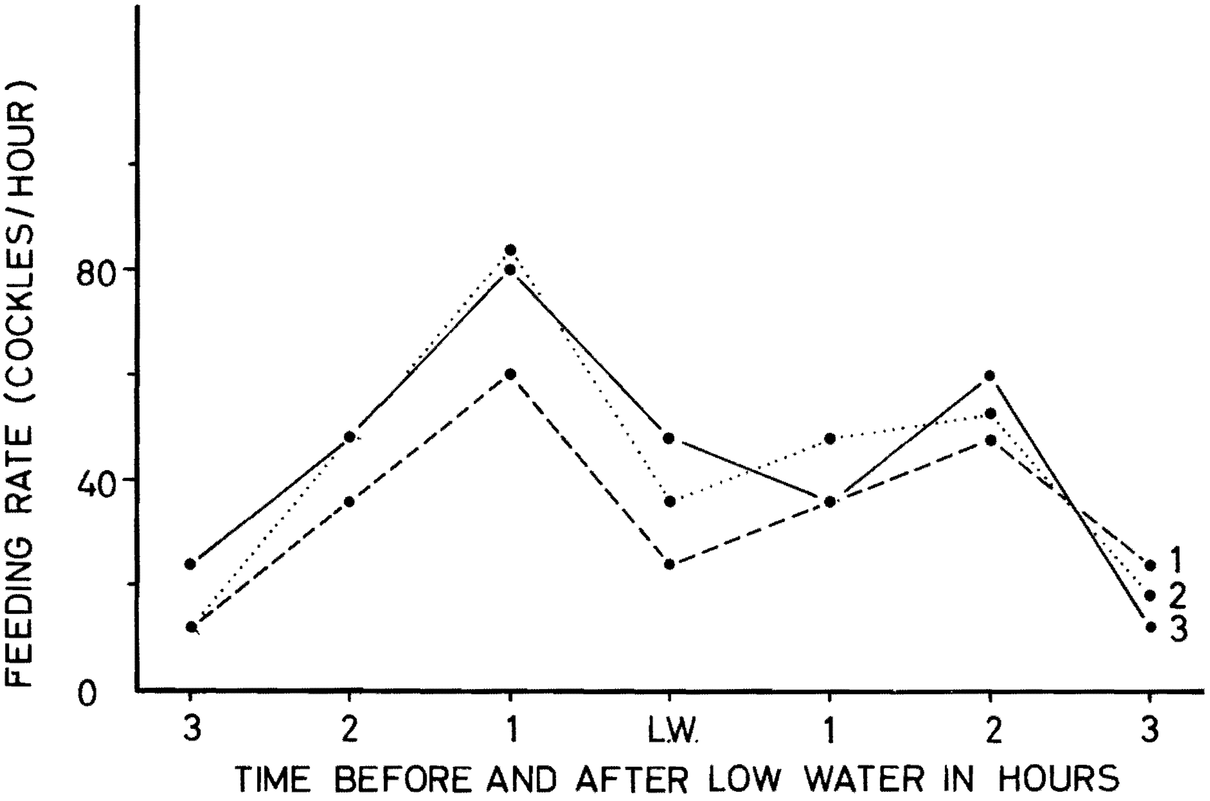

FEEDING RATE (COCKLES/HOUR)
80
40
0
3
2
1
L.W.
1
2
3
TIME BEFORE AND AFTER LOW WATER IN HOURS
1
2
3

Figure 3.18

Feeding rates of juvenile, sub-adult and adult South Island Pied Oystercatchers over a tidal cycle at the Heathcote-Avon estuary.

Key to numbers:

1. Juveniles
2. Sub-adults
3. Adults.

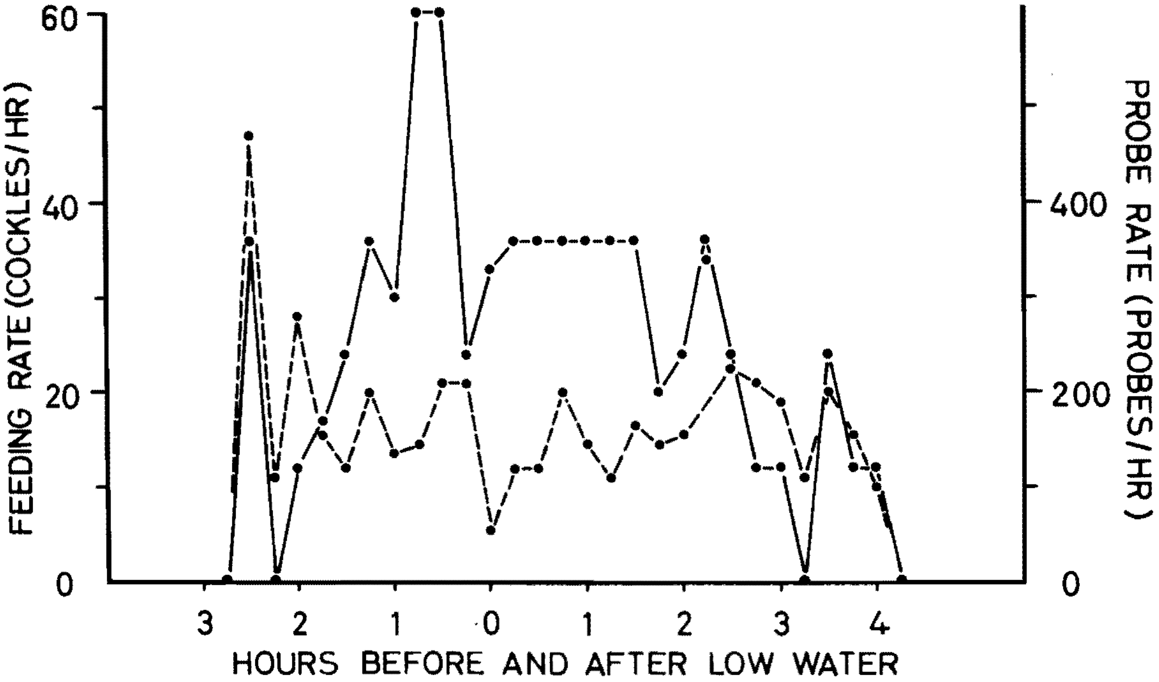

60
40
20
0
FEEDING RATE (COCKLES/HR)
400
200
0
PROBE RATE (PROBES/HR)
3
2
1
0
1
2
3
4
HOURS BEFORE AND AFTER LOW WATER

Figure 3.19

Variation of feeding and probe rates during a tidal cycle at the Heathcote-Avon estuary. The feeding rate is indicated by the solid line and the probe rate by the dotted line.

The feeding rates of juvenile first-year, second year sub-adult, and adult birds are shown in Fig 3.18. The mean feeding rate of juveniles over a particular tidal cycle was significantly lower than that of either sub-adults ($t_{48} = 2.71$, $0.01 > p > 0.001$) or adults ($t_{48} = 2.89$, $0.01 > p > 0.001$). The significance of this difference is sustained when feeding rates are used in making food intake estimations, as all age classes appear to feed for approximately the same time per tidal cycle. The similarity between the mean feeding rate of sub-adults (48.1 cockles/hr) and adults (49.4 cockles/hr) suggests that by their second year oystercatchers have learnt the various feeding behaviour patterns and are therefore as efficient at feeding as adults are.

VII. The Effect of Search Rate on Feeding Rates

Some of the fluctuations in feeding rates are attributable to either increased or decreased rates in food-searching. The search rate is most easily expressed in terms of probes per unit time. Variation of feeding and probes rates over a tidal cycle are shown in Fig 3.19. Probes rates are relatively constant during most of the feeding period, but small peaks of feeding near the commencement and end of the period are correlated with increased probe rates. At the beginning of the feeding period the peak in probe rate probably results from appetitive stimuli. The reduced and more constant probe rate during the central part of the feeding period would seem to indicate that the hunger reflex has been retarded, rest periods resulting from satiation of the appetite. The two peaks near the end of the period probably result from increasing appetitive stimuli, following the mid-period slump in feeding rates.

D. ESTIMATIONS OF FOOD INTAKE

It has been shown in the previous section that the rate at which oystercatchers feed is extremely variable due to the modifying effect of several factors. Several pertinent points arise from this variation. Firstly, since seasonal variation in feeding rates is so pronounced, it is unrealistic to extrapolate yearly food intake from feeding rates calculated only during one part of the year. Secondly, since feeding rates vary with prey size, comparative estimates of food intake can only be made for each race of oystercatcher providing there is no size selection of prey. The last condition can best be satisfied by taking records at a study area where all races are feeding on the same prey. Anomalous effects from differing levels of food availability will also be eliminated in this manner. Thirdly, because feeding rates vary with the state of the tide, it is important to base the mean feeding rate per tidal cycle on data collected from all states of the tide. Mean monthly rates can be extracted from the data, and a mean yearly rate calculated from the monthly means. Fourthly, fluctuations in feeding rates due to adverse weather make it imperative that data are recorded from a range of climatic conditions. Finally, interspecific and interracial comparisons will only be valid provided the same age classes of each species and race are compared.

At the Heathcote-Avon estuary during the winter months of June and July 1967, South Island Pied Oystercatchers ingested an average of 40.9 cockles/hour. Predated cockles had a mean valve length of 3.1 cm and a mean flesh volume of 1.9 ml. The average length of the daily feeding period was 12 hr, but half of this period occurred in darkness where the feeding rate was assumed to be half that during daylight hours (Drinnan, 1958b). Thus the birds ingested, on an average, 699.4 cockles a day. Since the percentage dry weight of cockles is 25 (Cole 1955, cited by Drinnan 1957), then the oystercatchers ingested 174.9 g of cockles daily (assuming the specific gravity of cockle flesh to be unity). Birds captured at the estuary had a mean body weight of 494 g so that the mean daily food intake corresponded to 35.2% of their body weight. The comparative feeding rate for the summer months of December and January was 29.0 cockles/hour, which was equivalent to a daily food intake of 124 g, or 25.1% of the body weight. The mean yearly feeding rate was 33.4 cockles/hour giving a daily food intake of 142.8 g of cockles and a mean yearly food intake of 52.12 kg (109,719 cockles) per bird.

Comparative food intake estimations were made for the New Zealand mainland races of oystercatcher feeding at Jackson Bay during the winter of 1967 (from the data of Fig 3.13). At this study area South Island Pied Oystercatchers ingested 255.9 g dry weight of tua-tuas daily, or 51.8% of their body weight. Black Oystercatchers had a daily food intake of 244.4 g which represented 35.8% of their body weight, while the values for Variable Oystercatchers were 246.2 g and 35.7% respectively. As all feeding rates were recorded when the birds were feeding on a sandy beach, it is apparent that South Island Pied Oystercatchers are at a distinct advantage to the other races when feeding there. Although Black and Variable Oystercatchers feed at approximately the same rate as their smaller South Island pied congener, they are at a competitive disadvantage due to their larger body size. Assuming that all three races have similar basal metabolic rates and conversion efficiencies, the larger Black and Variable Oystercatchers would require greater amounts of food than their pied congener to maintain energetic parity. Thus when feeding on soft substrates South Island Pied Oystercatchers appear to have a considerable competitive advantage over the other races.

When feeding on rocky substrates at Kaikoura Peninsula, Black and Variable Oystercatchers (data combined) ate an average of 298.3 g dry weight of limpets per day which was equivalent to 43.7% of their body weight. Although different foods are not strictly comparable in terms of dry weight (Hartley, 1948), Black and Variable Oystercatchers feeding on limpets at Kaikoura ingested more food per bird than the same races feeding on tua-tuas at Jackson Bay. These races appear much more efficient at utilising food on hard substrates than on soft substrates, and this factor could well be an important one influencing habitat selection especially where apparent competitive exclusion with South Island Pied Oystercatchers occurs.

3.7 WINTER DIET

Considered in its entirety, the winter diet of New Zealand oystercatchers is extremely varied, with 36 prey species being recorded during this study. Of the prey species, molluscs form 90 to 95% by weight of the diet although other foods may assume a larger content where they are locally abundant. An extreme example of this was noted at Collingwood beach where some South Island Pied Oystercatchers fed only on the sea-anemone (Isactinia olivacea) which was locally abundant on the shells of pipis (Amphidesma australe). Most of the birds, however, preferred to eat the pipis and completely ignored the anemones.

As New Zealand races of oystercatcher show differences in habitat selection, and since the substrate of the habitat strongly influences the type and variety of preys present, then it follows that the composition of the diet of predatory birds will show a correlation with substrate types. The winter diet of New Zealand mainland oystercatchers in relation to substrate is shown in Table 3.7.

Some of the differences in diet may be only apparent ones because the lack of a particular prey species in a diet could be due to insufficient numbers of observations at a large number of different feeding sites. This reservation particularly applies to the Variable Oystercatcher which was not studied in the northern part of its range. The following discussion is therefore restricted to similarities and differences in diet which are thought to be real rather than apparent.

Bivalve molluscs form the major part of the diet. Where South Island Pied, Black, and Variable Oystercatchers feed on the same substrate they take the same bivalves. Black and Variable Oystercatchers occupying the top trophic level of rocky sea shore ecosystems show a decided preference for mussels and limpets. The large shore limpet (Cellana denticulata) is extensively taken where it occurs abundantly, in preference to other limpets presumably because of its larger size and associated food content. Fresh

TABLE 3.6 THE WINTER DIET OF NEW ZEALAND OYSTERCATCHERS IN RELATION TO HABITAT.

Prey Species	Substratum	Race of oystercatcher		
		Haematopus ostralegus finschi	*H.o.unicolor*	*H.o.reischeki*
COELENTERATA : ACTINOZOA				
Isactinia olivacea	Rock	X	-	-
MOLLUSCA : BIVALVIA				
Chione stutchburyi	Mud and sand	X	X	-
Amphidesma australe	"	X	X	X
A. subtriangulatum	Sand	X	X	X
Macomona liliana	Mud	X	-	-
Dosinia anus	Sand	X	X	-
D. subrosea	"	X	X	-
Protothaca crassicosta	"	X	X	X
Hydridella menziesi	Gravelly sand and mud	X	-	-
Mytilus edulis	Rock	-	X	X
Perna canaliculus	"	-	X	X
Modiolus neozelanicus	"	-	X	X
Aulacomya maoriana	"	-	X	X
: GASTROPODA				
Cellana denticulata	Rock	-	X	X
C. radians	"	X	X	X
C. ornata	"	-	X	X
C. flava	"	-	X	X
Haliotis iris	"	-	-	X
Melagraphia aethiops	"	X	X	X
Amphibola crenata	Mud	X	-	-
Cominella lucida	Mud and rocks	X	X	X
Zediloma corrosa	"	X	X	X
: AMPHINEURA				
Amaurochiton glaucus	Rock	X	X	X
Sypharochiton pelliserpentis	"	X	X	X
CRUSTACEA : DECAPODA				
Palaemon affinis	Rock	X	-	-
Helice crassa	Mud	X	X	-
Hemigrapsis edwardsii	Rock	-	X	X
: AMPHIPODA				
Talorchestia spp.	Sand	X	X	X
: ISOPODA				
Dynamenella huttoni	Rock	X	X	X
ANNELIDA : POLYCHAETA				
Glycera americana	Mud	X	X	-
Nicon aestuariensis	"	X	-	-
Perinereis nuntia	Sand	X	X	X
* : OLIGOCHAETA				
Allolobophora caliginosa	Soil	X	X	-
* INSECTA : COLEOPTERA				
Costelytra zelandica (larvae)	Soil	X	-	-
: LEPIDOPTERA				
Wiseana spp. (larvae)	Soil	X	-	-
PISCES : ACTINOPTERYGII				
Rhombosolea plebeia	Sand	X	-	-

N.B. * - prey species taken from coastal fields only during wet weather.

water mussels were taken only by South Island Pied Oystercatchers feeding inland at Lake Tuakitoto, Kaitangata. Of the gastropods other than limpets, only the paua (Haliotis iris) and mudsnail (Amphibola crenata) are not common to the diets of each race. The one instance of a Variable Oystercatcher feeding on a small juvenile paua is probably insignificant as this prey is relatively uncommon in the littoral zone of New Zealand sea shores. Mudsnails form only a subsidiary food item for South Island Pied Oystercatchers, but neither Black nor Variable Oystercatchers were seen to utilise this prey.

Chitons were a common dietary item, being taken with approximately equal frequency by each race. The occasional taking of crabs was noted for mainland oystercatchers, but the single isolated instance of South Island Pied Oystercatchers taking the marine shrimp (Palaemon affinis) suggests that it is a rare "opportunist" prey. Sand-hopping amphipods (Talorchestia spp.) were taken in small numbers from the flotsam line at high water, but this habit is chiefly associated with Black and Variable Oystercatchers. Although isopods belonging to one species (Dynamanella huttoni) were found in the guts of all three races, it seems probable that other isopods are occasionally taken. Polychaetes were a common food, the species taken depending upon the substrates the birds were feeding on. Earthworms (Allobophora caliginosa), and porina larvae (Wiseana spp.) were exclusive to the diet of South Island Pied Oystercatchers as this species has developed the habit of terrestrial feeding in winter (see section 3.4). The single occurrence of a sand flounder (Rhomboselea plebeia) in the gut of a South Island Pied Oystercatcher chloroformed at the Heathcote-Avon estuary suggests that it is an uncommon prey.

Summarising, the winter diets of New Zealand oystercatchers are basically similar, with molluscs forming the main prey. Where limpets are locally abundant Black and Variable Oystercatchers take them in preference to bivalves. Although dietary differences indicate that New Zealand oystercatchers fall into two groupings

(South Island Pied or Black and Variable Oystercatchers), these groupings are more a reflection of differing habitat selection rather than differing ecological requirements.

3.8 SUMMARY

The feeding ecologies of the New Zealand oystercatchers are essentially similar as could be expected from their ecologically specialised mode of feeding. However, differences in habitat selection, feeding behaviour, food requirements and diet are evident which suggest a two-fold grouping of the birds. These differences, and their probable significance are discussed below:

I. Habitat Selection

South Island Pied Oystercatchers show a strong selection for habitats with soft substrates such as estuaries, mudflats and sandy beaches. Black, Variable and Chatham Island Oystercatchers show an equally strong selection for habitats with hard substrates such as rocky platforms and promontories. Strict adherence to these habitat types does not occur, principally because of the modifying influences of social gregariousness, habitat availability, food availability and interspecific competition. Any one of these last mentioned factors can make one particular type of habitat unattractive to oystercatchers and thus force them to use another type they would otherwise select against.

II. Feeding Behaviour

New Zealand oystercatchers, being littoral feeders, follow a tidal cycle of behaviour. The periods of activity and rest are timed to coincide with low water and high water respectively. Large flocks of South Island Pied Oystercatchers feeding at wintering haunts display a more advanced form of social behaviour in their movements to and from the feeding grounds. Specific groups of birds feed in distinct home ranges, gathering together at the end of each period to form intermediate sandflocks before flying back to the high water roost. Colour-marked birds were found to have remarkable tenacity to particular sandflocks throughout the winter. Although Black Oystercatchers will also associate themselves with specific sandflocks, where they and Variable Oystercatchers occur as populations discrete from their South Island pied congener, sandflocking behaviour does not occur. Further, black and variable birds do not appear to maintain home ranges in their feeding grounds, although some isolated mated pairs actively defend a territory all year round. Thus the maintenance of home ranges by large flocks of South Island Pied Oystercatchers seems to be an elaboration of gregarious behaviour, resulting in an efficient apportionment of food resources.

The three races of oystercatcher possess a wide range of prey-specific feeding behaviour patterns to cope with the various sizes and species of prey found on the sea shore. Each race possesses the same range of behaviour patterns, all of which are neatly adapted to the structure and habits of the prey. Development of these patterns varies from race to race; South Island Pied Oystercatchers show a strong tendency to hammer cockles, whereas Black and Variable Oystercatchers appear to restrict hammering to mussel species. In general, South Island pied birds are behaviourally adapted to prey on estuarine bivalves, and the rock-dwelling black and variable species possess well-developed behaviour patterns to exploit mussels and limpets on rocky shores. In heterogeneous rocky habitats the differential expression of these patterns could be directly responsible in lessening the effects of interspecific competition for food. The principle of habitat exclusion (Gause, 1934) as modified by Dobzhansky (1951) that "two closely related species can only co-exist in the same habitat provided it is heterogeneous" appears to be operating at two distinct levels for New Zealand oystercatchers: (i) between adjacent contrasting habitats; and, (ii) within a habitat.

Where sandy and rocky habitats meet, Black and Variable Oystercatchers will restrict their feeding to the latter (even though food is less available) providing large flocks of South Island Pied

Oystercatchers inhabit the sandy area. Superior prey-specific feeding patterns for preys of rocky shores apparently outweigh the disadvantages of decreased food availability under such competitive conditions. However, exclusion is rarely absolute, and an occasional black or variable bird is not uncommon in large flocks of South Island Pied Oystercatchers. Within a heterogeneous rocky habitat, direct competition for the same food source is largely prevented, due to the use of different prey-specific feeding behaviour patterns by the two species of oystercatcher. Black and Variable Oystercatchers are rarely seen feeding with large flocks of their South Island pied congener, presumably because under these conditions they take the same prey and thus are competing directly.

Large feeding flocks of South Island Pied Oystercatchers are subject to competitive harassment from "parasitic" Red-billed Gulls, especially during the initial ebbing of the tide. Black and Variable Oystercatchers were never seen to be harassed in this manner, probably because their larger body size inhibits the gulls' aggressive approaches. Intraspecific interactions within each race are not common, and only occasionally contain aggressive elements. The aggressive piping display, which is the major threat display of oystercatchers, appears to be identical in all New Zealand races.

III. Food Requirements

The rate at which oystercatchers ingest food is extremely variable due to the influence of several factors. The state of the tide, environmental conditions, seasonal temperature, food availability, prey size, age of the feeding birds and the rate at which food is searched for, all exert modifying effects on the rate of feeding.

South Island Pied Oystercatchers feeding at the Heathcote-Avon estuary in winter had a mean daily dry weight intake of 174.9 g of cockles, corresponding to 35.2% of their mean body weight. In midsummer the values were respectively 124 g and 25.1%. During 1967 the mean feeding rate was 33.4 cockles/hr, giving a mean daily food intake of 142.8 g dry weight and a yearly food intake of

52.12 kg per bird.

At Jackson Bay during the midwinter of 1967, South Island Pied Oystercatchers ingested 255.9 g dry weight (51.8% of body weight) of tua-tuas daily, Black Oystercatchers ingested 244.4 g (35.8%) and Variable Oystercatchers 246.2 g (35.7%). As all observations were made on a sandy beach habitat, Black and Variable Oystercatchers feeding there were at a considerable competitive disadvantage to their smaller pied congener. The reverse probably applies when the races are feeding on rocky habitats. At Kaikoura, Black and Variable Oystercatchers ingested 298.3 g dry weight of limpets daily, which was equivalent to 43.7% of their body weight. The increased efficiency of these two races at utilising foods on hard substrates could well be an important factor in habitat selection, especially where apparent competitive exclusion with South Island Pied Oystercatchers occurs.

IV. Winter Diet

The winter diets of New Zealand races of oystercatcher are essentially similar with molluscs forming the main prey. South Island Pied Oystercatchers show a distinct preference for bivalves, whereas black and variable birds prefer limpets. Each race has a wide range of prey species representing many of the major invertebrate phyla in its diet.

3.9 TAXONOMIC CONCLUSIONS

New Zealand oystercatchers have similar feeding ecologies resulting from their specialised mode of feeding. Assessment of similarities and differences supports the taxonomic categories adopted by the Checklist of New Zealand Birds (1953). Differences of species magnitude in habitat selection, feeding behaviour, food requirements and diet, occur between South Island Pied Oystercatchers (*Haematopus ostralegus finschi*) on the one hand, and Black and Variable Oystercatchers (*H. u. unicolor* and *H. u. reischeki* respectively) on the other. Expected interracial differences between

Black and Variable Oystercatchers were not recorded, both races appearing to have identical ecological requirements. Black, intermediate and pied phases of the Variable Oystercatcher all behave as if one race, and black phases appear ecologically inseparable from the southern black race (*H. u. unicolor*).

Chapter 4

THE BREEDING BIOLOGY OF NEW ZEALAND OYSTERCATCHERS

4.1 INTRODUCTION

The breeding biology of oystercatchers has not been the subject of intensive research which characterises that of the altricial nidicolous bird species. Most workers have directed their efforts at determining general breeding parameters such as clutch-size, incubation period and brood-size. Breeding studies of the European Oystercatcher (Haematopus ostralegus) have been conducted by Dewar (1920), Dircksen (1932), Buxton (1939), Keighley & Buxton (1948), Grosskopf (1964) and Harris (1967). Comparable research has been carried out on the American Pied Oystercatcher (H. o. palliatus) (Tomkins, 1954), the North American Black Oystercatcher (H. bachmani) (Webster, 1941; Legg, 1954) and the South African Black Oystercatcher (H. moquini) (Hall, 1959). Clutch, nest-site, and pair bond details of the European Oystercatcher have been recorded by Haverschmidt (1946), Campbell (1947), Keighley (1948), Drost & Hartman (1949), Neddermann (1954), and Jungfer (1954). Mortality and fertility estimates have also been made for this species (Boyd, 1962).

General breeding data have been collected for American oystercatchers (Kaeding, 1905; Ridgway, 1919; Murphy, 1925; Bancroft, 1927; Bent, 1929; Murphy, 1936; and Kenyon, 1949), and Australian oystercatchers (Campbell, 1900; North, 1913; Serventy & Withell, 1951; and Warham, 1955).

Records of growth and development of oystercatchers are rare, the only published accounts being those of Dewar (1920) and Webster (1942). Downy young of world forms were compared by Webster (1943). Parental feeding has been described only for the European Oystercatcher (Lind, 1965).

Breeding behaviour has attracted much attention from ethologists, mainly because of the spectacular nature of distraction displays in defense of eggs and young (Huxley & Montague, 1925; Makkink, 1942; Williamson, 1943; Armstrong, 1947; Edwards, Hoskine & Smith, 1948; Duffey, Creasey & Williamson, 1950; and Hall, 1959). Bigamous behaviour was noted by Webster (1941), Barnes (1950), Ticehurst (1950), Nevin & Ticehurst (1951), and Harris (1967).

Complete breeding studies of New Zealand oystercatchers are lacking. The first description of the breeding habits of the South Island Pied Oystercatcher was that of Potts (1869), later confirmed by Travers (1871) and Buller (1888). Further details of this species' breeding were recorded by Stead (1927) and Falla (1939). Falla also produced the first authoritative account of the breeding of Black and Variable Oystercatchers, which was later recapitulated and expanded by Oliver (1955). Breeding habits of the Chatham Island Oystercatcher have not been studied.

The limited knowledge of the breeding biology of New Zealand oystercatchers necessitated comparative studies for each species, especially since taxonomy at the species level ultimately depends upon critical assessment of the major species criterion; that of reproductive isolation in nature from other species. Comparative population ecology studies were not attempted because of wide breeding dispersion within and between each race. Research was therefore restricted to general breeding parameters not requiring the collection of voluminous data.

4.2 METHODS

A. Assessment of Breeding Data from General Sources

General breeding data such as the duration of breeding seasons, breeding dispersal and dispersion, territory retention, nest-site preferences, laying dates, clutch size, incubation period and brood size were extracted from the following sources:

1. the early literature of ornithological discovery in New Zealand;
2. Classified Summarised Notes (in New Bird Notes and Notornis);

3. the Recording Scheme of the Ornithological Society of New Zealand;
4. nest-record cards of the O.S.N.Z.; and,
5. personal communications and records.

B. Breeding Activity at Winter Haunts

The Heathcote-Avon estuary was visited once a week over the period May to November 1967 to record breeding activity. At each visit the types and numbers of nuptial activities of South Island Pied Oystercatchers were recorded over 60 min recording periods, a mean taken from five such records. One visit of three days duration was made to Jackson Bay and Farewell Spit in August, and the nuptial activities of Black and Variable Oystercatchers recorded as for the above species.

C. Breeding Activity at the Breeding Grounds

Breeding activity of South Island Pied Oystercatchers at the Ashley River study area was observed for five days a week during August and September, 1967. One day surveys at weekly intervals were conducted in October, November and December. Arrivals of breeding pairs at the area were noted, and once territories were established all further observations were made from a portable hide. Comparative studies of Black and Variable Oystercatchers were conducted in a similar manner at Jackson Bay in January, 1968.

D. Identification of Nest-scrapes, Eggs, and Chicks

Nest scrapes were identified by white marking pegs driven into the substrate 10 m north of their actual location. Each peg was serially numbered so that data from each pair could be assigned a numerical code.

Freshly laid eggs were serially numbered on both ends with a felt marking pen. Eggs of unknown age were designated with an = sign alongside relevant numbers. Numbers lasted throughout incubation in all cases except one, in which case the number was replaced by reference to the other eggs in the clutch.

Chicks were initially marked at hatching by applying black enamel paint to the inside of the left tarsus. Stripes were painted horizontally across the tarsus, the number of the stripes corresponding to the order of hatching. Recovered chicks were repainted if the enamel showed signs of wear. At the age of three weeks all chicks were banded with Dominion Museum monel K bands.

E. Measurement of Clutches and Broods

Egg and clutch dimensions of complete clutches were recorded in the field. Additional egg measurements were obtained from eggs in the Dominion Museum collection. Maximum length and diameter of eggs were measured with vernier calipers accurate to the 0.1 mm. Eggs were weighed within 24 hr of laying so that error arising from weight losses during incubation could be eliminated. Weights were taken with a 50 g balance accurate to 1 g. Egg weight loss during incubation was recorded by daily weighings of a small number of clutches.

Chick weights were recorded at hatching and thereafter at weekly intervals until fledging. Chicks up to two weeks old were weighed on a 100 g pan balance accurate to 1 g. Older chicks were weighed on a 500 g spring balance accurate to 5 g. Growth rates of chicks were recorded by taking standard measurements of the body appendages as outlined by Gurr (1947). Each chick was measured at weekly intervals from hatching to fledging.

4.3 THE STUDY AREAS

A. The Ashley River Study Area

This study site, covering an area of approximately 2 km^2, is centred at 43° 15' South, 172° 12' East near the foothills of the Puketeraki Range (see Fig 4.1). The bed of the Ashley River is composed largely of greywacke pebbles and boulders interspersed at intervals by banks of river sand (see Plate 4.1). Shingle regions of the riverbed are intersected with numerous river channels, between which silt islands are common. The islands are densely

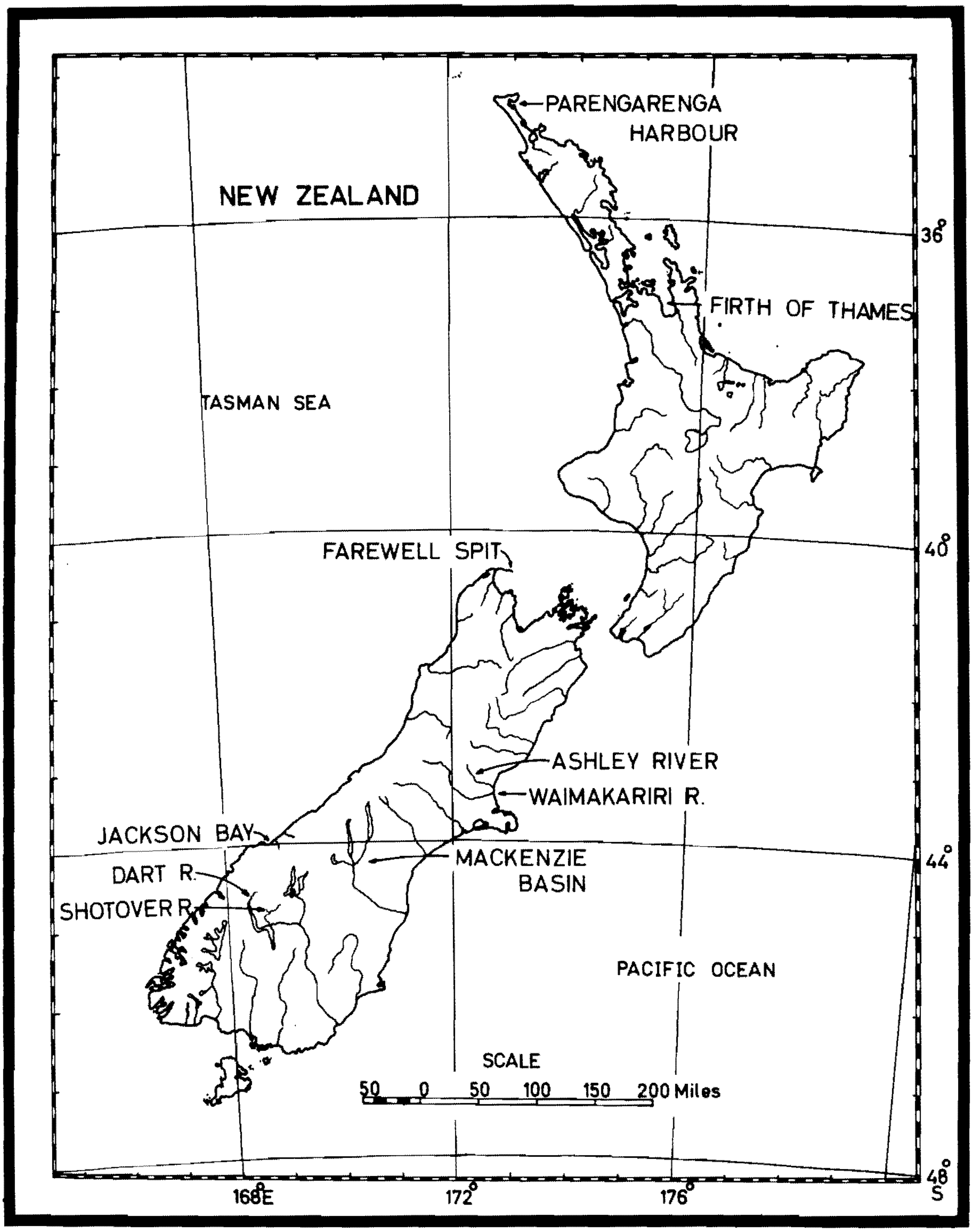

NEW ZEALAND
PARENGARENGA HARBOUR
FIRTH OF THAMES
TASMAN SEA
FAREWELL SPIT
ASHLEY RIVER
WAIMAKARIRI R.
JACKSON BAY
MACKENZIE BASIN
DART R.
SHOTOVER R.
PACIFIC OCEAN
SCALE
50 0 50 100 150 200 Miles
36°
40°
44°
48° S
168°E
172°
176°

Figure 4.1

The location of the study areas, and localities mentioned in the text.

Plate 4.1

General view of the Ashley River study area.

September, 1967.

clothed with gorse (Ulex uropaeus) and broom (Cystisus scoparius).

The riverbed at the study site is subject to an equable climate during the breeding season, being in a region of low rainfall (58 to 78 cm) and experiencing warm summers with occasional hot "Norwest" Foehn winds of approximately 30° C.

Grasslands in the immediate vicinity of the riverbed are established on yellow-grey earths superimposed above recent sedimentary basement strata. Erosion of these soils at the margins of the riverbed provides a ready source of flood silt.

B. Farewell Spit and Jackson Bay Study Areas

The general topography, location, and climate of these two study sites have been discussed previously (see Ch.3.3 C and E). The general nature of the breeding habitats in each of these study areas is shown in Plates 4.2 and 4.3.

4.4 BREEDING SEASONS

New Zealand's two species of oystercatcher have markedly different breeding seasons. South Island Pied Oystercatchers are relatively early breeders, the earliest nesting record being 17th July (Royds, 1955). Most nesting occurs in August and September with egg-laying reaching a peak in September. Chicks are raised chiefly during October and November, and are usually fully fledged by the end of December. However, breeding birds with unfledged young have been recorded as late as January, but in most cases these represent repeat clutches. Thus for this species the breeding season extends from July to January.

Black and Variable Oystercatchers breed much later than their South Island pied congener, but the breeding season of the two species partly overlap. Egg-laying begins at the end of October, the earliest record for variable and black birds being 22nd October (Oliver, 1955) and 3rd November respectively. A peak is reached in December and chicks are common in January and February. Black and Variable Oystercatchers breed earlier (October to February) in

Plate 4.2

Breeding habitat at the Farewell Spit study area.
December, 1968.

Plate 4.3

Breeding habitat at the Jackson Bay study area.
January, 1968.

the southern South Island than they do in the northern North Island (December to February). Chicks are raised in December and January and fledge during January and February. The breeding season of this species therefore extends from October to February.

New Zealand species of oystercatcher have different breeding seasons of which approximately three months are common to both. Breeding peaks, however, are separated by a period of at least two months. To a large extent then, these asynchronous breeding seasons largely ensure reproductive isolation between the species, irrespective of their breeding dispersion.

4.5 BREEDING AND NON-BREEDING POPULATIONS

The wide nesting dispersion of New Zealand oystercatchers (see section 4.7) allied with the complete lack of breeding censuses have made accurate estimates of breeding and non-breeding populations within the country impossible. For this reason only the characterisation of breeders and non-breeders are discussed below.

A. BREEDING BIRDS

Breeding populations of European Oystercatchers are composed of birds all possessing adult plumage and characteristic bill, leg, iris and eye ring colouration (Witherby, Jourdain, Ticehurst & Tucker, 1940). New Zealand species and races of oystercatcher possess identical adult colouration, but the configuration of black and white areas of the plumage differs with each race (see Ch.1.6). The bill and eye ring are bright orange, the iris scarlet, and the legs and feet bright pink. During the breeding season, following the pre-nuptial moult (see Ch.5.3 B), black areas of the plumage have a glossy appearance often reflecting greenish or purplish hues (see Plates 4.4 and 4.5). This glossiness has in the past been the source of taxonomic confusion noted by Falla et al.(1966), who commented, "It has been stated that the black form of reischeki is a browny black and lacks the purple gloss of true unicolor, but this needs verification. The plumage of black oystercatchers

Plate 4.4

Adult plumage and body colouration of the South Island Pied Oystercatcher.

Plate 4.5

Adult plumage and body colouration of a smudgy phase Variable Oystercatcher.

breeding on the northern coast of the North Island can be distinctly glossy; and black oystercatchers seen in flocks on Stewart Island are not noticeably glossy." The explanation of this difference is simple; the northern breeding birds had acquired glossy plumage following the pre-nuptial moult while the Stewart Island birds were still in duller winter plumage following the post-nuptial moult (winter being the only time at which the birds form flocks).

B. NON-BREEDING BIRDS

Non-breeding populations are composed of birds belonging to three age classes; first year, second year, and adult birds.

1. First year juveniles

Juvenile South Island Pied Oystercatchers maintain their fledging plumage until midwinter when they moult their first plumage (see Ch.5.3 B). Up to this stage the dark parts of the plumage are suffused with brown, the scapulars and upper wing coverts being edged with buff. Distal portions of the bill are dusky and the legs and feet are a dull grey-pink. Eye colouration is characteristic, the eyelid being yellowy-orange and the iris brown (see Plate 4.6).

Juveniles of Black and Variable Oystercatchers were described by Oliver (1955). Immature black birds had a blackish brown plumage, the feathers being edged with buff. Bill colouration was dull orange turning dusky at the tip, and the legs and feet were greyish purple. Variable Oystercatcher juveniles were noted to have a similar plumage to the adult except that the back and wing coverts were dark brown with whitish edges to the feathers. The breast had a wide mottled band at the junction of black and white areas.

2. Second and third year sub-adults

Following their first moult in midwinter, juvenile South Island Pied Oystercatchers assume sub-adult plumage. Dorsal dark parts have less brown, the iris changes to light orange, and the legs and

Plate 4.6

First winter juvenile plumage of the South Island Pied Oystercatcher.

Plate 4.7

Second year sub-adult plumage of the South Island Pied Oystercatcher.

feet become pale pink. Similar colour changes occur in Black and Variable sub-adults (see Plate 4.7).

Sub-adult plumage and body colouration is maintained throughout the second year of life, and occasionally the third year. Of thirty-three sub-adult South Island Pied Oystercatchers colour banded at the Heathcote-Avon estuary during 1967, thirty moulted into adult plumage during 1968. The remaining three birds maintained their sub-adult plumage during the same period, although their third year plumage contained considerably less brown dorsally. Thus for the great majority of birds in the sample (90.0%), the plumage and colour change sequence was juvenile (first year), sub-adult (second year), and adult (third year). Identical changes with age were noted for the conspecific European Oystercatcher (Witherby et al., 1941; M.P. Harris, pers. comm.). Black and Variable Oystercatchers probably follow a similar maturation pattern, as three plumage groups are discernible within their flocks.

3. Adult non-breeders

In addition to juveniles and sub-adults, flocks of non-breeding oystercatchers also contain small numbers of birds in adult plumage and body colouration. The latter presumably have either been unsuccessful in finding mates or they have not undergone psychological or physiological changes necessary to bring them into breeding condition.

4. Age composition of winter flocks prior to breeding

The age composition of some winter flocks of oystercatchers in New Zealand prior to breeding dispersal is shown in Table 4.1.

For both H. ostralegus and H. unicolor approximately 70 to 80% of the total wintering flocks are potential breeding birds. Of these adults approximately 1 to 3% (from Heathcote-Avon census) will be non-breeders. The remaining 20 to 30% is composed of immature birds, juveniles and sub-adult birds occurring in approximately equal numbers.

TABLE 4.1 AGE COMPOSITION OF WINTER FLOCKS OF NEW ZEALAND OYSTERCATCHERS

Species	Locality	Age Groups 1st yr juveniles	 2nd & 3rd yr sub-adults	 Adults
South Island Pied Oystercatcher (*Haematopus ostralegus finschi*)	Heathcote-Avon estuary	446 (11.6%)	405 (10.4%)	3,100 (78.2%)
"	Manakau Harbour	1883 (26.9%)		5,509 (73.1%)
	Firth of Thames	365 (14.6%)		2,138 (84.4%)
Black Oystercatcher (*H. u. unicolor*)	Jackson Bay	8 (13.6%)	10 (15.0%)	41 (71.4%)

Note: Comparable data on the Variable Oystercatcher are not available.

C. AGE OF FIRST BREEDING

The age at which oystercatchers first breed is not known with certainty. European Oystercatchers have been recorded breeding in their third year (Dircksen, 1932; Jungfer, 1954; Grosskopf, 1964), but the recent work of Harris (1967) has indicated that the majority of birds probably breed in their fourth year. The latter author suggested that, as in the Yellow-eyed Penguin *Megadyptes antipodes* (Richdale, 1951), females breed, on average, earlier than males. He also noted the third year birds prospected for territories but did not actually breed until their fourth year. As Harris's study was conducted on the small island of Skokholm where nest-sites were limited, it seems likely that many of the three year old birds would have bred in their third year had nesting densities been lower.

New Zealand oystercatchers probably breed in their third year. Since the majority of South Island Pied Oystercatchers attain adult plumage and body colouration during their third year, and as nearly all adult-plumaged birds migrate to breeding areas, it seems probable they breed at an age of three years. Also, as this species breeds inland on shingle riverbeds where nest sites are plentiful, delayed maturity (Wynne-Edwards, 1962) until the fourth year is unlikely. For the same reasons, Black and Variable Oystercatchers probably first breed at a similar age.

4.6 BREEDING DISPERSAL AND DISPERSION

A. Dispersal to Breeding Areas

The two New Zealand species of oystercatcher have different dispersal patterns from their winter haunts to the breeding grounds. South Island Pied Oystercatchers possess a well developed migratory instinct. Breeding birds wintering at North Island localities begin their southward migration in July (Falla et al., 1966). Full-scale migration is usually preceded by "trial flights" in which small groups of birds ascend to great height above the wintering area, and may venture several miles away before returning to roost (see Plate 4.8). Such flights are undertaken only by small groups of birds, usually between 20 and 50 per flock. Migration begins for each flock where they continue southward instead of returning to the wintering area. Birds wintering in northern New Zealand could possibly migrate as far as 800 miles. Buxton (1957) recorded a similar maximum migration distance for the conspecific European Oystercatcher.

Breeding birds wintering in South Island localities begin their migration later than northern birds. Migration of the Farewell Spit and Heathcote-Avon estuary breeding populations begins in early August. This suggests that the northern birds are reaching their

Plate 4.8

A "trial flight" of South Island Pied Oystercatchers
prior to migration to breeding areas.

August, 1967.

breeding grounds well in advance of the South Island birds, and since colonisation of breeding birds occurs firstly in Southland and Otago, it would appear that these areas could be the breeding grounds of the northern birds. Canterbury wintering birds undertake shorter migrations, flying along river beds rather than moving directly southwards (Dawson, 1949; J.D. Coleman, pers.comm.). Salamonsen (1955) described a similar migration pattern for the nominate race of *H. ostralegus* in Europe, which he termed leap frog migration. He further postulated that this type of migration could be of importance in the formation of races.

Black and Variable Oystercatchers do not undertake migrations to their respective breeding areas. Where flocks have been formed during winter, dispersal of breeding pairs to nearby territories begins in September. The lack of a migratory instinct in this species is a complete contrast to that of its smaller pied congener. At the Jackson Bay and Farewell Spit study areas, Black and Variable Oystercatchers dispersed only short distances away from the winter roost, the maximum recorded distance being 15 km. Isolated pairs remain in their territories throughout the year and do not therefore undertake pre-breeding dispersal movements.

B. Breeding Dispersion

New Zealand oystercatchers fall into two natural groups on the basis of their breeding dispersion;

1. Inland breeders
2. Coastal breeders

1. Inland Breeders

South Island Pied Oystercatchers are, with very few exceptions, inland breeders. They nest on the beds of all major snow-fed rivers in the South Island. Apart from one breeding record at Haupiri in Westland, this species nests east of the main divide. Coastal breeding birds are rare, and when they do so the nest-sites are associated with lagoons, lakes and marshy fields (see Fig 4.2). The inland breeding habitat appears to have been established and

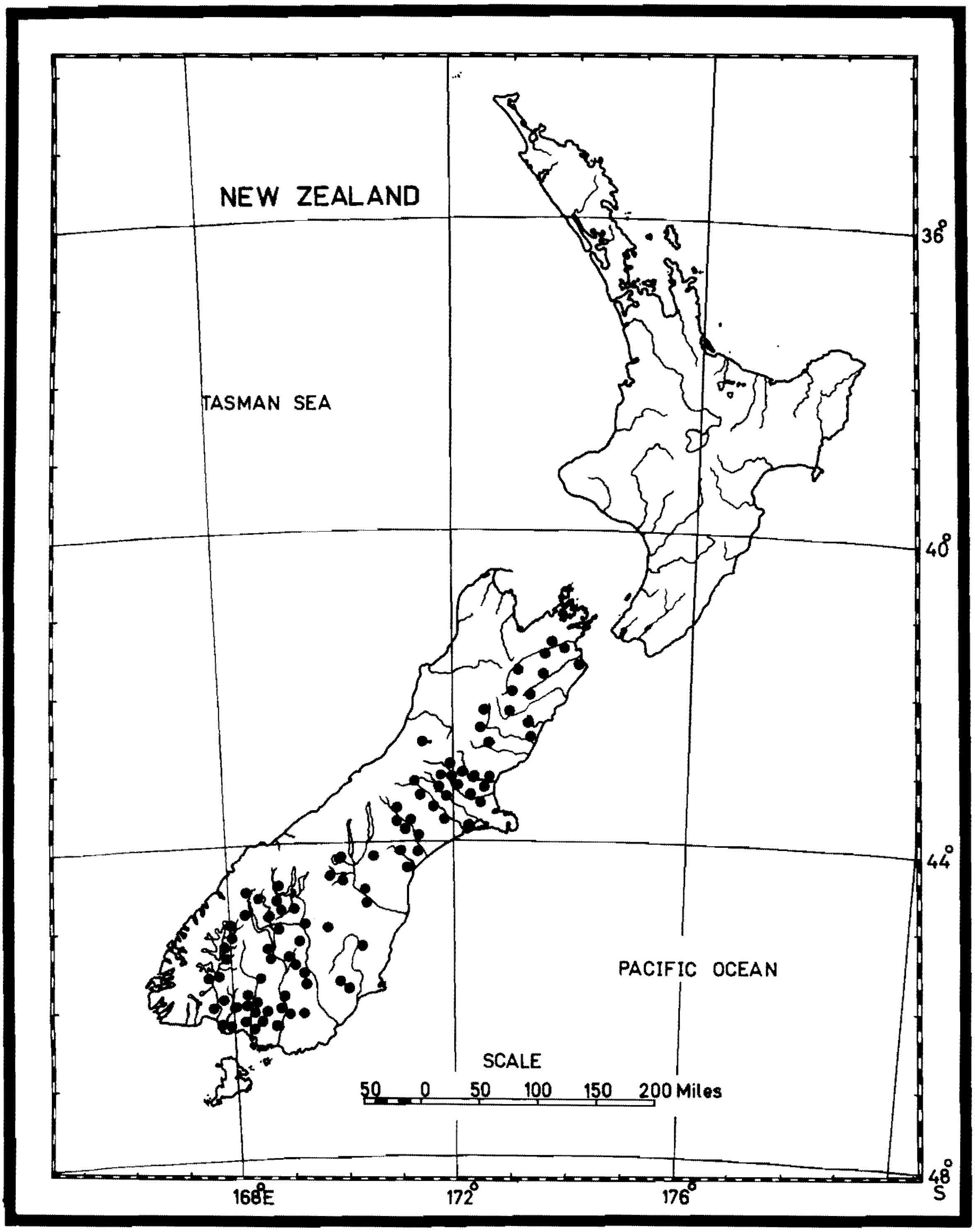

NEW ZEALAND
TASMAN SEA
PACIFIC OCEAN
SCALE
50 0 50 100 150 200 Miles
36°
40°
44°
48° S
168°E
172°
176°

Figure 4.2

Breeding distribution of South Island Pied Oystercatcher.

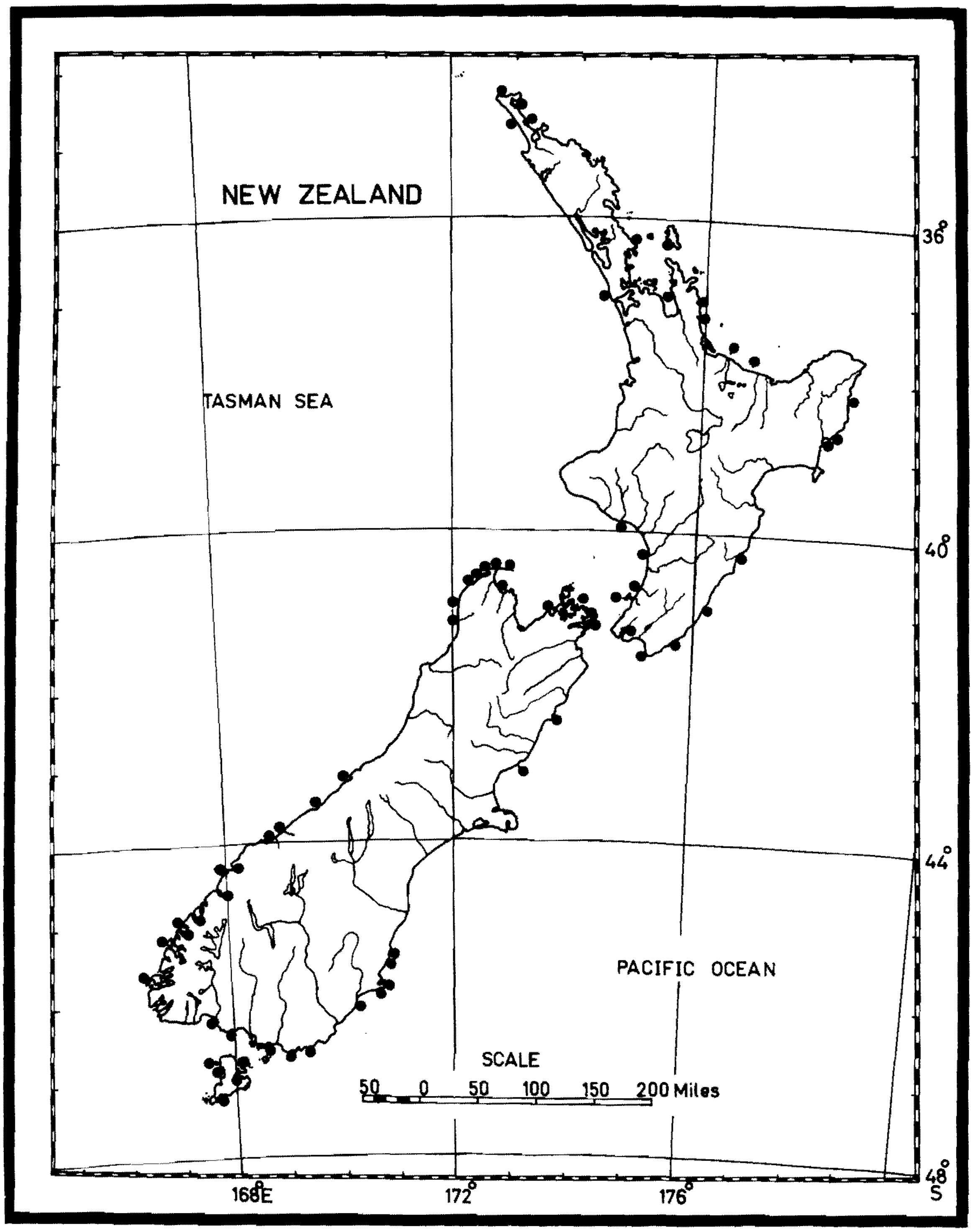
maintained in New Zealand for at least the last 100 years. Potts (1869) noted that South Island Pied Oystercatchers were common breeders on Canterbury riverbeds at that time.

The absence of coastal breeding populations over such a length of time is unexpected when the breeding dispersion of the conspecific European Oystercatcher is considered. At the start of the 19th century oystercatchers were breeding around virtually the entire coast of England, and did not breed inland at all. Between 1880 and 1910 they spread inland by way of the river systems (Buxton, 1962). At a later stage in their colonisation oystercatchers began to disperse away from riverain shingle beds to nest on surrounding farmlands. Similar recent extension of breeding range inland has been noted in Holland, Germany, Denmark and southern Sweden (Voous, 1960). In spite of this tendency to breed inland, however, European Oystercatchers still extensively use coastal areas as breeding habitats.

2. Coastal Breeders

Black and Variable Oystercatchers breed only in coastal habitats (see Fig 4.3 and 4.4). Breeding dispersion is essentially similar to the distribution of wintering flocks, as it would be expected from their limited pre-breeding dispersal (see section 4.6 A). Isolated breeding pairs of this species frequently breed on small offshore islands.

Reproductive isolation of the two New Zealand species of oystercatcher is ensured by their allopatric breeding dispersion. This factor, combined with their asynchronous breeding seasons, has clearly made reproductive isolation absolute. The extent of overlap in the breeding dispersion of black and variable races of _H. unicolor_ is difficult to assess. Phenotypic similarity between the southern Black Oystercatcher (_H. u. unicolor_) and the black phase of the Variable Oystercatcher (_H. u. reischeki_) has made accurate racial delimitation impossible. It seems certain, however, that the races overlap during the breeding season, as the pied phase of


NEW ZEALAND
TASMAN SEA
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176°

<u>Figure 4.3</u>

Breeding distribution of "black" (Southern Black and black phase of Variable) oystercatchers.

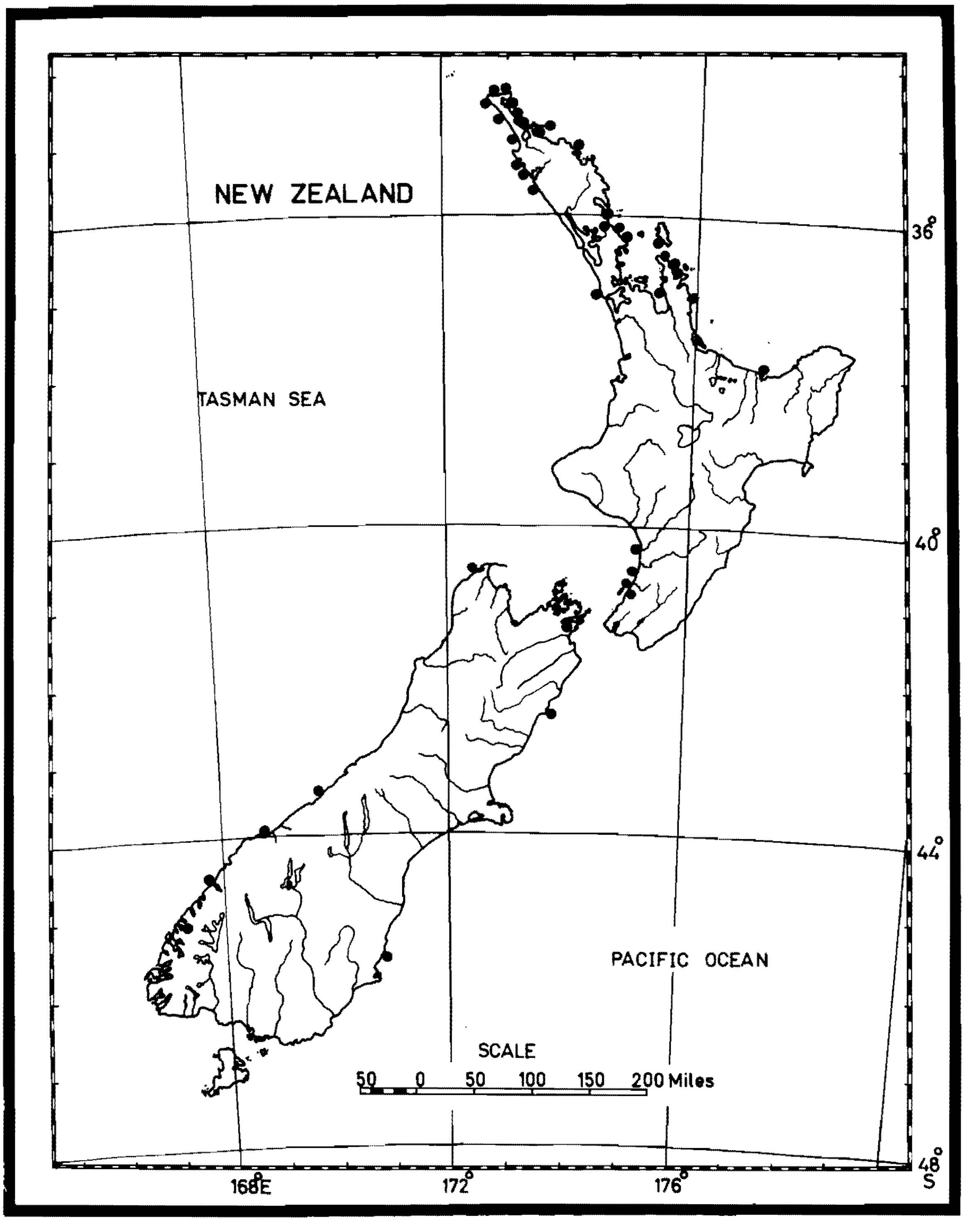
NEW ZEALAND
TASMAN SEA
PACIFIC OCEAN
SCALE
50 0 50 100 150 200 Miles
36°
40°
44°
48° S
168°E
172°
176°

Figure 4.4

Breeding distribution of Variable Oystercatchers.

the Variable Oystercatcher has been recorded breeding with black birds as far south as Charles Sound in Fiordland.

C. Recent Trends in Breeding Dispersion

The irruption of South Island Pied Oystercatchers which followed the ban prohibiting the shooting of shorebirds in 1941 has brought about changes in breeding dispersion. In the first half of the current century, this species was rarely recorded breeding away from riverbeds. Since 1950, however, there has been an increasing tendency to breed in pastural habitats, and the habit now appears well established. Natural grasslands such as tussock-covered plains of the MacKenzie Basin have also become recent breeding habitats. Oystercatchers have been recorded breeding at 1,600 m above sea level in the Old Man range in Otago (Austin, 1954).

The spread away from traditional riverbed breeding habitats has presumably resulted from the population irruption, which has in turn reduced nest-site availability. As South Island Pied Oystercatchers are strongly territorial, and since arable and pastural land contains plentiful supplies of invertebrate foods, population pressure from rising nesting densities has been reduced by colonisation of this new readily available habitat. A parallel colonisation, again correlated with an expanding population, has been described for the European Oystercatcher in Britain (Dare, 1966).

4.7 BREEDING BEHAVIOUR

A. Courtship and Pair Formation

Pair formation in both New Zealand species of oystercatcher is usually effected whilst the birds are still in their winter flocks. Courtship leading to pair formation manifests itself primarily in vocalised piping displays (see Plate 4.9). Such piping contains a dominant social element in contrast to aggressive piping which is agonistic in nature (see Ch.3.5 C). Social and aggressive piping also differ in that the former is mutually stimulative to several birds, groups of up to six birds being common in displays. Fighting

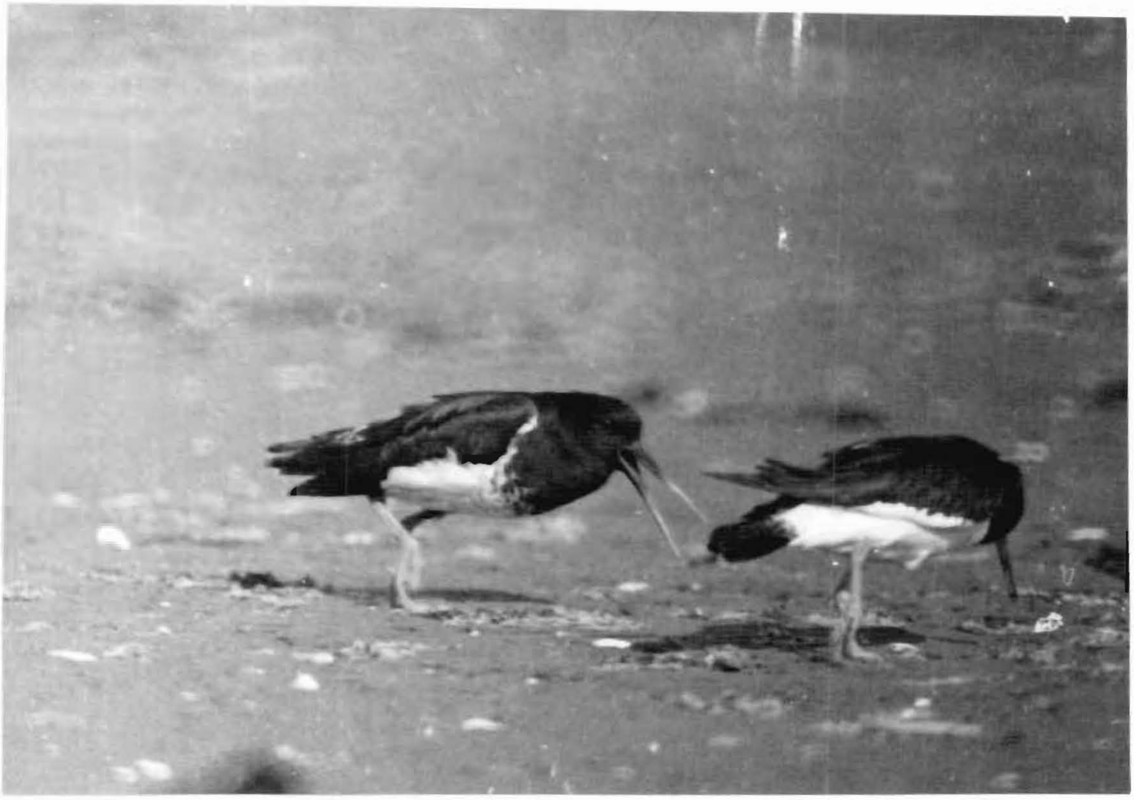

Plate 4.9

Social piping display of the Variable Oystercatcher. During such displays, the participating birds pipe in unison and frequently turn towards each other.

between the members of a group following social piping is extremely rare whereas it frequently follows aggressive piping. The sexual nature of social piping of the South Island Pied Oystercatcher was apparent during this study. At the Heathcote-Avon estuary piping was restricted to adult-plumaged birds (presumably sexually mature) and the occurrence of displays increased markedly with the onset of the breeding season (see Table 4.2).

TABLE 4.2 OCCURRENCE OF SOCIAL PIPING DISPLAYS BY SOUTH ISLAND PIED OYSTERCATCHERS AT THE HEATHCOTE-AVON ESTUARY DURING 1967.

Month	May	June	July	August	Sept.	Oct.	Nov.
Mean No. of displays/ 1 hr obs. period	0	2	11	19	5	3	0
% of total	0	5	27.5	47.5	12.5	7.5	0

Ceremonial social piping parties of the European Oystercatcher have received a great deal of attention from ornithologists (Selous, 1901; Huxley & Montague, 1925; Dircksen, 1932, 1938; Perry, 1938; Armstrong, 1940; Makkink, 1942). Two to a dozen birds were noted to participate, though three was the usual number, especially during the months of February, March, April (August, September and October of the New Zealand breeding season). Social piping of the conspecific South Island Pied Oystercatcher seems similar in both form and timing to that of the European bird.

Courtship behaviour of South Island Pied Oystercatchers begins in June, reaches its greatest development in August, and ends in October. Similar social piping, involving identical posturing (Watt, 1955) reaches a peak in September for Black Oystercatchers at Jackson Bay (D. Greeney, pers. comm.). The later seasonal development of piping activity in this species is in accordance with its later breeding season. Falla et al. (1966) noted that the piping ceremony accompanied pair formation and courtship of the

Variable Oystercatcher.

Pair formation marks the culmination of courtship behaviour, and is indicated by copulation between members of the pair. Makkink (1942) found that pair formation and early nuptial activities of the European Oystercatcher were associated with the casting of straws with the bill and the making of nest-scrapes. No such comparable behaviour prior to pair formation was noted for New Zealand oystercatchers during this study.

Most pair formation of South Island Pied Oystercatchers is accomplished by mid-August. Prior to inland migration, pairs became discernible at wintering localities, frequently feeding and roosting together. Further evidence of pair formation at wintering areas is provided by the size of migrating flocks. Individual pairs of birds were frequently sighted on migration, especially above the Ashley and Waimakariri riverbeds. Larger flights of 20 to 50 birds which occur earlier in the breeding season presumably represent groups of pairs en route to a common breeding area.

Pair formation of Black and Variable Oystercatchers is accomplished by September, and precedes the establishment of territories. Pairs formed at this time gradually disperse away from the wintering flock to breeding localities. Thus pair formation in New Zealand oystercatchers is sociogamous[1] rather than territorigamous[2].

B. Copulatory Behaviour

Copulation is usually, but not always, preceded by specific posturing. South Island Pied Oystercatchers at the Heathcote-Avon estuary were noted to adopt two distinct postures previous to copulation. Males (as determined by taking the active role in copulation) and females showed approximately equal tendencies to initiate copulatory behaviour. The male posture involved a stealthy approach, with the head withdrawn between the shoulders and held to one side of the body. This hunched-up attitude was accentuated by a general lowering of the body, and a pressing down and fanning of the tail. Females willing to copulate assumed a

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1 & 2 - terminology of Makkink (1942)

passive posture, raising the body higher above the ground than is usual and at the same time erecting the tail feathers above the horizontal. The male mounted from behind and during coition maintained balance by flapping the wings. Coitus was always of short duration, lasting only a few seconds. After the male dismounted normal behaviour was resumed again. Occasionally copulations were noted in which the male did not adopt the pre-copulatory posture, but walked normally up to the female and mounted.

Only one copulation was observed between Black Oystercatchers, and in this case no specific posturing preceded the act. Webster (1941) noted that copulation of American Black Oystercatchers did not involve any special preliminary ceremony, the male flying onto the female's back from a distance. Copulatory behaviour of the Variable Oystercatcher does not appear to have been studied.

South Island Pied Oystercatchers were observed copulating at the Heathcote-Avon estuary at least five weeks in advance of egg-laying. Huxley & Montague (1925) noted the same behaviour in European Oystercatchers and concluded that the physiological capacity of the eggs to be fertilised was not synchronous with the psychological readiness for insemination. Applying this reasoning, Makkink (1942) suggested that early copulations were part of the behavioural mechanism whereby pair-bonds were established and secured. Copulations at the wintering haunts probably assist pair-formation of New Zealand oystercatchers, especially since at this time they are unlikely to effect fertilisation. Further, copulations were noted on the breeding grounds up to the time of egg-laying, and it seems probable that these later acts bring about fertilisation of the eggs.

C. Territorial Behaviour

New Zealand oystercatchers are intensely territorial. Territories are actively defended against intraspecific intruders, but other bird species transgress territorial boundaries with impunity. Territorial display is restricted to aggressive piping (see Ch.3.5 C), very rarely culminating in fighting. During this study piping displays between neighbouring pairs were commonest near territorial boundaries. Males, distinguished on their smaller size (see Ch.5.3A), were found to be more active in territorial defense than females. Of 29 observed territorial displays, 19 were initiated by males and 10 by females. The most frequent number of birds involved in these displays was two, but three (one pair and an intruder) and four (two pairs) were not unusual. Resident birds always stood their ground against intruders, the latter retreating when threatened.

In the rare cases that fighting occurred, combat was usually preceded by the adoption of a specific posture, the diplomatist attitude (see Plate 4.10). This attitude was first described by Makkink (1942) for European Oystercatchers, and he found that it was always indicative of hostility. The posture appears to be identical in both New Zealand species. The body was drawn erect and the neck extended so that the body took on an oblique attitude. The bill was extended horizontally towards the opponent, and the feathers depressed against the body and wings. Opposing birds which had assumed this posture frequently circled each other flank to flank before attacking.

D. Mutual Behaviour

Following the establishment of territories, mutual displays between the members of a pair are common. This behaviour is of two types:

1. balancing; and,
2. allopreening.

1. Balancing

Mutual balancing involves a particular stance in which both birds of a pair stand close together and rock their bodies in a seesaw motion about the axis of their knee joints. In this action they resemble weighting balances. Similar mutual balancing was noted for the European Oystercatcher by Dircksen (1932) and Makkink (1942), the latter concluding that it reflected general excitement associated with the early stages of nesting. All New Zealand races perform this type of behaviour.

Plate 4.10

The diplomatist attitude of the Variable Oystercatcher. The hostile nature of this posture is indicated by the raised hackle feathers on the neck.

2. Allopreening

Allopreening has been defined by Landsborough Thompson (1964) as preening of another bird, usually of the same species and commonly a mate, often mutual. Just prior to egg-laying, South Island Pied Oystercatchers were often observed roosting close together and indulging in allopreening. Preening was restricted to the feathers of the head, and was performed by both sexes. Neither Black nor Variable Oystercatchers were observed allopreening, but further observation would be required to satisfactorily exclude this activity from their behavioural repertoire.

E. Distraction Display

Distraction displays have been defined by Landsborough Thompson (1964) as "elaborate stereotyped activities performed by a parent bird that tend to concentrate the attention of potential predators on it and away from the nest and young". These displays arise from conflicting motivations; those concerned with parental behaviour involve remaining close to the nest or chicks and defending them on the one hand, and the impulse to escape on the other. Oystercatchers possess elaborate distraction displays as might be expected from the ground nesting habit. As Armstrong (1956) has pointed out, distraction displays are most adaptive for species with relatively inconspicuous nests in vulnerable situations primarily exposed to ground predators. They therefore reach their highest development in ground nesting birds. Distraction displays of New Zealand oystercatchers belong to three categories:

1. injury-feigning;
2. false-brooding; and,
3. false-feeding.

1. Injury-Feigning

Injury-feigning is by far the most prevalent type of distraction display when hard-set eggs or young are threatened. Potential predators are lured away from the brood or clutch by the adults feigning injury. Feigning South Island Pied Oystercatchers lie prostrate on the ground, flapping both wings and calling plaintively. The display becomes even more effective when the birds run with wings extended (the so-called broken wing display) to reveal vivid white markings on the wings and rump (see Plate 4.11). Black and Variable Oystercatchers will also injury-feign when predators are present, but both the intensity and duration of their displays do not approach that of their smaller South Island pied congener. Hall (1959) suggested that the South African Black Oystercatcher (*H. o. moquini*) warranted separate species status from the European Oystercatcher (*H. o. ostralegus*) on the basis of its relatively undeveloped distraction behaviour.

The urge to simulate injury varies with breeding phenology. Prior to and immediately after egg-laying, oystercatchers were never seen to injury-feign. Towards the middle of the incubation period injury-feigning behaviour began to develop, and at hatching distraction displays of this type were invariably used against predators. Similar intensification of distraction displays with advance of incubation was noted for the Killdeer Plover (*Charadrius vociferus*) (Friedmann, 1934).

2. False-brooding

False-brooding is a form of distraction display in which the displaying birds attempt to lure predators away from the nest by brooding at a "false nest-site". All New Zealand races of oystercatcher appear equally adept at this display. False-brooding of oystercatchers has been the source of controversy as to its correct behavioural classification. Tinbergen (1940) considered that false-brooding was a displacement activity, as both birds of a pair, and not only the bird which had been interrupted in brooding, may act thus. Makkink (1942) rejected this explanation and regarded false-brooding as an impulse seeking satisfaction in the absence of an adequate object. Neither view appears to fit the facts as ascertained in this study. Oystercatchers were observed to false-

Plate 4.11

Broken wing distraction display of the South Island Pied Oystercatcher. Note how the wings are extended to reveal the vivid white markings of the alar bars and the rump.

brood when either their clutch was threatened by a predator or when one bird of a pair was reluctant to leave the nest during nest-relief. In either case, by false brooding at successively increasing distances away from the nest, the display served as a lure or distraction display.

3. False-feeding

False-feeding functions as a distraction display when used to lure predators away from the nest (Armstrong, 1947). It consists of probing and sometimes swallowing movements in the absence of food, with each successive 'feeding station' being further away from the nest. False-feeding was performed equally well by both Black and Variable Oystercatchers, but was never recorded for the South Island pied species. The only other record of false-feeding is for the South African Black Oystercatcher (Hall, 1959).

F. Displacement Activities

Displacement activities were defined by Tinbergen (in Landsborough Thompson, 1964) as "movements that, as regards their causation and function, seem to occur out of context; they are in both respects unexpected". Breeding oystercatchers commonly perform two main types of displacement activity other than those already described under different headings:

1. throwing straws; and,
2. the pseudo-sleeping attitude

1. Throwing Straws

This type of displacement activity usually denotes agitation. Straws, small stones, or twigs are picked up between the mandibles and thrown backwards with a violent flick of the head. Both New Zealand species of oystercatcher throw small objects when alarmed. Similar behaviour has been recorded for the Australian Sooty Oystercatcher (*Haematopus fuliginosus*) (Warham, 1955) and the European Oystercatcher (*H. ostralegus*) (Makkink, 1942).

2. The Pseudo-sleeping attitude

The pseudo-sleeping attitude is a displacement posture which can also function as a threat display (Tinbergen, 1951). During territorial fighting, oystercatchers may suddenly cease hostilities and assume this posture. In this posture, the bird stands upright and rotates the head horizontally through 180° before placing the bill under the scapular feathers (see Plate 4.12). This is similar to the true sleeping attitude (see Ch.3.5 A) except that the eyes are never closed, both feet remain on the ground, and the bill is frequently removed from the scapulars. The functioning of the pseudo-sleeping attitude as a threat display is supported by two independent observations. Firstly, the bird assuming this posture frequently followed it with an attack or was itself attacked, and secondly, breeding birds unable to adequately attack their own image in a mirror placed by their nest, responded by adopting the pseudo-sleeping attitude (Edwards et al., 1948).

4.8 THE PRE-EGG STAGE

A. Arrival at the Breeding Area

South Island Pied Oystercatchers begin arriving at their inland breeding areas in July (Heather, 1961). The main peak of arrivals occurs in August, gradually diminishing and ending in late September. In contrast to many other charadriiform species where the male precedes the female by several weeks, both birds of a pair arrive together. The arrival of pairs at the Ashley River study area is shown in Table 4.3.

At this study area the first pair of birds arrived in the first week of August. Most pairs arrived in the fourth week of August, and the last pair arrived by the end of the month. Although a small population such as this is of limited value in depicting general trends, the staggered nature of the arrivals is still apparent.

Black Oystercatchers arrive in their breeding areas in September,

Plate 4.12

Pseudo-sleeping attitude of the European Oystercatcher, functioning here as a threat display to a mirror image. Note how the eye is open and that the bird is standing on both legs. This posture is indistinguishable from that of New Zealand oystercatchers.

(from Edwards et al., 1948)

TABLE 4.3 ARRIVAL OF SOUTH ISLAND PIED OYSTERCATCHERS AT THE ASHLEY RIVER STUDY AREA

Date	No. of pairs sighted	No. of new pairs sighted
27/7/67	0	0
3/8/67	1	1
10/8/67	2	1
17/8/67	7	5
24/8/67	9	2
31/8/67	11	2
7/9/67	11	0
14/9/67	11	0

October and November, the main occupation occurring in October. Variable Oystercatchers follow a similar pattern of arrival, but on the whole arrive later than their southern conspecifer, a peak of arrivals occurring in November.

B. Territories

1. Territory Establishment

At the Ashley River study area, South Island Pied Oystercatchers took up territorial residence on arrival, but did not actively defend the territory during the first week of occupation. Early arrivals spent much of their first week feeding in communal non-territorial feeding areas several kilometres away from the riverbed. Heather (1961) noted that flocks of this species appeared on Southland farmlands and riverbeds, presumably prior to territory establishment. Similarly, at Skokholm Island off southwest Wales, European Oystercatchers formed flocks before taking up their territories (Harris, 1967).

In contrast, Black and Variable Oystercatchers breeding at Jackson Bay defended their territories from the date of occupation and were never seen in communal feeding flocks.

2. Territory Size

As in many other territorial birds, the size of territories occupied by oystercatchers is proportional to nesting density. At the Ashley River study area 11 pairs of South Island pied Oystercatchers nested along 4 km of riverbed, whereas at the Dart River in Southland 87 pairs nested along 14 km (Child, 1967). Ashley territories had a mean area of 0.14 km^2 which is probably double the size of Dart territories (the two rivers have approximately equal nesting habitats/km). The distribution and size of territories at the Ashley River are shown in Fig 4.5. The size of territories here is closely related to nesting density, smaller territories occurring at higher nesting densities and vice versa.

Black and Variable Oystercatchers breeding at Jackson Bay and Farewell Spit maintained slightly larger territories than South Island Pied Oystercatchers. Twelve territories delimited during this study had a mean area of 0.18 km^2. Insufficient data were gathered to allow adequate comparison of territory sizes of Black and Variable Oystercatchers.

3. Retention of Territories

Although colour-banded birds are necessary to conclusively demonstrate tenacity to territories, sufficient reports have accumulated in New Zealand literature to allow some generalisation. Territory retention has been recorded for all mainland races. Soper (1962) noted that two pairs of South Island Pied Oystercatchers previously photographed by him retained the same territories on the Shotover River for four and six years respectively. Similar territorial tenacity was recorded for birds breeding at inland Southland localities (Heather, 1962). At the Ashley River study area, nine of the 11 pairs occupying territories in 1967 re-occupied the same territories in 1968. The two territories not re-occupied were subject to flood erosion and were thus unsuitable for nesting.

Variable Oystercatchers probably retain territories from year to year. A pair in smudgy plumage at Kaikoura Peninsula have

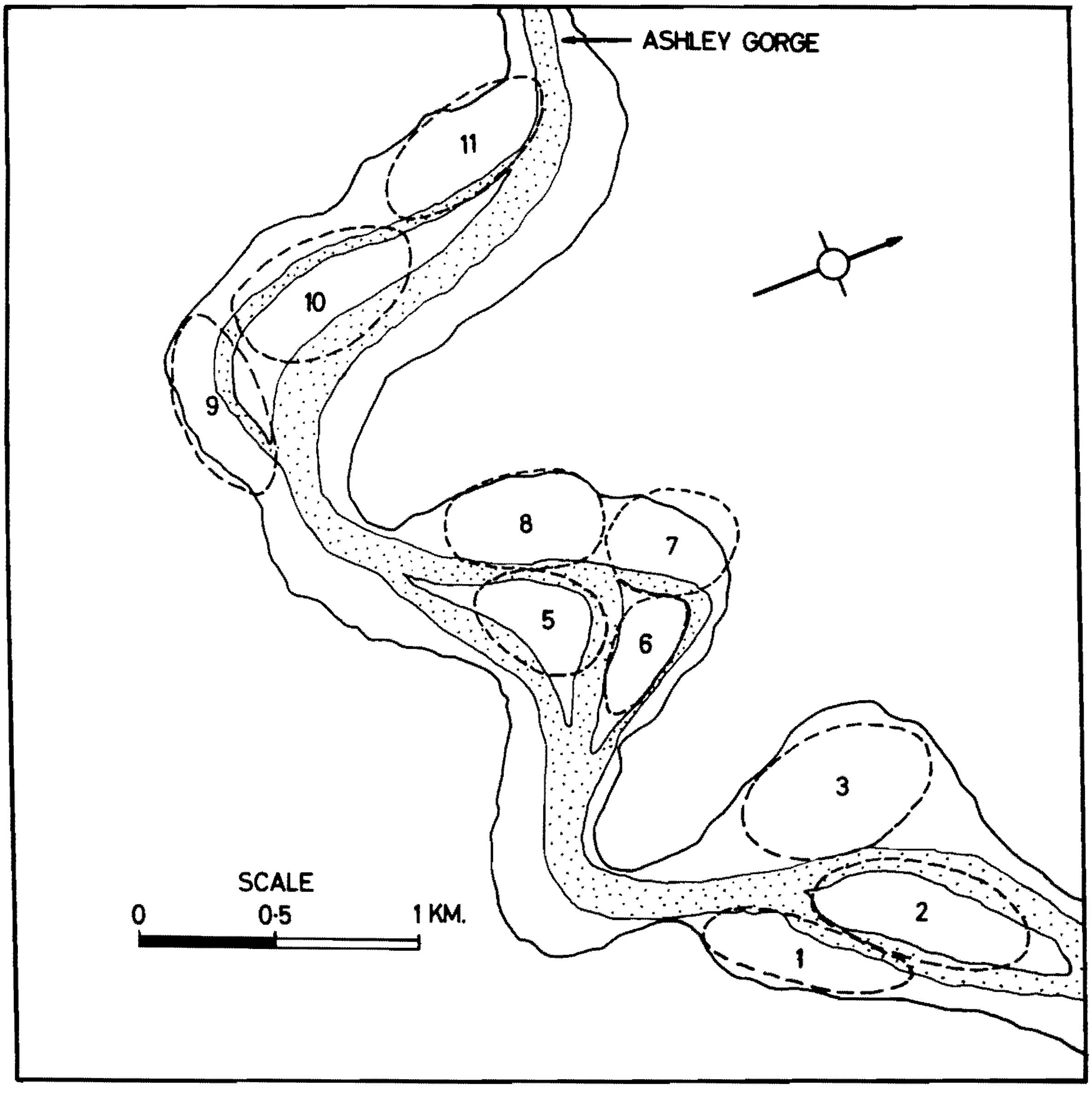

ASHLEY GORGE
11
10
9
8
7
5
6
3
2
1
SCALE
0
0·5
1 KM.

Figure 4.5

The distribution and size of territories of South Island Pied Oystercatcher breeding at the Ashley River study area.

maintained the same territory for six successive seasons. Moon (1967) described a pair which retained the same territory for nine years. Black Oystercatchers also show similar territorial tenacity (Soper, 1966).

In general then, New Zealand oystercatchers possess a well developed tenacity to territories. Establishment of new territories is likely to occur when floods or storms render existing territories unsuitable for nesting, or when birds are breeding for the first time.

C. Construction of Nest-Scrapes

At the Ashley River study area, South Island Pied Oystercatchers began making nest-scrapes approximately two weeks after occupying their territories and two weeks before laying. A maximum of 10 nest-scrapes were recorded in one territory, four being constructed within a day of laying. The nest-scrape in which eggs were laid was always constructed less than 24 hr before the commencement of egg-laying.

Black and Variable Oystercatchers at Jackson Bay also made several "trial" or "play" nest-scrapes prior to laying (see Plate 4.13).

New Zealand oystercatchers use identical methods in constructing nest-scrapes. The breast is pressed against the substrate, the posterior end of the body elevated, and the legs extended backwards at an angle to give downward thrust. This action is repeated several times in different directions until a suitable depression is pressed in the substrate.

D. Nest-Scrape Dimensions

The form of the nest-scrape was determined by two measurements, greatest diameter and depth. The dimensions of the nest-scrapes of New Zealand oystercatchers are shown in Table 4.4.

The mean dimensions of the nest scrapes of Black and Variable Oystercatchers are obviously very similar. There is no significant difference between the diameters of nest-scrapes of South Island

Plate 4.13

"Trial" or "play" nest-scrapes of the Variable Oystercatcher at Jackson Bay.

TABLE 4.4 DIMENSIONS OF NEST-SCRAPES OF NEW ZEALAND OYSTERCATCHERS

Race	Locality	Mean Diameter (cm)	Mean Depth (cm)	No. of measurements
South Island Pied Oystercatcher	Ashley River	13.9	5.1	13
Black Oystercatcher	Jackson Bay & Farewell Spit	15.2	7.6	10
Variable Oystercatcher	Jackson Bay & Kaikoura	15.0	7.1	6

Pied Oystercatchers on the one hand, and black and variable birds on the other ($t_{21} = 1.95$, $0.1 > p > 0.05$, and $t_{17} = 1.81$, $0.1 > p > 0.05$ respectively). However, the nest-scrapes of Black and Variable Oystercatchers are significantly deeper than those of their smaller pied congener ($t_{21} = 3.78$, $0.01 > p > 0.001$, and $t_{17} = 3.21$, $0.01 > p > 0.001$). This difference in depth probably results from the use of softer substrates (beach sands) by black and variable birds.

E. Nest Materials

Nest-scrapes are rarely lined with nesting materials. South Island Pied Oystercatchers nesting in fields occasionally line their nest-scrapes with grasses (Bond, 1965). Twigs and small stones often serve as "decorations" in and about the nest; a nest at the Ashley River study area contained 150 g of small pebbles and 8 g of faecal pellets of the Hare (Lepus europaeus). One Black Oystercatcher nest was unusually lavish in its decoration, being surrounded by driftwood and shells of the bivalve Spisula aequilateralis which had been collected from the flotsam line (see Plate 4.14). Variable Oystercatchers frequently construct nest-scrapes near washed-up pieces of kelp (Durvillea antarctica); choice of such sites might aid in detracting from or concealing the nest-scrape.

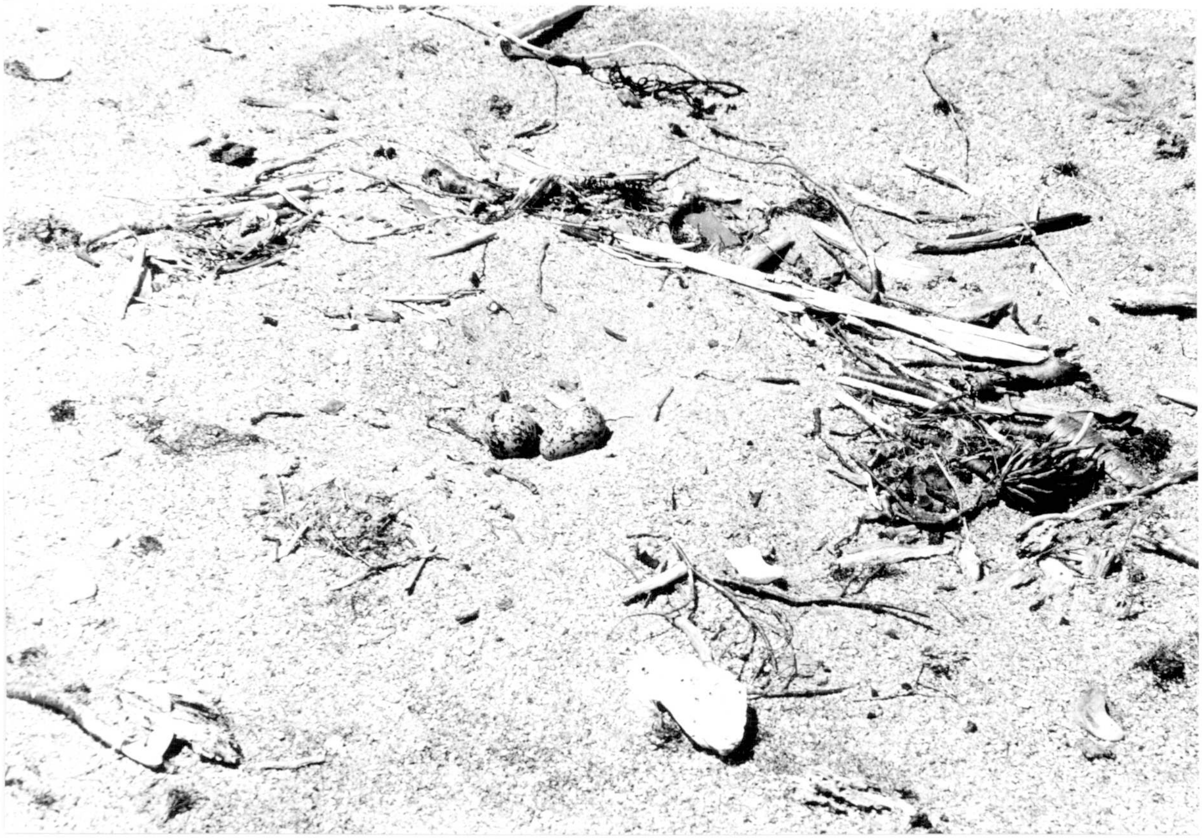


Plate 4.14

Nest-scrape and clutch of the Black Oystercatcher at Jackson Bay. Note the lavish "decoration"; driftwood and shells were carried to the scrape from the flotsam line approximately 50 m distant.

F. Nest-Sites

Major species differences in nest-site preference occur in coastal and inland breeding habitats (see Table 4.5).

TABLE 4.5 NEST-SITE PREFERENCES OF NEW ZEALAND OYSTERCATCHERS

Race	River-bed	Tussock	Arable land	Lake & Lagoon	Sandy beach	Shingle beach	Rocky Platform
South Island Pied Oystercatcher	145 (67.9%)	13 (5.9%)	41 (19.2%)	15 (7.0%)	-	-	-
Black Oystercatcher	-	-	-	1 (1.3%)	56 (72.2%)	14 (17.8%)	7 (8.7%)
Variable Oystercatcher	-	-	-	-	47 (87.2%)	6 (11.1%)	1 (1.7%)

Since 1950 South Island Pied Oystercatchers have begun to nest away from riverbeds; moving particularly onto arable land and high country tussock. This expansion has presumably arisen as a result of the population irruption since 1941 which increased nesting densities. Black and Variable Oystercatchers have similar nest-site preferences, but the latter show a stronger preference for sandy nesting areas, and are rarely found breeding on rocky platforms.

4.9 THE EGG STAGE

A. Laying Dates

Laying date histograms for each mainland race of oystercatcher are shown in Fig 4.6. The separation in the laying seasons of the two species is clearly evident. South Island Pied Oystercatchers begin laying in the second week of August, reach a peak of egg production in September, and extend their laying season to the first week in December. Repeat clutches are laid from September onwards and probably account for many of the layings which occur in November

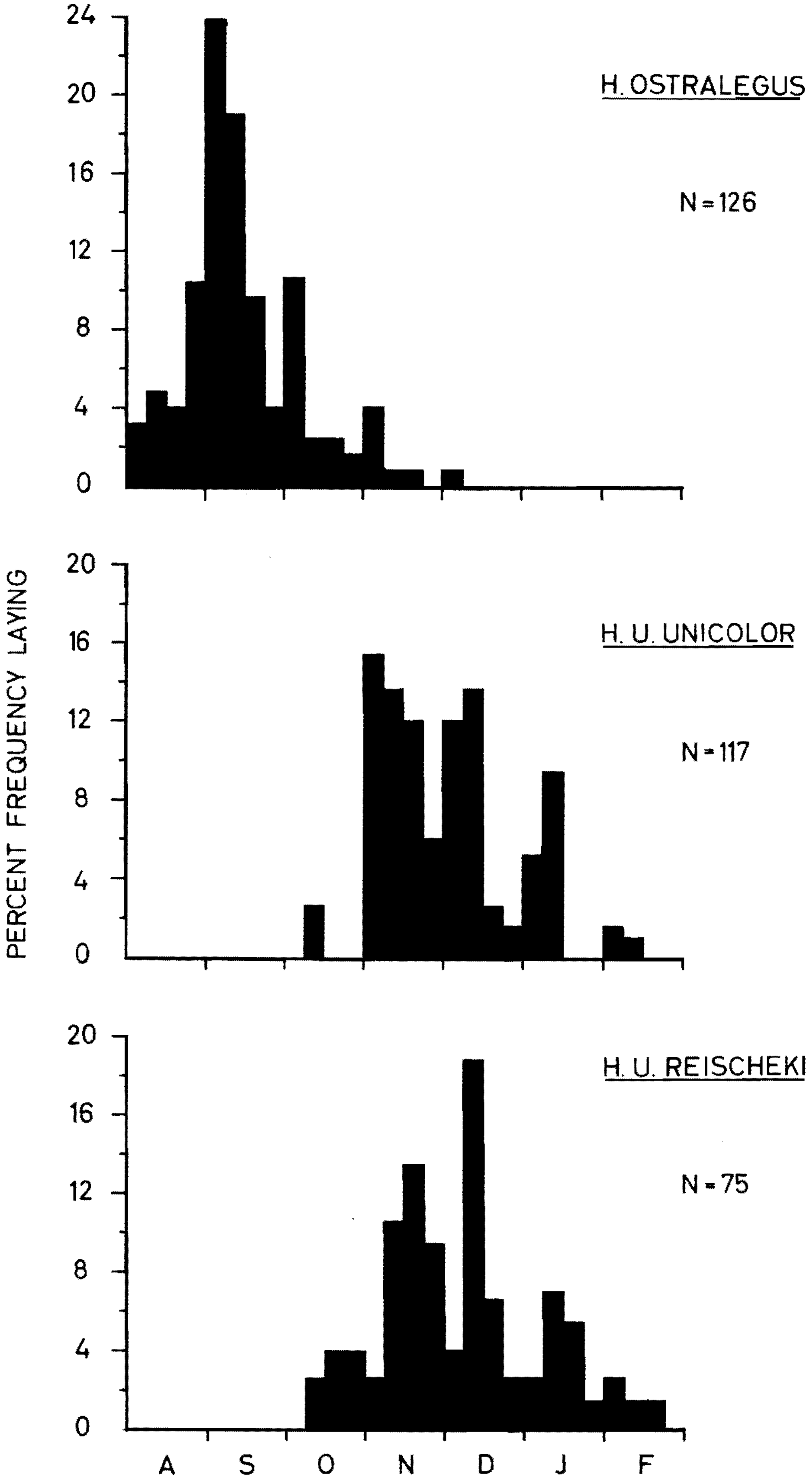

PERCENT FREQUENCY LAYING
H. OSTRALEGUS
N = 126
H. U. UNICOLOR
N = 117
H. U. REISCHEKI
N = 75
24
20
16
12
8
4
0
A
S
O
N
D
J
F

Figure 4.6

Laying date histograms of New Zealand oystercatchers.

and December.

Black and Variable Oystercatchers both have similar laying seasons which are distinct from that of their smaller southern congener. Laying begins in the second week of October and extends through to the first week of February. Most eggs are laid in the period November to December inclusive. Layings in January and February probably contain a number of repeat clutches.

B. Time of Laying and Laying Interval

The time at which eggs are laid differs with the two species. South Island Pied Oystercatchers at the Ashley River study area laid their eggs in the early morning between 5 a.m. and 10 a.m. Black and Variable Oystercatchers at Jackson Bay laid eggs chiefly in the afternoon. Moon (1967) also recorded Variable Oystercatchers laying in the afternoon. This interspecific difference in laying time is similar to that noted by Skutch (1925) for 40 species of Central American land birds, where each species was found to have its own time of laying. In addition he found that birds laying near sunrise were subject to less variation in the hour of laying than those which laid later in the day.

The interval between the laying of successive eggs of a clutch is the same for both New Zealand species of oystercatcher and is normally 48 hr. Extremes of 24 hr and 72 hr have been recorded for the South Island Pied Oystercatcher (Soper, 1957, 1962). Similar variation was noted for the conspecific European Oystercatcher, but again the normal laying interval was 48 hr (Keighley & Buxton, 1948). Black and Variable Oystercatchers at Jackson Bay most commonly laid their eggs at 48 hr intervals, with extremes of 36 hr and 52 hr.

C. Clutch-Size

Oystercatchers are determinate layers as they lay a set number of eggs per clutch. When eggs from an incomplete clutch are lost, only the remaining eggs in that clutch are laid and not a complete new clutch. For this reason clutch-size data are often subject to error and should be treated with reservation. Only completed clutches have been included, and no distinction is made between first and repeat clutches.

The frequency distribution of clutch-sizes of New Zealand oystercatchers are shown in Table 4.6.

TABLE 4.6 FREQUENCY DISTRIBUTION OF CLUTCH SIZES OF NEW ZEALAND OYSTERCATCHERS

Race	No. of clutches analysed	Clutch Size				Mean Clutch size
		C/1	C/2	C/3	C/4	
South Island Pied Oystercatcher	55	5 (9.2%)	31 (56.3%)	17 (30.9%)	2 (3.7%)	2.3
Black Oystercatcher	50	5 (10.0%)	24 (49.0%)	18 (36.0%)	0	2.3
Variable Oystercatcher	35	4 (11.4%)	21 (60.0%)	10 (28.6%)	0	2.2

The frequency distributions and percentage composition of clutch sizes are similar for each race. Two egg clutches are by far the most common and one egg clutches are relatively rare. Four egg clutches are the rarest clutch size, being recorded only for South Island Pied Oystercatchers. Mean clutch sizes of the races are remarkably similar, indicating identical fecundities.

During this study repeat clutches were found only for South Island Pied Oystercatchers, although repeat layings have been recorded for black and variable birds (Sibson & McKenzie, 1948). All five repeat clutches of the former species were laid within two weeks of the loss of the first clutch. Each was smaller than the initial clutch; one three egg clutch was replaced with a two egg clutch, and four two egg clutches were replaced with one one egg clutch. Reduction in clutch size with repeated layings is not an invariable result however, as Jackson (1964) found a repeat clutch of two eggs replacing a first clutch of the same size.

D. Seasonal Variation in Clutch Size

Mean clutch sizes of New Zealand oystercatchers decrease as the breeding season progresses (see Table 4.7).

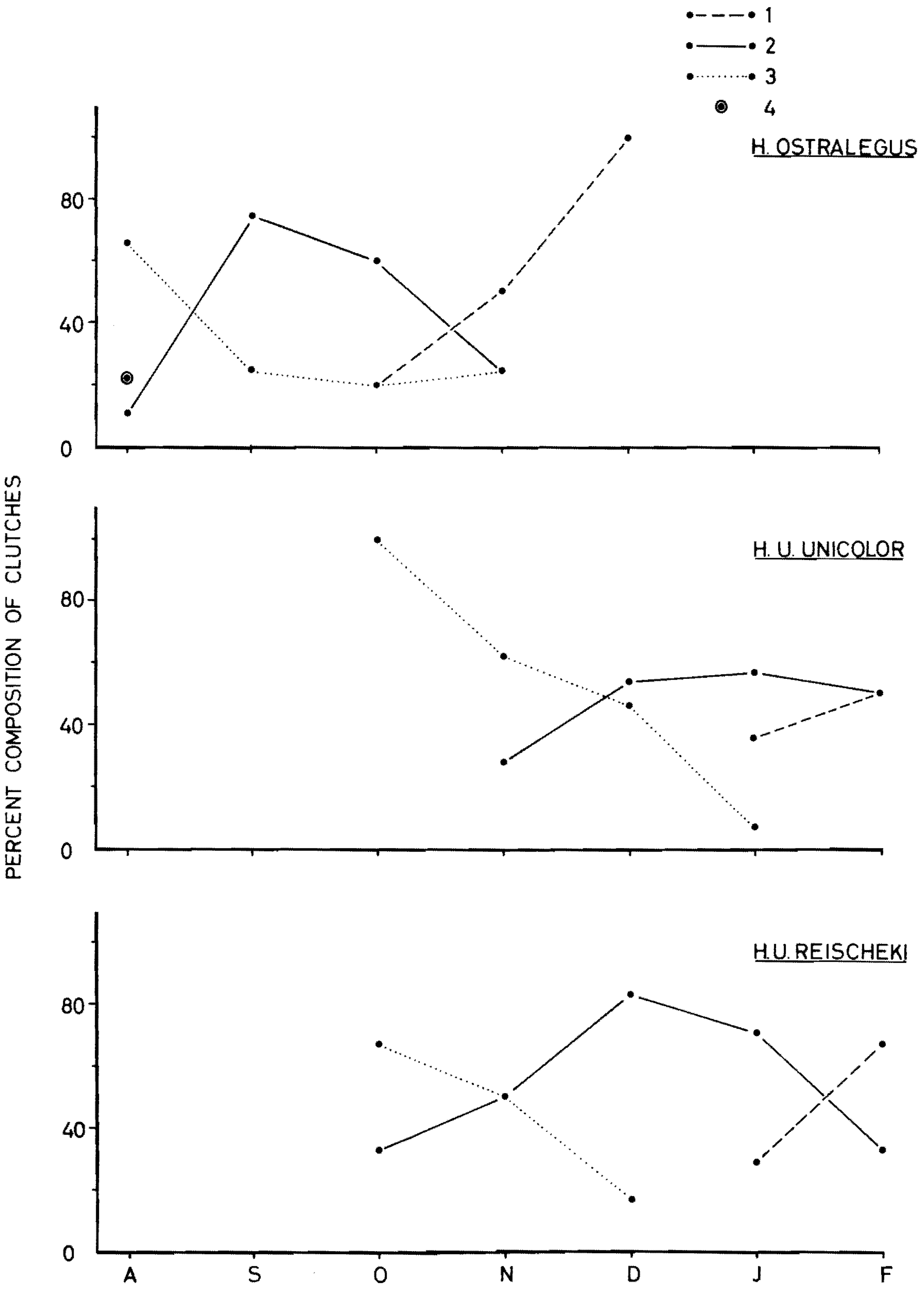
TABLE 4.7 SEASONAL VARIATION IN CLUTCH SIZE OF NEW ZEALAND OYSTERCATCHERS

Race	Mean Monthly Clutch Sizes						
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
South Island Pied Oystercatcher	3.11	2.26	2.00	1.75	1.00	-	-
Black Oystercatcher	-	-	3.00	2.62	2.46	1.72	1.00
Variable Oystercatcher	-	-	2.66	2.55	2.17	1.72	1.33

Clutches of each size class were also subject to seasonal variation (see Fig 4.7). Three and four egg clutches of each race are restricted to the first half of the breeding season, while one egg clutches are common in the second half. Two egg clutches are laid throughout the season, but are most abundant in the peak egg-laying months. Similar seasonal variation in clutch size was noted for the European Oystercatcher (Harris, 1967).

E. Discussion

Lack (1968) considered that through natural selection each nidifugous species, like each nidicolous one, must have evolved an optimum clutch size which on average results in its leaving most descendants. He further suggested that in nidifugous species the limit to the clutch size was not set by the food which the parents could bring to the brood. Hence the critical factor was probably the average amount of food available to the laying hen, modified by the size of the egg.


1
2
3
4
H. OSTRALEGUS
H. U. UNICOLOR
H.U. REISCHEKI
PERCENT COMPOSITION OF CLUTCHES
80
40
0
80
40
0
80
40
0
A
S
O
N
D
J
F

<u>Figure 4.7</u>

Seasonal variation in clutch size of New Zealand oystercatchers.

Seasonal decline in clutch size has been shown to be an adaptation to seasonal decline of food availability (usually to the brood) (Lack, 1954). However, in nidifugous species, seasonal variation in clutch size is probably correlated with variation in food availability to the laying female. Harris (1967) suggested that European Oystercatchers lay larger clutches as they grow older; he noted a seasonal decline in clutch size, which was probably due to older birds breeding earlier in the season.

Lack (1947) has pointed out that birds breeding for the first time are probably less efficient at food gathering (whether for themselves or for their broods), and appear to adjust to it by laying smaller clutches. Hence the seasonal decline in clutch size of New Zealand oystercatchers is probably due to older birds being more efficient feeders, and therefore coming into breeding condition in advance of first year breeders. The greater breeding success of oystercatchers breeding early in the season (Harris, 1967) would also appear to be a consequence of more experienced birds breeding first.

F. Egg Dimensions and Weight

Dimensions of eggs for each mainland race of oystercatcher are shown in Table 4.8. For each egg the length and greatest diameter were measured.

TABLE 4.8 DIMENSIONS OF EGGS OF NEW ZEALAND OYSTERCATCHERS

Race	Egg Dimensions (mm)				No. of eggs
	Mean Length	S.D.	Mean Breadth	S.D.	measured
South Island Pied Oystercatcher	55.8	2.1	38.6	1.0	22
Black Oystercatcher	58.6	2.0	40.8	3.1	26
Variable Oystercatcher	58.7	1.7	41.2	0.9	10

Eggs of both Black and Variable Oystercatchers are extremely similar in size, differences in the mean length and breadth being statistically insignificant (Length : $t_{34} = 0.16$, $p > 0.9$; Breadth : $t_{34} = 0.47$, $0.7 > p > 0.6$). South Island Pied Oystercatchers lay smaller eggs than the aforementioned species, with significant differences occurring in length ($t_{46} = 4.61$, $p < 0.001$; $t_{30} = 3.82$, $p < 0.001$) and breadth ($t_{46} = 3.16$, $0.01 > p > 0.001$; $t_{30} = 6.62$, $p < 0.001$).

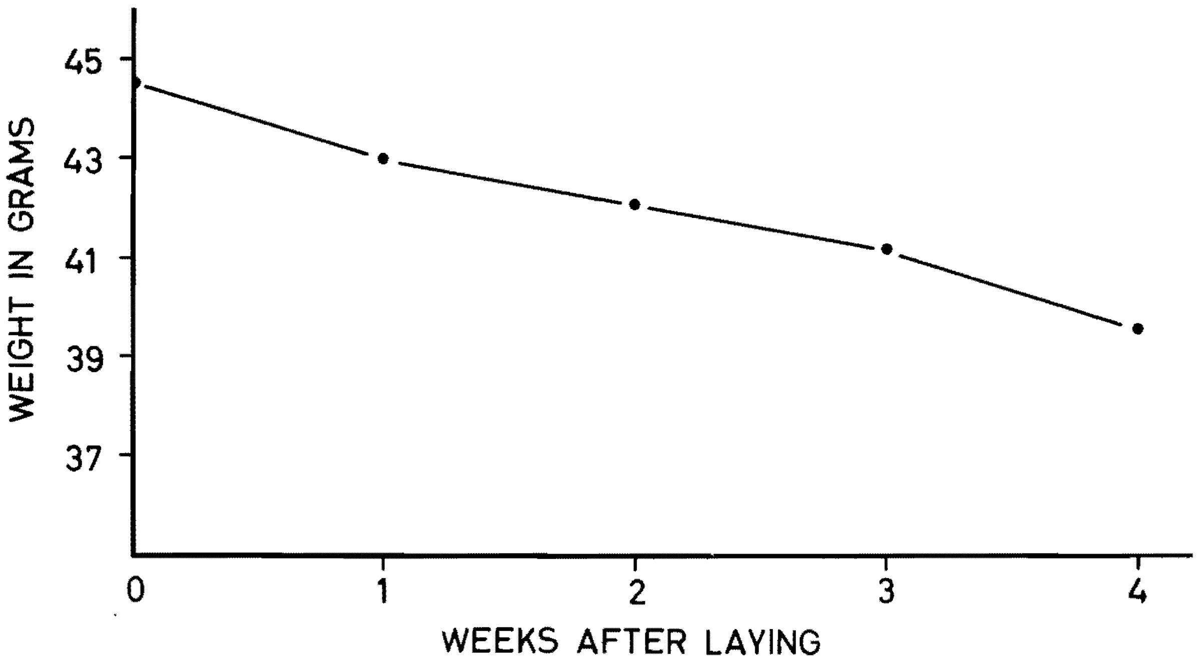
Commensurate with the species differences in the length and breadth of the eggs differences occur in the weight of freshly laid eggs (see Table 4.9).

TABLE 4.9 WEIGHTS OF EGGS OF NEW ZEALAND OYSTERCATCHERS

Race	Mean Egg Wt (g)	S.D.	No.of eggs weighed
South Island Pied Oystercatcher	43.1	2.2	18
Black Oystercatcher	48.3	1.8	14
Variable Oystercatcher	48.1	1.7	9

Black and Variable Oystercatchers lay eggs of similar mean weight, but the eggs of South Island Pied Oystercatchers are significantly lighter ($t = 9.9$, $p < 0.001$; and $t = 9.2$, $p < 0.001$ respectively).

The comparison of egg weights of different races must be based only on data gathered for freshly laid eggs as egg weights decline markedly with increased incubation (see Fig 4.8). Although data were gathered only for the eggs of the South Island Pied Oystercatchers, similar trends could be expected for black and variable birds. The loss in weight of eggs during incubation results from the conversion of food into energy and the loss of water vapour through the porous shell (Harris, 1964).



WEIGHT IN GRAMS
45
43
41
39
37
0
1
2
3
4
WEEKS AFTER LAYING

Figure 4.8

Loss of weight of eggs during incubation. Data for South Island Pied Oystercatchers only.

G. Egg Colour

Eggs of New Zealand oystercatchers vary in colour, but the variation is relatively restricted. Colours of eggs vary as much within a species as between different species. Typical egg colours for each New Zealand race are shown in Plate 4.15

The greatest variation in egg colour occurs in the ground colours of the shell. With reference to Ridgway's Colour Standard (1912), ground colours range between yellowish stone and ochreous. Ground colours of the eggs of South Island Pied Oystercatchers at the Ashley River study area seemed to vary with the colour of the substrate in which nest-scrapes were situated. Eggs laid in light gray sand nest-scrapes had a pale mustard ground colour, whereas eggs laid in nest-scrapes in darker river gravel were olive.

Superficial markings on the eggs occur as irregular blotches and streaks. They are distributed all over the shell, but tend to be slightly more concentrated towards the larger end of the egg. The markings vary in colour from rufous brown to sepia black. The nature and distribution of these markings afford the egg protective colouration by breaking their regular outline (Cott, 1940).

The general similarity in egg colour of New Zealand species of oystercatcher was noted by Potts (1885). He also noted that the colours of New Zealand eggs were virtually indistinguishable from those of the European Oystercatcher. The conservative variation in the colours of oystercatcher eggs as noted by Bent (1929) is undoubtedly due to their role in protective colouration. Since oystercatchers nest in similar habitats throughout their range, the eggs are of necessity similar in colour.

H. Incubation and Hatching

1. Incubation spells

Incubation may be defined as the process by which heat necessary for embryonic development is applied to the egg after it is laid (Beer, in Landsborough Thompson, 1964). Oystercatchers incubate

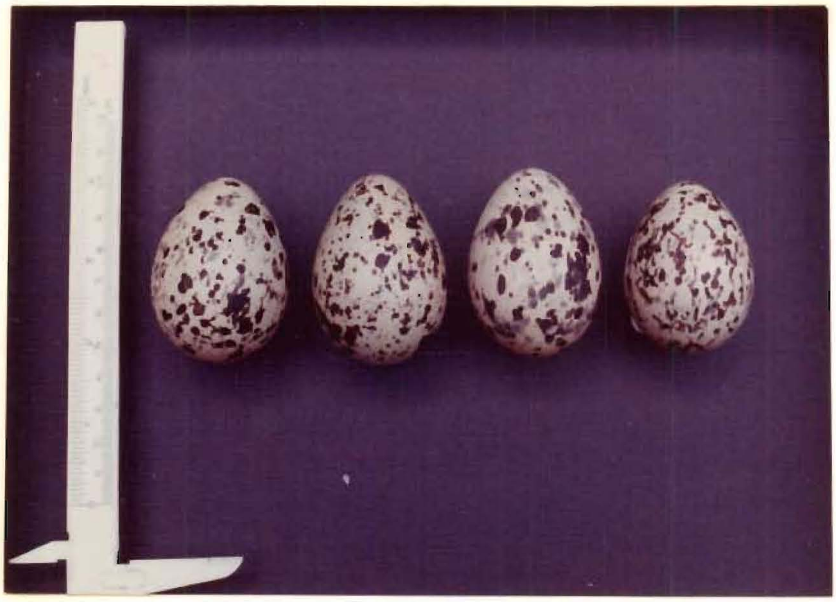


Plate 4.15

Eggs of New Zealand Oystercatchers. Key to eggs (left to right): South Island Pied Oystercatcher, Black Oystercatcher, Variable Oystercatcher, Chatham Island Oystercatcher.

Plate 4.16

South Island Pied Oystercatcher turning eggs prior to resuming incubation.

by bringing their brood patches in contact with the eggs. At nest-relief, the relieving bird usually turns the egg with its bill (see Plate 4.16). Before sitting on the eggs the bird lowers the feathers surrounding the brood patch to expose the vascularised surface (see Plate 4.17). Settling movements include shuffling with the wings, probably to bring the eggs in closer contact with the brood patch (Beer, 1961).

Incubation spells, the time spent incubating between successive nest reliefs, are of unequal length for each sex. Females carry out the major portion of incubation, usually sitting for 2 hr and sometimes as long as 4 to 5 hr. Males perform shorter incubation spells, frequently sitting for only 1 hr. Each New Zealand race has similar incubation spells and associated sex differences in incubating behaviour. The dominant role of the female in incubation has also been noted for the European Oystercatcher (Bent, 1929).

2. Nest Relief

New Zealand races of oystercatcher display identical methods of nest relief. The change-over between incubation spells is usually accomplished by the sitting bird leaving the nest on the approach of its mate (see Plate 4.18). When the eggs are near hatching the sitting bird is often reluctant to leave the nest-scrape. On approach of the relieving bird, its sitting mate may pipe loudly before rushing off the nest to attack the approaching bird. Occasionally the sitting bird has to be prised off the nest by its mate. In extreme cases the relieving bird will attempt to entice the sitting bird off the nest by injury-feigning. Warham (1955) noted Australian Sooty Oystercatchers injury-feigning to effect nest relief.

3. Incubation period

The incubation period was defined by Heinroth (1922) as the time from the laying of the last egg of a clutch to the hatching of that egg. Oystercatchers begin incubation when the clutch is completed, except in the case of four egg clutches where incubation

Plate 4.17

South Island Pied Oystercatcher lowering brood patch feathers before settling on eggs.

Plate 4.18

Nest relief of Black Oystercatchers at Jackson Bay.

begins with the laying of the third egg (Harris, 1967).

During this study no four egg clutches were found (although they have been recorded in O.S.N.Z. nest record cards), so that incubation always began with the completion of the clutch. The mean incubation periods of New Zealand oystercatchers are shown in Table 4.10.

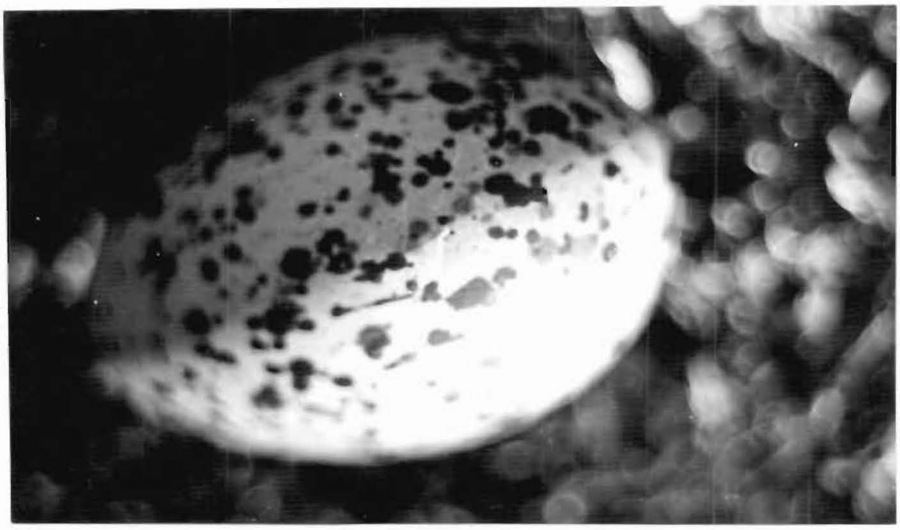
TABLE 4.10 INCUBATION PERIODS OF NEW ZEALAND OYSTERCATCHERS

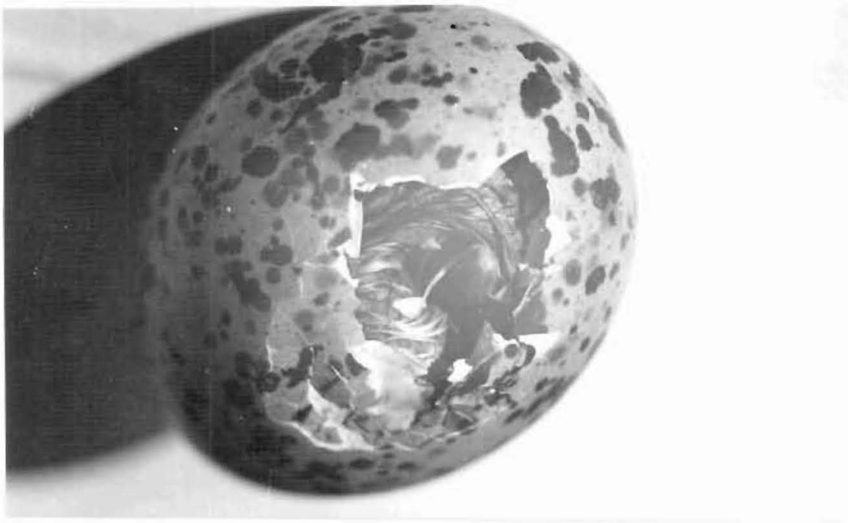
Race	Mean incubation period (Days)	S.D.	Range	Sample Size
South Island Pied Oystercatcher	27.5	3.7	24-30	12
Black Oystercatcher	28.1	5.0	25-32	8
Variable Oystercatcher	28.7	2.6	27-31	7

Racial differences in mean incubation period are not statistically significant (Black v. S.I.P.O., $t_{18} = 0.62$, $0.6 > p > 0.5$; Variable v. S.I.P.O., $t_{17} = 1.26$, $0.3 > p > 0.2$; Black v. Variable, $t_{13} = 0.59$, $0.6 > p > 0.5$).

4. Hatching

Hatching is the period during which the chick frees itself from the egg. Stonehouse (1962) has shown that hatching begins well before the appearance of any external signs on the egg shell. The hatching of oystercatcher eggs first becomes externally apparent when the egg tooth of the chick creates fracture lines near the broad end of the egg (see Plate 4.19). Gradually the chick hammers a circular hole at a point on one of the fracture lines, puncturing the shell membranes in the process (see Plate 4.20). The hole is expanded until a circumpolar crack develops about the large end of the egg, at which this part of the shell falls away allowing the chick to escape (see Plate 4.21).





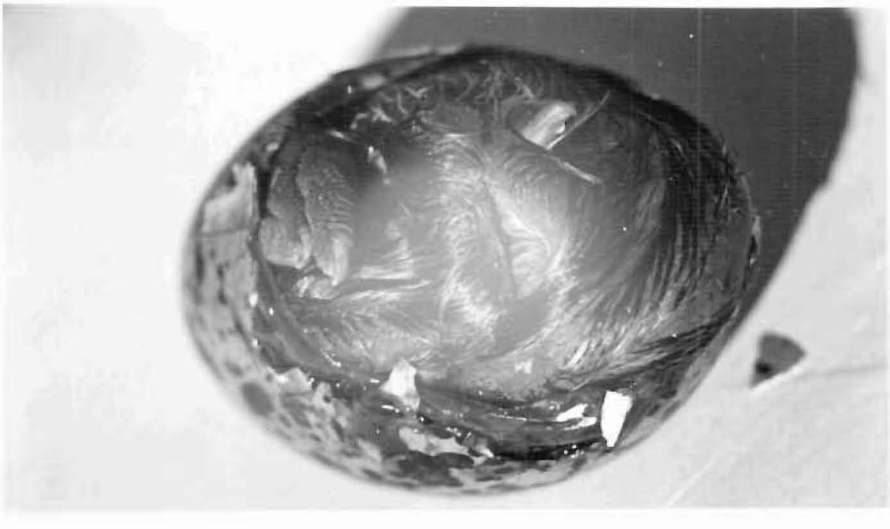


Plate 4.19

Initial stage of hatching, fracture line appearing on the broad end of the egg.

Plate 4.20

Pipped egg with hole hammered along a fracture line.

Plate 4.21

Egg with broad end of shell removed prior to the escape of the chick.

From the first outward sign of pipping, eggs of New Zealand oystercatchers each take approximately 36 hr to hatch, although this time is subject to considerable variation. Soper (1958) noted a two egg clutch of the South Island Pied Oystercatcher which took 6 days to hatch.

The hatching period, defined by Ward (1965) as the time within which all eggs in a clutch hatch, is shown in Table 4.11 for South Island Pied Oystercatchers breeding at the Ashley River study area.

TABLE 4.11 HATCHING PERIOD OF SOUTH ISLAND PIED OYSTERCATCHERS IN RELATION TO CLUTCH SIZE

Clutch Size	No. of clutches examined	Mean Hatching Period (hr)
C/1	3	36.5
C/2	6	49.5
C/3	4	60.0

Note: Time taken to the nearest half hour.

Hatching periods increase with clutch size, but not in a linear manner. Although eggs were laid 48 hr apart they hatched at much closer intervals. This is due in part to incubation commencing at the completion of the clutch so that each egg had a similar incubation period. Oystercatcher chicks begin calling loudly from within the egg two to three days prior to hatching. This may help to partially synchronise hatching as Vince (1964) has shown that eggs of the Bobwhite Quail (Colinus virginianus) that are a day or two behind others in development still hatch on the same day due to auditory stimulation from more advanced young. Nevertheless hatching is still somewhat asynchronous (see Plate 4.22). Hatching periods of Black and Variable Oystercatchers were not recorded, but they are probably of the same order. Hatching of eggs of this species is also asynchronous (Cunningham, 1951).

Plate 4.22

Asynchronous hatching of a clutch of the South Island Pied Oystercatcher. The chick on the right is dry, the one in the centre is still wet after hatching, and the egg is just pipping.

4.10 THE CHICK PHASE

A. Chick Development

Chick development can be conveniently described in weekly intervals from hatching. Unless otherwise stated, descriptions refer only to chicks of the South Island Pied Oystercatcher.

1. First week

Newly hatched chicks are brooded continuously for the first 36 to 48 hr, during which time the down dries out and the pendant yolk sac is resorbed (see Plate 4.23). At this time the upper mandible is decurved and distinctly plover-like in appearance (see Plate 4.24). The calcareous egg-tooth is clearly visible on the dorsal tip of the upper mandible. Natal down of South Island Pied Oystercatcher chicks has a buffy grey ground colour on the head, foreneck, and dorsal aspect of the trunk. Darker blackish down occurs in a loral and postocular stripe, and in a medium crown stripe. Two broad distinct stripes continue along the back and converge on the rump. Down of the underparts is white.

Chicks of Black and Variable Oystercatchers have very similar natal down, which differs from that of their South Island pied congener. The basic ground colour is light grey. Darker markings occur all over the back, not being localised into stripes (see Plate 4.25).

Chicks of all races at this age have dark brown bills, brown irides, and grey legs.

2. Second week

The egg-tooth drops off the bill between the seventh and eleventh days. Juvenile plumage begins to develop on the flank and underparts, the primary wing feathers piercing the skin though they are not visivle unless the down is parted. Flesh colours begin to change at the end of the second week, the legs and mandibles developing yellow undertones (see Plate 4.26).

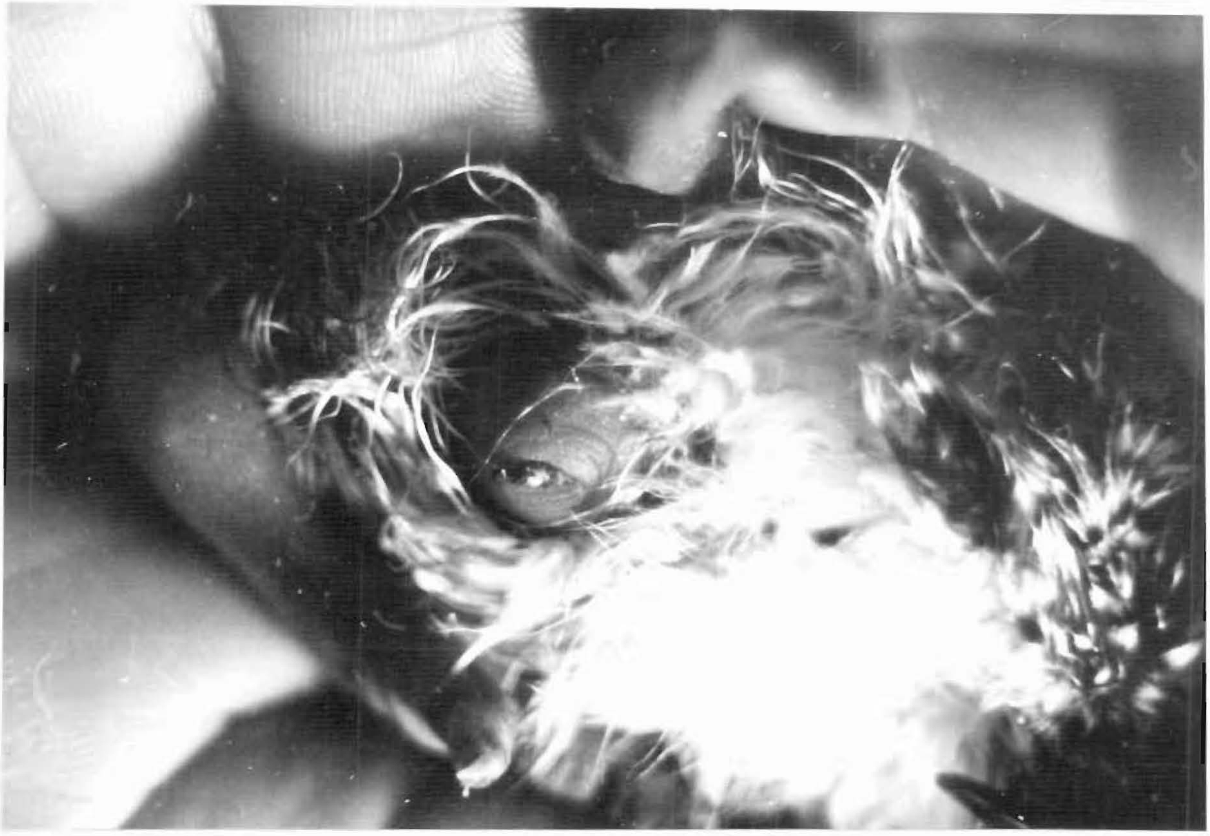


Plate 4.23

Ventral view of a newly hatched South Island Pied Oystercatcher chick showing the yolk sac which is resorbed during the first day of life.

Plate 4.24

A one week old three chick brood of the South Island Pied Oystercatcher. Note that the upper mandible of the chick on the right is distinctly decurved at the tip, and that the chick on the left has already lost its egg-tooth.

Plate 4.25

Young downy chick of the Variable Oystercatcher (after Moon, 1967).

Plate 4.26

Two week old chick of the South Island Pied Oystercatcher.

3. Third week

The general body cover remains buffy grey, but the darker juvenile plumage begins to appear. Feather shafts of the primaries elongate considerably and the vanes begin erupting from the shafts. Much of the down moults, especially on the dorsal aspect of the chick, leaving the feather shafts exposed (see Plate 4.27).

4. Fourth week

The chick's fourth week of life is characterised by the proliferation of the juvenile plumage, with primaries, secondaries, secondary coverts, scapulars, rectrices, auriculars, and feathers of the pileum appearing. The alar bars on the wing become apparent as white markings on the secondaries. Both mandibles become orange over their proximal portions, with only the distal tip remaining dusky (see Plate 4.28).

5. Fifth week

During the fifth week the flight feathers lengthen rapidly, the down wears off the tips of the body feathers, and the juvenile plumage becomes virtually complete except in small areas on the inner sides of the thighs, on the back of the neck, and under the chin. The appearance of a bright yellow eye ring identifies chicks of this age. Of the flesh colours, only the legs change from the four week condition, taking on a pinkish hue (see Plate 4.29).

6. Sixth week

The juvenile plumage becomes fully developed during the sixth week as the chick completes fledging. Feathers of the mantle, the scapulars, and the upper wing coverts are all tipped with ochreous buff. Flesh colours are similar to those of first winter juveniles with the exception of the eye ring which is still yellow rather than orange (see Plate 4.30).

B. Chick Growth

Growth of chicks can be considered from two standpoints:

Plate 4.27

Three week old chick of the South Island Pied Oystercatcher.

Plate 4.28

Four week old chick of the South Island Pied Oystercatcher.

Plate 4.29

Five week old chick of the South Island Pied Oystercatcher.

Plate 4.30

Six week old chick of the South Island Pied Oystercatcher.

1. changes in weight with age; and,
2. changes in body dimensions i.e. standard measurements.

Each of the above parameters is discussed separately below. Growth studies were made only on chicks of the South Island Pied Oystercatcher as time did not permit interspecific comparison.

1. Growth depicted by weight measurements

Hatching weights of 21 chicks ranged from 31 g to 40 g, with a mean of 36.6 g. For the first week after hatching growth is relatively slow, but between the second and fifth weeks weights increase rapidly until a peak is reached at the end of the sixth week. At approximately this time the chicks begin to fly, and body-weights decline slightly due to heavy energy expenditure associated with initial attempts at flight. Weights of six-week old chicks range from 407 g to 441 g, with a mean of 423 g.

Chick growth rates vary with brood-size and season. Differential weight gains occur in broods of one, two, and three chicks (see Fig 4.9). Growth rates are maximal in broods of two chicks where parents are able to keep up with the food demands of their brood. Three chick broods are characterised by differential weight gains of chicks within the brood. Growth rates here are markedly affected by hatching asynchrony. The oldest chick in the brood, having hatched 12 to 24 hr in advance of the second one, is first fed approximately 24 hr before its nearest brood-mate. The second chick has a similar advantage over the third chick, and maintains it throughout the entire chick period (see Fig 4.9). Differences in body-weight at hatching are accentuated during the chick stage, presumably as a result of competition for food. Since food-begging behaviour develops in the third week of life, the oldest chick probably begs more strongly than its brood-mates, obtains more food, and thus grows faster. The decreased growth rates of the second and third chicks probably result from their receiving disproportionately smaller amounts of food. Active competition for food between brood-mates of European Oystercatchers commences in their first week (Dewar, 1920). Older chicks threaten each other (Lind, 1965) and

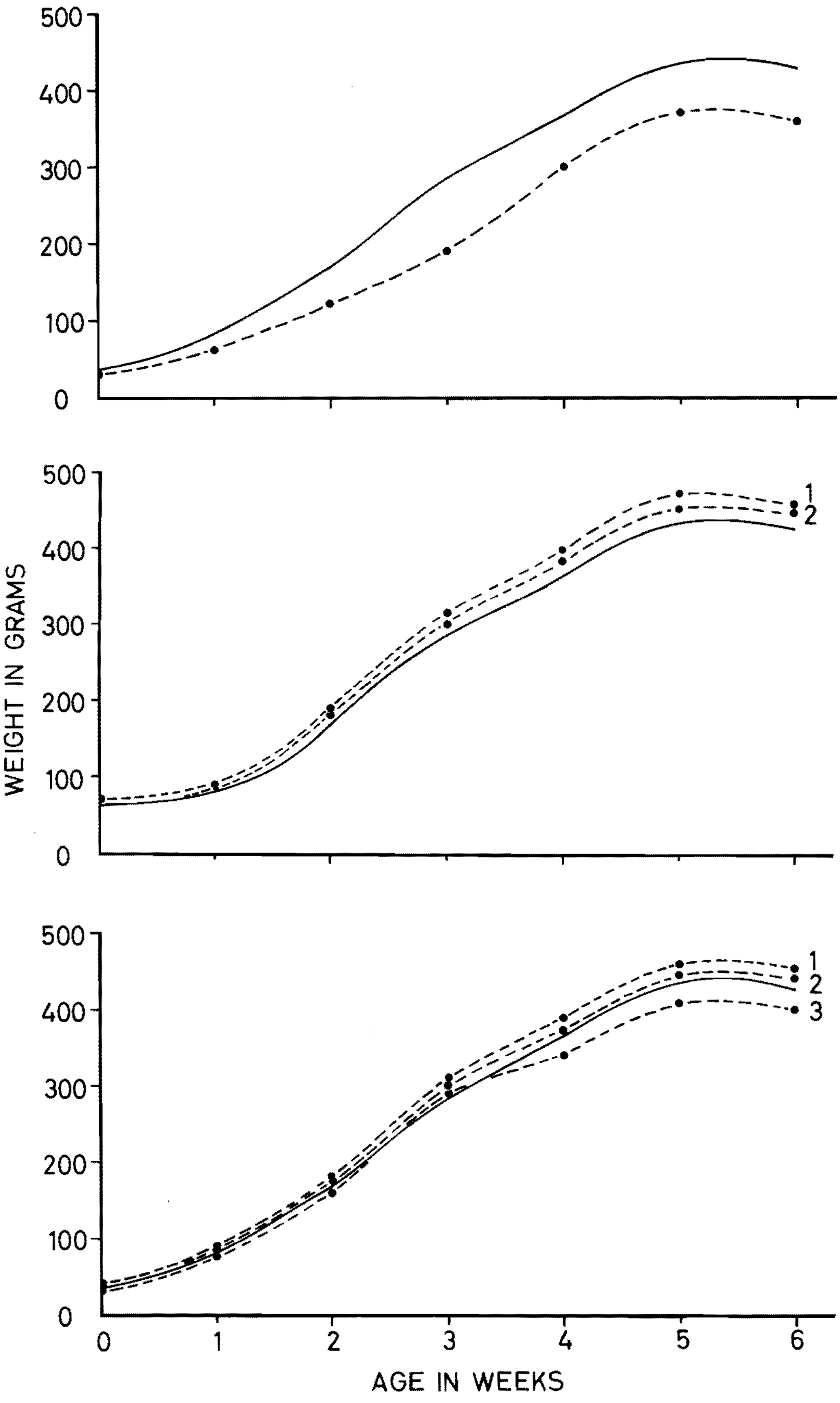

500
400
300
200
100
0
500
400
300
200
100
0
1
2
WEIGHT IN GRAMS
500
400
300
200
100
0
1
2
3
0
1
2
3
4
5
6
AGE IN WEEKS

Figure 4.9

Growth rates of South Island Pied Oystercatcher chicks as depicted by weight changes in one, two and three chick broods. The mean growth curve is shown as a solid line, and chicks are distinguished by a number indicating their hatching order.

Data from 3 broods of each size.

in extreme instances the oldest chick will kill its brood-mates (Heinroth, 1928). Lack (1968) has suggested that the asynchronous hatching of eggs of wading birds could result in some young dying quickly if food is sparse. The slower growth rate of the youngest chick in three chick broods supports this contention.

Two chick broods show less discrepancy in growth rates of brood-mates (see Fig 4.9). Presumably, the greater average amount of food available per chick allows similar weight gains. One chick broods have surprisingly slow growth rates (see Fig 4.9). This is probably due to the occurrence of those broods late in the breeding season when food is less available to the chicks.

2. Growth depicted by standard measurements

Growth rates of oystercatcher chicks are most clearly depicted by two measurements:

(a) tarsus length; and,

(b) bill length, measured from the bill tip to the gape. This measurement was taken in preference to that of the exposed culmen as it is subject to less error (see Ch.5.3 A).

(a) Tarsus Growth

Growth of the tarsus occurs most rapidly during the two weeks immediately following hatching. Between the second and fifth weeks the tarsus elongates at an approximately constant rate. Near fledging tarsus growth rates decrease as adult dimensions are approached. In a similar manner to body weight, tarsus growth varies with brood-size and season (see Fig 4.10). One chick broods show the slowest growth, two chick broods grow fastest with both chicks having similar growth curves, and three chick broods are characterised by the lagging growth rate of the third chick.

(b) Bill Growth

Growth of the bill proceeds at an even rate during most of the growth period, decreasing only near the time of fledging (see Fig 4.11). For this reason, bill growth (in conjunction with changes

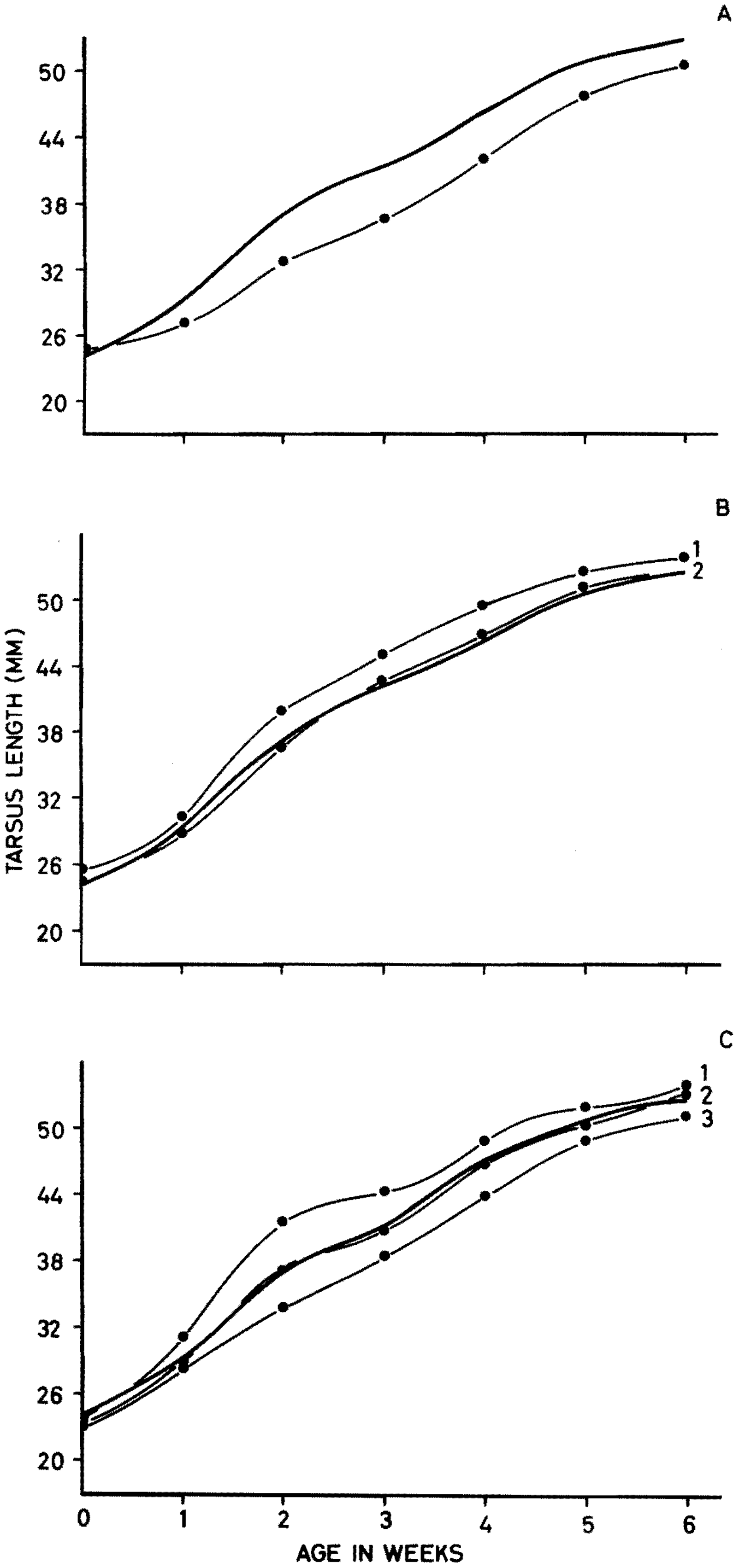

A
B
C
1
2
1
2
3
TARSUS LENGTH (MM)
20
26
32
38
44
50
0
1
2
3
4
5
6
AGE IN WEEKS

Figure 4.10

Growth rates of South Island Pied Oystercatcher chicks as depicted by tarsus elongation in one, two and three chick broods. Data from 3 broods of each size.

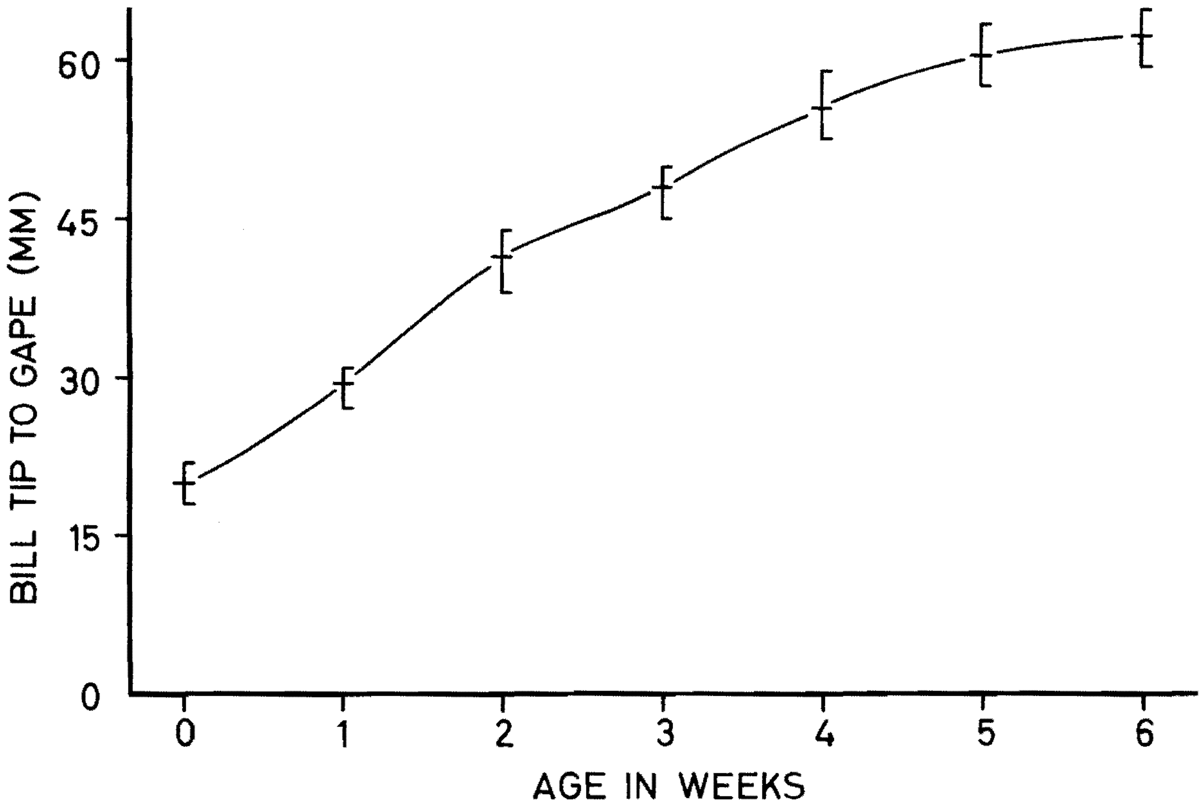

BILL TIP TO GAPE (MM)
0
15
30
45
60
AGE IN WEEKS
0
1
2
3
4
5
6

Figure 4.11

Mean growth curve of South Island Pied Oystercatcher chicks as depicted by bill elongation. Vertical lines indicate the range of measurements at each age grouping, and the curve passes through the means. Data from 9 broods.

in plumage and flesh colours) is the most reliable parameter for estimating the age of chicks captured in the field.

C. Parental Care

1. Feeding of small chicks

Chicks of the South Island Pied Oystercatcher are first fed approximately 24 hr after they hatch. During the first three weeks they are fed from a specific feeding posture. Adult South Island Pied Oystercatchers possess a feeding posture identical to that of the conspecific European Oystercatcher (Lind, 1965). The parent stands motionless with the bill pointing almost vertically downward. Food items are held in the tip of the bill just above the surface of the substrate, the chick taking the food from this position. As long as the adult is searching for food the chick does not respond to it, but follows slowly at a distance.

Lind (1965) has shown that the adult oystercatcher bill, as demonstrated in the feeding posture, releases and directs a pecking response in the chick. Among the releasing stimuli are colour, form, and position of the bill. The pecks of the chick are directed at the tip of the bill where the adult holds the food.

2. Feeding of older chicks

When the chicks are approximately three weeks old the parental feeding system changes. The adult more frequently stops presenting food and starts self-feeding when the chick does not at once react to the feeding posture. Also at this age, the chick starts to show distinct begging behaviour, assuming a characteristic posture in doing so. The neck is withdrawn, the head is held at or below the level of the back, and the body is puffed out. Begging chicks frequently rub their heads against the breast of the adult as they run back and forward in front of it. Occasionally the chick will stop and jerk its head upwards to peck at the head of the parent. Begging is always accompanied by a soft "mewing" call.

As fledging is approached the chick is often left to feed itself, and only rarely is fed by the parents. This suggests that the final breakdown in the parental feeding mechanism is timed to coincide with the completion of fledging. The fledgling therefore becomes largely independent of its parents before post-breeding migration to winter haunts commences.

3. Protection of chicks against predators

The hostile response of adults to predators includes alarm calls, the chick responding by seeking cover or by crouching in a "frozen" attitude on the substrate (see Plate 4.30). Cryptic colouration of the dorsal aspect of the chick renders this behaviour particularly effective as an anti-predator reaction. Harrier Hawks (*Circus approximans*) appear to be the major predator of oystercatcher chicks, and are vigorously attacked and driven from the territory by the parents. Each New Zealand race possesses identical anti-predator behaviour. Distraction displays also play a major part in the protection of chicks against predators (see section 4.7 E).

D. Progeny from Cross-matings of Black and Variable Oystercatchers

Without quantitative data on mating combinations and their associated progeny, it is impossible to determine the genetics of colour phase inheritance in *H. unicolor*. All possible mating combinations occur in nature; the three colour phases of the Variable Oystercatcher (*H. u. reischeki*) freely interbreed with each other and with the Black Oystercatcher (*H. u. unicolor*). Progeny of all recorded matings between "black" (Black Oystercatcher and the black phase of *reischeki*) and pied phases of *H. unicolor* are intermediate in plumage. Matings of intermediate phases produce either parental black and pied phases or further intermediates. Backcrosses of parental pied or black phases with an intermediate phase results in progeny with parental characteristics. Brathwaite (1950) noted that a cross between a black male and an intermediate phase female produced two pied offspring.

Whether the phenotypes outlined above are the only ones produced for each mating combination is uncertain. However, it is clear that

Plate 4.31

"Frozen" attitude of a South Island Pied Oystercatcher chick in response to parental alarm calls.

the genes controlling plumage colour of the Black Oystercatcher and the black phase of the Variable Oystercatcher are extremely similar, if not identical. Intermediates produced between these two "black" oystercatchers and the pied phase of the Variable Oystercatcher are phenotypically indistinguishable.

The lack of a fixed plumage pattern in the intermediate phase birds has been regarded by Oliver (1955) as evidence for their hybrid nature. On this basis alone he raised reischeki and unicolor to full species status. However, as these "hybrids" appear to be always fertile, and in other respects except plumage are identical to their parents, the hypothesis that they are interspecific hybrids has little supporting evidence. A more rational explanation is that the variation in the intermediate phase plumage is due to a primary pair of genes whose expression is controlled by a pleiotropic set of modifying genes or polygenes acting additively. Irrespective of the actual genetic mechanism involved, the high frequency of cross-matings between Black and Variable Oystercatchers allied with the production of fertile offspring from such matings supports the contention that Black and Variable Oystercatchers are separate races.

4.11 POST-BREEDING DISPERSAL

Following the successful fledging of chicks at the age of six to seven weeks, a further period of approximately two weeks is spent at the breeding area. During this time the flight of the juveniles becomes much stronger. Juveniles of the South Island Pied Oystercatcher are usually independent of their parents at the end of this period, and commonly form flocks prior to migration (see Plate 4.31). Although adults frequently associate with these flocks it is not unusual for them to leave the breeding area before their offspring.

Migration of South Island Pied Oystercatchers from their breeding areas to winter haunts begins in December, reaches a peak in January and February, and continues through until April (Falla et al., 1966). Although the major movement is northwards, some birds fly southwards to winter on Stewart Island. The bulk of the

Plate 4.32

A post-breeding flock of juvenile South Island Pied Oystercatchers in pastures near the Makarora River.

January, 1968.

population migrates to winter haunts on the east and north coasts of the South Island, but several thousand birds move further north to the Auckland province, a few annually reaching Parengarenga Harbour near the tip of the North Auckland Peninsula. Juveniles show a tendency to migrate further northwards than their parents, the percentage of juveniles in wintering flocks increasing on transition south to north through New Zealand (see section 4.5 B).

Black and Variable Oystercatcher juveniles often remain with their parents throughout their first winter, especially where the family group is an isolated one (Moon, 1967). Towards the end of the winter the juveniles leave the breeding territory and become fully independent of their parents. Williams (1927) observed American Black Oystercatchers feeding their young three to four months after hatching, noting that the juveniles had not then mastered the technique for removing limpets and small chitons from the rocks. At Jackson Bay, where a comparatively large population of Black and Variable Oystercatchers occurs, parents and their young return to the winter flocking area three to four weeks after the young have fledged. There is no apparent association of family groups within the flock, and young appear to be independent of their parents.

4.12 SUMMARY

The breeding biologies of the New Zealand races of oystercatcher are essentially similar in their broader perspectives. Breeding birds of each race are characterised by bright flesh colours; the bill and eye ring are bright orange, the iris scarlet, and the legs and feet bright pink. Non-breeding birds are divisible into three groups, first year juveniles, second year sub-adults, and adult non-breeders. Juveniles are recognisable by their dull greyish pink legs, dusky bill tips, brown irides, and buffy tips to the scapular feathers. Sub-adults have darker dorsal plumage and characteristic orange irides.

New Zealand oystercatchers probably first breed at an age of three years since it is then that they assume adult plumage. The small number of adult-plumaged birds which remain at winter haunts during the breeding seasons suggests that the greater majority of three year adults are breeding.

Courtship and pair formation occurs at the winter haunts before dispersal to breeding areas begins. Courtship manifests itself in the form of social piping, which ultimately leads to sociogamous pair formation and copulation. Successful copulations are usually preceded by specific posturing, the male approaching in a crouched stealthy walk and mounting when the female stands erect with the tail feathers raised.

Territories are taken up by both birds of a pair on arrival at the breeding area. The only form of territorial defence other than direct combat appears to be aggressive piping, an agonistic form of behaviour which frequently occurs at territorial boundaries. Pair-bonds in the pre-egg stage are strengthened by mutual behaviour such as allopreening and balancing. Territory size is inversely proportional to nesting density, territories being large when nesting densities are low, and vice versa.

Many nest-scrapes are constructed in the territory, construction commencing approximately two weeks before egg-laying. Nest-scrapes in which the eggs are eventually laid are constructed usually within 24 hr of laying. The hollow cup-shape of the nest-scrape is due to the method of formation, the breast of the bird being pressed into the substrate. Nest-scrapes are rarely lined with nesting material, but on occasion are decorated with twigs, small pebbles and mollusc shells.

Although the laying seasons of the two New Zealand species are largely asynchronous, they are of similar duration, each lasting approximately five months. Eggs are normally laid at intervals of 48 hr, although extremes of 24 hr and 72 hr have been recorded. Oystercatchers are determinate layers as they lay only a set number of eggs per clutch, and will not replace eggs lost from an incomplete clutch. The most common clutch size is two eggs, followed by three, one, and four. Repeat clutches are laid if the first clutch is destroyed, and in most cases they contain less eggs than their predecessor. Mean clutch size decreases as the season proceeds, probably as a result of older birds laying larger clutches in the early part of the season. The increased frequency of repeat clutches later in the season probably enhances this variation.

Egg colours show a conservative range of variation due to their function of protective colouration. Since oystercatchers nest in similar habitats throughout their range, the eggs are of necessity similar in colour.

Incubation spells are performed by both members of a pair, but the major part of incubation falls to the female. Nest-relief is usually a passive process, being accomplished by the approach of the relieving bird and the withdrawal of the sitting bird. The incubation period is similar in each race, being approximately 28 days.

Hatching of eggs is asynchronous. Each egg takes approximately 36 hr to hatch, but the hatching period of a clutch varies with the clutch-size. Hatching periods of eggs in larger clutches are shorter than would be expected from their laying interval, partial synchronisation of hatching being due to incubation commencing with the laying of the last egg and auditory stimulation of less developed young by their more advanced brood-mates.

Chick growth-rates vary with brood-size and season. Two chick broods grow fastest, three chick broods are characterised by lagging growth of the third chick, and one chick broods achieve the slowest growth-rate. The latter presumably results from the occurrence of one chick broods late in the season when food is less available. Bill length measured from the bill tip to the gape, in association with plumage characters and flesh colours, is the most reliable method of aging chicks.

Parental care of chicks involves the use of a specific feeding posture, the parent standing motionless near the chick with a food item held in its vertically directed bill. Chicks begin food-begging at an age of approximately three weeks, but are largely able to support themselves two weeks after fledging. Protection of the young involves alarm calls and distraction displays; injury-feigning, false-brooding, and false-feeding being prominent.

Although the aspects of breeding biology outlined above are common to all species and races of New Zealand oystercatchers, important differences occur between them. These differences, and their probable significance are discussed below;

I: Breeding Seasons

New Zealand species of Oystercatcher have different breeding seasons of which approximately three months are common to both. South Island Pied Oystercatchers breed from July to January, and Black and Variable Oystercatchers from October to February. Peaks in breeding activity, however, are separated by a period of at least two months, being respectively September and November to December. This asynchrony of the species breeding seasons is a major factor in ensuring reproductive isolation between them.

II: Dispersal to Breeding Areas

The two New Zealand species of oystercatcher have different dispersal patterns from their winter haunts to the breeding grounds. South Island Pied Oystercatchers possess a well developed migratory instinct, migration commencing in July and continuing until September. Distances as great as 800 miles are probably traversed during migration.

Black and Variable Oystercatchers are non-migratory. They either undertake local dispersal movements from their winter flocking areas, or they retain isolated territories throughout the year.

III: Breeding Dispersion

The breeding dispersion of New Zealand oystercatchers differs for the two species. South Island Pied Oystercatchers are, with very few exceptions, inland breeders. They nest exclusively in the South Island, the major nesting habitats being provided by the shingle beds of snow-fed rivers. Since 1950 this species has spread away from the traditional riverbed nesting sites to breed on arable land and high country tussock grasslands. This has presumably resulted from the contemporary population irruption which has in turn increased competition for nest-sites. Coastal breeding birds of this species are rare, and where they occur their nest-sites are associated with lagoons, lakes, and marshy fields.

Black and Variable Oystercatchers are exclusively coastal breeders, and are commonly found breeding on small offshore islands. Breeding dispersion of this species is essentially the same as the distribution of winter flocks due to their limited pre-breeding dispersal.

IV: Egg Weights and Dimensions

Egg weights and dimensions for New Zealand Oystercatchers are species-specific. The eggs of the South Island Pied Oystercatchers are significantly smaller in both length and breadth than those of the Black or Variable Oystercatchers. Commensurate with the species differences in egg dimensions, corresponding differences occur in the weights of the freshly laid eggs. Eggs of both Black and Variable Oystercatchers are extremely similar in size and weight.

V: Post-breeding Dispersal

Following the fledging of broods, South Island Pied Oystercatchers undertake full-scale migrations back to winter haunts. Movement begins in December, reaches a peak in January and February, and continues until April. Juveniles tend to migrate greater distances than adults.

Black and Variable Oystercatchers either remain in their territories throughout the year or undertake local movements back to nearby flocking areas.

4.13 TAXONOMIC CONCLUSIONS

New Zealand oystercatchers have similar breeding biologies with many features common to each race. Assessment of the similarities and differences support the taxonomic categories adopted in the Checklist of New Zealand Birds (1953). Two good species can be recognised; South Island Pied Oystercatchers (*H. ostralegus finschi*) are reproductively isolated from Black and Variable Oystercatchers (*H. unicolor* subspp.) by their allopatric breeding dispersion and asynchronous breeding seasons. Black and Variable Oystercatchers are best considered as separate races since they overlap in their breeding dispersion, interbreed freely, and produce fertile offspring from their cross-matings. Progeny of interracial matings are phenotypically identical to the intermediate phase of the Variable Oystercatcher. This suggests that the colour phase polymorphism of this species is under the control of a relatively simple genetic mechanism. Intermediates should not, therefore, be regarded as interspecific hybrids since the latter are usually characterised by disharmonious genotypes resulting from the incompatibility of parental gene recombinations.

Chapter 5

EXTERNAL MORPHOLOGY, MOULTS, AND MALLOPHAGA OF NEW ZEALAND OYSTERCATCHERS

5.1 INTRODUCTION

Animal taxonomy was dominated during the 19th and early 20th centuries by the morphological species concept, but in recent years it has been superseded by the biological species concept. Mayr (1963) pointed out the vulnerability of a purely morphological classification of species, noting that conspicuous morphological differences occur among conspecific individuals and populations, and that sympatric sibling species are morphologically indistinguishable. In spite of these objections it seems reasonable to use morphological characters to assist recognition of species delimited by other criteria.

Descriptions and measurements of the external morphology of oystercatchers are common in ornithological literature (Audubon, 1840; Ridgway, 1886, 1919; Mathews, 1913; Murphy, 1925, 1936; Stresemann, 1927; Bent, 1929; Salamonsen, 1930; Witherby et al., 1941; Webster, 1942; Wetmore, 1965; Harris, 1967). Similar descriptions of New Zealand oystercatchers are numerous (Buller, 1872; Martens, 1897; Hartert, 1921, 1927; Falla, 1939; Fleming, 1939; Oliver, 1955; Williams, 1963; Falla et al., 1966).

Moults have been described for the European Oystercatcher (Witherby et al., 1941), the American Black Oystercatcher (Webster, 1942), and the American Pied Oystercatcher (Bent, 1929). Mallophagan ectoparasites of oystercatchers have been reviewed by Timmermann (1954).

5.2 MATERIALS AND METHODS

Thirty-six South Island Pied Oystercatchers were mist-netted at the Heathcote-Avon estuary during the winter months of May, June, July and August, 1967. Twenty skins of this species were examined from the collections in the Canterbury and Dominion Museums. A further 15 specimens were shot, five each during the summer months of December, January and February.

Ten Black and two Variable Oystercatchers were mist-netted for comparative study. In addition 10 skins of the Variable Oystercatcher, seven from the Black Oystercatcher and one of the Chatham Island Oystercatcher were examined from museum collections.

For each bird standard measurements were taken as outlined by Gurr (1947), but the two measurements total length and extent of wings were omitted as they could not be satisfactorily measured from museum skins. The plumage was examined and the extent of moult (if any), recorded. Mallophaga were collected from five Black Oystercatchers, seven black phase and one intermediate phase of the Variable Oystercatcher.

5.3 A. External Morphology

The plumages of New Zealand Oystercatchers have been described previously (see Ch. 1.4 and Ch. 4.5). Each plumage is species-specific, and allows positive identification in the field. Since the Black Oystercatcher and the black phase of the Variable Oystercatcher are identical in appearance, further investigation of their external morphology was desirable to either support or refute their present racial status. Results of this investigation can be conveniently grouped under two headings:

1. general standard measurements; and,
2. sexual dimorphism.

1. General Standard Measurements

The use of standard measurements for taxonomic purposes is basic to avian systematics. However, the measurement exposed culmen appears to be an inexact one for oystercatcher bills, and its taxonomic value open to doubt. White and Gittins (1964) found that the exposed culmen of European Oystercatchers was subject to seasonal

TABLE 5.1 STANDARD MEASUREMENTS OF ADULT NEW ZEALAND OYSTERCATCHERS

Race	Sex	WING		TAIL		BILL		TARSUS		MIDDLE TOE		N
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	
South Island Pied Oystercatcher	Male	252.2	8.2	96.7	4.4	82.4	3.4	44.1	3.5	34.3	2.4	23
	Female	254.6	11.2	98.0	3.5	93.6	4.5	45.7	1.7	33.3	7.6	28
Black Oystercatcher	Male	268.1	10.5	107.9	5.4	79.6	7.8	56.2	2.0	37.1	3.2	10
	Female	272.4	10.3	105.6	3.8	89.4	5.1	54.9	2.7	38.2	3.5	7
Variable Oystercatcher	Male	271.4	18.7	109.0	6.4	81.3	2.5	55.5	4.0	35.4	10.4	5
	Female	276.1	10.9	108.1	4.6	91.3	3.2	59.5	3.0	37.9	2.3	7

variation, its length increasing in the winter months. They concluded that the bill grew faster during the winter months to compensate for the increased bill tip abrasion from probing in frozen beaches. Harris (1967) rejected their explanation on the basis that their sample of measurements was small, and suggested that most of the seasonal changes they detected could be attributed to feather abrasion at the base of the bill (from whence the measurement is taken) and observer error. As oystercatchers probe deeply in the substrate for bivalve molluscs, often completely submerging their bills, abrasion of feathers in the frontal apterium can be extensive. It therefore seems desirable to use a measurement of bill length not including error from feather abrasion, such as bill tip to gape. In a relative evaluation test, the exposed culmen and bill length from the tip to the gape was measured for 30 South Island Pied Oystercatchers. From this data comparative coefficients of variability were calculated (Simpson, Roe & Lewontin, 1960). The coefficient for the exposed culmen (V = 7.57) was greater than that for the bill tip to gape measurement (V = 6.91). This indicates that the latter measurement is a more reliable one, containing less variation about the mean. Accordingly, this measurement was adopted in preference to exposed culmen.

Standard measurements of adult oystercatchers are shown in Table 5.1. Disregarding sexual dimorphism temporarily, it is evident at a cursory glance that the two species are clearly distinguished on all body dimensions except bill length. Black and Variable Oystercatchers have markedly larger wings, tails, tarsi and middle toes than their South Island pied congener, statistical tests not being necessary to make distinction. Each race possesses bills of similar length, which could be expected from their similar ecologically specialised modes of feeding (Grant, 1968). As bill length is an important factor in determining feeding success when probing for bivalves, it may contribute toward their adaptive superiority in utilising habitats with soft substrates (see Ch. 3.6 D).

Black and Variable Oystercatchers have similar standard measurements, none of the differences in the means being statistically significant (wing : $t_{27} = 0.92$, $0.4 > p > 0.3$; tail : $t_{27} = 0.96$, $0.4 > p > 0.3$; bill : $t_{27} = 0.90$, $0.4 > p > 0.3$; tarsus : $t_{27} = 1.74$, $0.1 > p > 0.05$; middle toe : $t_{27} = 0.52$, $0.6 > p > 0.5$). Insufficient data are available on standard measurements of the Chatham Island Oystercatcher to allow statistical analysis. Measurements of two adult females and one adult male given by Fleming (1939) fall within the range of those given for Black and Variable Oystercatchers, with the exception of the exposed culmen and middle toe. Since the exposed culmen represents most of the measurement bill tip to gape, then it appears that bill length in this race is substantially smaller than that of mainland races. The middle toe of the Chatham Island Oystercatcher is much longer than that of mainland races; both of these differences have been attributed by Falla et al. (1966) to a rock-dwelling habit.

2. Sexual Dimorphism

Although females are generally larger than males in most standard measurements (see Table 5.1), the extent of overlap in each dimension is too great to allow certain sex determination. Of 51 South Island Pied Oystercatchers sexed during this study (from museum skins and dissections) 11 birds (21.6%) could not be distinguished from their standard measurements. Similar overlap would probably occur in a large sample of Black or Variable Oystercatchers. On a population basis, a comparable magnitude of overlap was found for males and females of the European Oystercatcher by Harris (1967). However, he was able to sex breeding pairs with 99% accuracy on bill length, males never having longer bills than females of respective pairs.

B. Moult Cycles

The moult cycles of New Zealand oystercatchers were not investigated in detail, but it was possible to construct a general outline of moult from birds examined during this study. Adult South Island Pied Oystercatchers undergo an incomplete pre-nuptial moult at their winter haunts prior to migration to breeding areas. This moult extends from July to August inclusive, and involves most feathers except the scapulars, flight feathers and outer tail feathers. Faded worn feathers of the mantle are replaced by darker ones which make the dorsal aspect of the adult breeding plumage distinctly glossy, often reflecting greenish or bluish hues.

Black and Variable Oystercatchers also probably have a partial pre-nuptial moult, as an adult black bird trapped at Jackson Bay in August was in strong body moult.

On arrival back at the winter haunts following breeding, New Zealand oystercatchers undergo a complete post-nuptial moult. All the body feathers appear to be moulted. The darker parts of the resultant winter plumage are much browner than those of the nuptial plumage due to their buff undertones. The duration of this moult period is uncertain for each race, but South Island Pied Oystercatchers probably moult earlier (January to February) than Black or Variable Oystercatchers (February to March). Similar moult cycles were described for the European Oystercatcher by Witherby et al. (1941), but they occurred later in the year than those of New Zealand species.

First year juveniles arriving at winter haunts for their first winter undergo a partial post-juvenile moult (February to March) with only the flight feathers, scapulars, central tail feathers and wing coverts not being moulted. At the end of the first winter (July to September) a more extensive "sub-adult" moult occurs in which all feathers except the scapulars are moulted. The retention of most of these buff-tipped juvenile scapulars in the sub-adult plumage accounts for its dorsal brown colour. Similar post-juvenile moult cycles were described for the American Black and Pied Oystercatchers (Webster, 1942; and Bent, 1929, respectively).

C. Mallophaga

The use of Mallophaga as supporting evidence for taxonomic studies is a recent innovation. Clay (1951) has pointed out the limitations of applying the general principle that "the phylogenetic relationships of the Mallophaga reflect those of their hosts" to birds, as similarity of feather structure between unrelated birds can result in them having identical Mallophaga. However, she concluded that Mallophaga were often valuable as supporting evidence where the taxonomic status of a bird was in doubt.

Three genera and four species of lice occur on the feathers of New Zealand mainland races of oystercatcher. The largest of these, *Saemundssonia haematopi*, occurs on the head and upper breast of each race (see Plate 5.1). Two body lice (*Actornithophilus grandiceps* and *Quadraceps auratus*) are common to each race, occurring on the feathers of the trunk and wings (see Plates 5.2 and 5.3). The southern Black Oystercatcher possesses a fourth species of louse (*Q. ridgwayi* (?) - T. Clay det.) although a smudgy phase Variable Oystercatcher from a mixed mating of a Black and pied phase Variable Oystercatcher also had this louse (see Plate 5.4). Since only five Black Oystercatchers and seven black phase variable birds were examined for lice, the validity of this different lice species distribution has yet to be fully substantiated. At this stage it appears that the southern Black Oystercatcher and the black phase of the Variable Oystercatcher may be separated on their Mallophaga, and suggests a method of accurate racial delimitation in future research. Even if this distinguishing feature can be unequivocally substantiated in the future, it seems unlikely that species distinction exists between the two New Zealand black oystercatchers. The overwhelming ecological evidence supporting their racial status suggests that these birds represent two different colonisations of the same species, widely separated in time, during which one race lost or the other acquired the unique species of louse.

5.4 SUMMARY AND TAXONOMIC CONCLUSIONS

The New Zealand species of oystercatcher can be clearly separated on standard measurements of their external morphology except bill length. The similar bill length of each mainland race probably

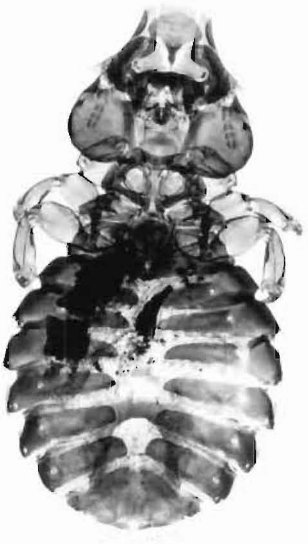


Plate 5.1

Head louse (Saemundssonia haematopi) of New Zealand oystercatchers (male left, female right).

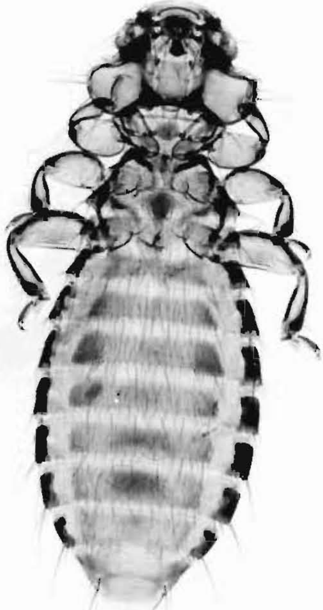
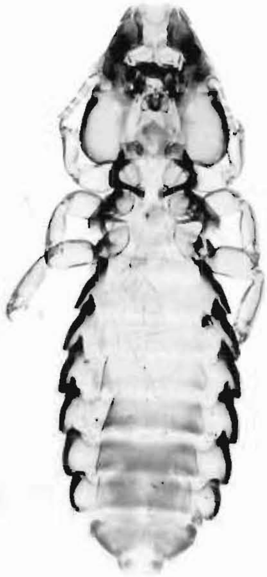
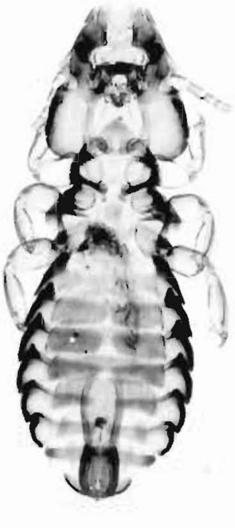
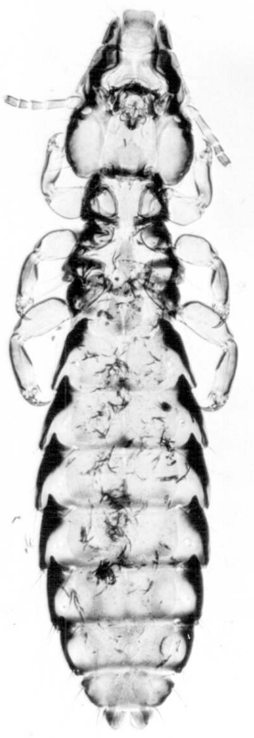





Plate 5.2

Body louse (*Actornithophilus grandiceps*) of New Zealand oystercatchers (male left, female right).

Plate 5.3

Body louse (*Quadraceps auratus*) of New Zealand oystercatchers (male left, female right).



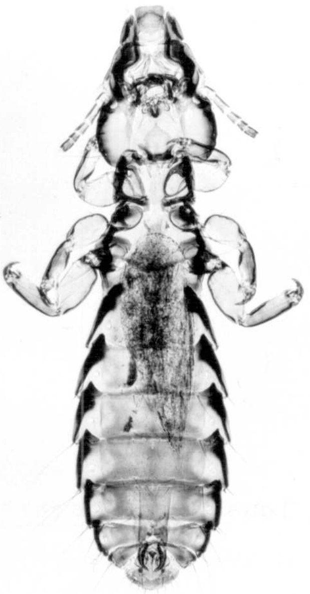


Plate 5.4

Body louse (*Quadraceps ridgwayi* ?) which has been collected only from Black Oystercatchers and a smudgy phase cross between Black and Variable Oystercatchers. (male left, female right) accounts for the adaptive superiority of the otherwise smaller South Island Pied Oystercatcher when feeding on soft substrates. Sexual dimorphism in size occurs for each race, with females being larger than males in most body measurements. Sex determination from comparative standard measurements is unsatisfactory as the region of overlap between the sexes is too large. Moult cycles appear to be similar for each race, but South Island Pied Oystercatchers probably moult in advance of Black or Variable Oystercatchers. Three genera and three species of Mallophaga are common to each race, whilst a fourth species appears to be restricted to the Black Oystercatcher. All of the above findings support the scheme of classification proposed in the Checklist of New Zealand Birds (1953).

CONCLUSIONS

In the preceding chapters the biology of New Zealand oystercatchers has been discussed on a comparative basis. By way of conclusion the results of this study are briefly recapitulated below and their taxonomic significance assessed.

New Zealand races of oystercatcher are widely distributed along the shore, each possessing similar winter ranges. South Island Pied Oystercatchers possess well developed gregarious behaviour, commonly gathering in large flocks at major harbours and estuaries. Black, Variable and Chatham Island Oystercatchers are less gregarious and therefore occur mainly in isolated pairs or small flocks. South Island Pied Oystercatchers show a strong selection for winter feeding habitats with soft substrates, whereas black, variable and Chatham races show a preference for rocky habitats.

Each race is adapted for an ecologically specialised mode of feeding. South Island Pied Oystercatchers have strongly developed behaviour patterns for preying on bivalve molluscs, whilst the rock-dwelling Black and Variable Oystercatchers possess behaviour patterns which enable them to exploit limpets and mussels. Competitive exclusion, although not always absolute, occurs between South Island pied birds on one hand, and black and variable birds on the other. This probably results from the superior ability of South Island Pied Oystercatchers in utilising habitats with soft substrates. In such habitats they feed at the same rate as black and variable birds, but are at a competitive advantage since they are smaller. The reverse probably applies in rocky habitats.

New Zealand oystercatchers have similar breeding biologies with many features common to each race. Courtship and pair formation are accomplished at the winter haunts, and once pair bonds are established the pairs disperse to their breeding areas. South Island Pied Oystercatchers, however, undertake large-scale migrations, whereas Black and Variable Oystercatchers lack a migratory instinct, dispersing only short distances away from their winter haunts to breed. Some isolated pairs of Black, Variable and Chatham Island Oystercatchers remain in their territories throughout the year.

South Island Pied Oystercatchers are reproductively isolated from Black and Variable Oystercatchers by their allopatric breeding dispersion and asynchronous breeding seasons, the former breeding inland from July to January and the latter breeding coastally from October to February. Each race has a similar pattern of egg-laying, incubation and hatching. Egg weights and dimensions are species-specific, those of Black and Variable Oystercatchers being similar in size, but considerably larger than those of the South Island Pied Oystercatcher.

Interracial plumage differences are supported by comparative standard measurements. South Island Pied Oystercatchers are smaller in all respects except bill length, whereas Black and Variable Oystercatchers have similar body dimensions. The Chatham Island Oystercatcher is unusual in that it has a short bill and extremely elongated middle toe, but both factors can probably be accounted for in terms of genetic drift since the initial colonisation from mainland stock. All other standard measurements of this race concur with those of Black and Variable Oystercatchers.

Moult cycles appear to be similar for each race, but moults probably occur earlier each year in the South Island pied species. Three genera and three species of Mallophaga are common to the inland races, but a fourth species has so far been collected only from the Black Oystercatcher, suggesting a method of distinguishing this bird from the black phase of the Variable Oystercatcher.

In appraising the species criteria of Maslin (1968) as outlined in the aims of this thesis, the following deductions can be made on the taxonomic status of New Zealand oystercatchers:

I. two good species can be recognised; South Island Pied Oystercatchers (Haematopus ostralegus finschi) are reproductively isolated from Black and Variable Oystercatchers (H. unicolor subspp.); and,

II. Black and Variable Oystercatchers are best considered as separate races of *H. unicolor* since they have similar ecological requirements, overlap in their breeding ranges, interbreed freely and produce fertile offspring from their cross-matings. From the evidence available, the Chatham Island Oystercatcher also represents a race of *H. unicolor*, having closest affinities with the pied phase of the Variable Oystercatcher.

The scheme of classification proposed in the Checklist of New Zealand Birds (1953) is therefore supported by the results of this study.

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