PREY-SPECIFIC FEEDING METHODS OF NEW ZEALAND OYSTERCATCHERS

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ABSTRACT

New Zealand oystercatchers use specialised prey-specific methods to feed on common prey found in the marine littoral zone. Methods of locating and dealing with bivalves, limpets, chitons, gastropods, and crabs are herein described. Feeding behaviour may be modified by climatic factors, physical factors of the environment, and competition for food. The mainland species of oystercatchers have similar repertoires of feeding methods, but the South Island Pied Oystercatcher is behaviourally adapted to exploit estuarine bivalves whereas the Variable Oystercatcher is adaptively superior in exploiting limpets and chitons on rocky shores. The Chatham Islands Oysstercatcher seems behaviourally intermediate to its mainland congeners in feeding habits, possibly in response to widely varying feeding habitats in the islands. Differential niche utilization may therefore have been an important factor in the speciation of New Zealand oystercatchers.

INTRODUCTION

Oystercatchers have attracted the attention of both ecologists and ethologists because of their specialised mode of feeding. Many authors have described foods and feeding habits (Dewar 1908, 1910, 1913, 1915, 1922, 1940; Bayne 1941; Webster 1941; Tomkins 1947; Legg 1954; Norton-Griffiths 1967; Heppleston 1971; Dare & Mercer 1973). Despite this wealth of literature, most of which pertains to the European Oystercatcher (*Haematopus ostralegus* L.), very little is known about the feeding habits of the New Zealand species of oystercatchers. The only published account of feeding in these species is that of Oliver (1955) which contains only a brief mention of foods taken by the Variable Oystercatcher *(H. unicolor)*. The present paper reports on some prey-specific feeding methods which were observed during the course of a study of the comparative feeding ecology of the New Zealand species of oystercatchers.

METHODS

Time and location of observations:

Field observations of feeding habits of mainland New Zealand oystercatcahers were made primarily in the winters of 1966 and 1967, and supplementary observations were made in the winters of 1968

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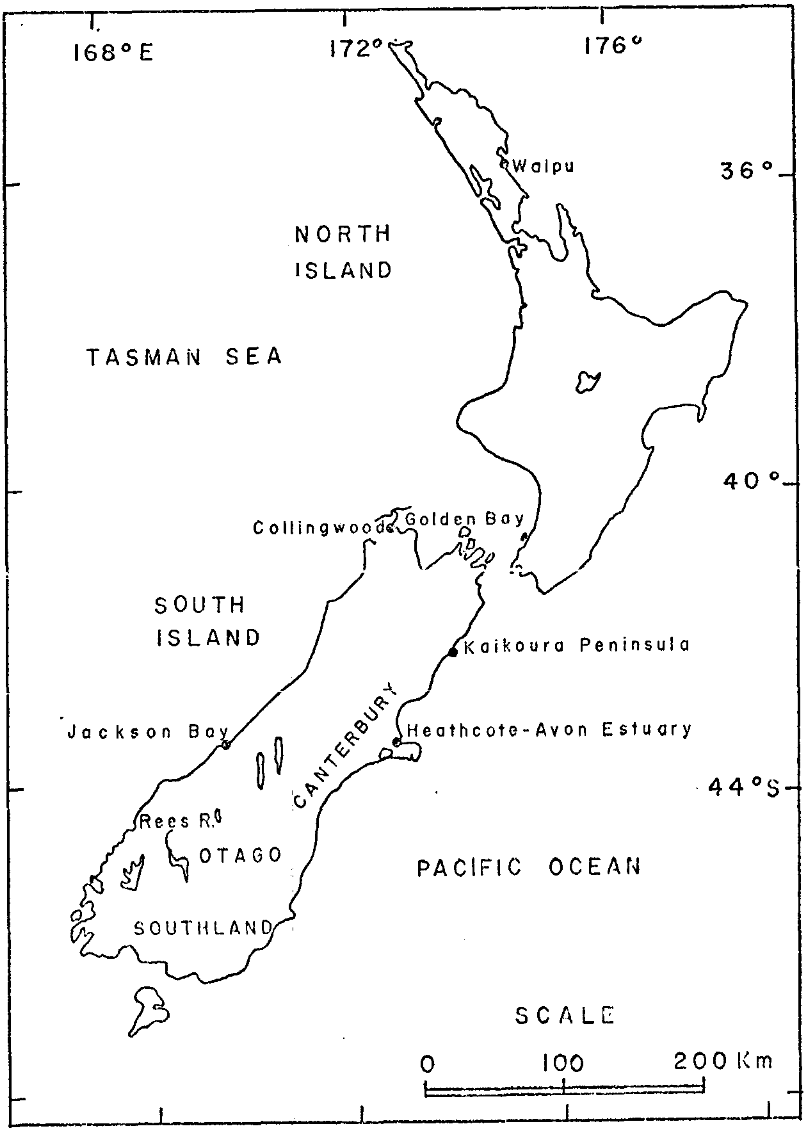

FIGURE 1 — Map of New Zealand showing location of study areas and localities mentioned in the text.

through to 1971. Feeding of the Chatham Islands Oystercatcher was observed only in early November 1970 when the author was fortunate to be a member of the Wildlife Service expedition to the Chatham Islands. The South Island Pied Oystercatcher *(H. ostralegus finschi)* was studied in detail at the Heathcote-Avon estuary in Canterbury, and comparative observations of the Variable Oystercatcher *(H. unicolor)* were made at Golden Bay, Kaikoura Peninsula and Waipu estuary (Fig. 1).

Feeding behaviour:

Individual birds were observed feeding from distances of about 10 to 50 m through 7 x 50 mm fieldglasses. Each bird was followed for 10 min. and the number of probes in search of food were recorded, the number of successes marked, and the food identified where possible. Two experiments were conducted on a dense bed of cockles to test if the observed feeding success of birds was consistent with touch or sight location of the cockles. The success of touch location (random probing) was estimated by walking slowly along probing in the substrate with an oystercatcher bill held in the hand, and counting the number of times a live cockle was located. Similarly, the expected success of visual location was determined by probing at siphons of the cockles which were extended to the surface when shallow water covered the cockle bed. In each test 10 samples of 20 probes were made to allow statistical analysis of data.

Statistical analysis:

Differences between percentages were tested with the angular transformation which yields a test statistic t^s (Sokal & Rohlf 1969). The G - statistic (rather than X^2) was used to test differences in frequencies as it is easier to compute and is more accurate at lower sample sizes (Sokal & Rohlf, 1969). The significance level was set at 0.95, and probability ranges were designated as follows: $* = 0.05 > P > 0.01$, $** = 0.01 > P > 0.001$, $*** = P < 0.001$, ns = not significant, $P > 0.05$.

LOCATION OF PREY

Visual location:

The most abundant bivalve mollusc at the Heathcote-Avon estuary is the cockle *(Chione stutchburyi)*, which also forms the major item of the oystercatchers' diet. Cockles (and many other bivalves) usually burrow beneath the surface of the substrate and feed by extending siphons to the surface. The siphons are extended from the gaping shell only when water covers the substrate, and when the tide uncovers the area they are retracted into the closed shell. It is therefore possible to detect feeding cockles by looking for siphons at the surface (see Fig. 2D). Oystercatchers feeding on cockle beds which were covered by shallow water seemed to locate cockles visually. The acute sight of the birds is illustrated by birds striking at a potential food source and then halting the strike at the waterline on seeing that the source was unsuitable. Birds were occasionally seen turning completely about to investigate something sighted in passing. Further evidence for visual location of prey was obtained by calculating estimates of feeding success, defined as the percentage of probes which were successful in locating prey (see Table 1).

Table 1. Feeding success of South Island Pied Oystercatchers at the Heathcote-Avon estuary.

Date	N	Mean No. of probes per 10 min. ± S.E.	Mean No. of cockles taken per 10 min.± S.E.	Mean % feeding success ± S.E.
12 June 1967	20	15.2 ± 0.31	8.1 ± 0.46	53.2 ± 1.86
30 June 1967	20	10.4 ± 0.96	6.2 ± 0.67	57.3 ± 2.01
25 June 1968	20	17.7 ± 1.10	9.3 ± 0.26	52.6 ± 1.77
21 June 1967	20	19.5 ± 0.37	11.7 ± 0.68	60.2 ± 1.59
3 July 1967	20	22.8 ± 1.34	12.5 ± 0.39	54.7 ± 1.75
27 June 1968	20	16.6 ± 0.72	8.4 ± 0.27	51.6 ± 1.42

The figures 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 during the optimum period, i.e. in the period an hour either side of low water (Baker 1969). Under such conditions, South Island Pied Oystercatchers were successful in locating a cockle at approximately every second attempt. This represents a much higher rate of success than would be expected if probing were random and no visual location was involved. The experimental random probing test with an oystercatcher bill gave a mean feeding success of 9.0%, compared with 51.6% for oystercatchers in June 1968. The difference between these two means was statistically significant ($t^{s} = 3.13^{**}$) 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 trials did not locate any gaping cockles at all. The visual location experiment in which the probe with the oystercatcher bill was made at the siphons produced results which were more consistent with feeding success figures of the birds. When conditions were ideal for sighting cockle siphons (bright sunshine, no wind, cockles covered by 1 to 10 cm of water) the mean percentage of successful piercing probes was 46.2%. The difference in the means for the birds and the experimental trial was not significant ($t^{s} = 0.342$, ns.). The higher recorded success rate of the birds was probably due to their more co-ordinated and better directed piercing probe than that attained manually with the oystercatcher bill.

Both mainland New Zealand species of oystercatcher appear to sight feeding bivalves, judging from the comparative feeding success calculations made at peak feeding periods near low water (see Table 2). The difference between the feeding success means of the two species was not significant ($t^s = 0.055$, ns.), indicating that they possess similar ability at locating gaping cockles.

Table 2. Comparison of feeding success of mainland New Zealand species of oystercatchers at Golden Bay.

Species	N	Mean No. of probes per 10 min.	Mean No. of cockles taken per 10 min.	Mean % feeding success
South Island Pied Oystercatcher	16	18.4 ± 1.20	8.6 ± 0.59	46.6 ± 2.22
Variable Oystercatcher	22	15.6 ± 0.88	7.2 ± 0.62	45.7 ± 2.45

The location of other bivalves was also probably visual. The pipi *(Paphies australe)*, the tuatua *(Paphies subtriangulatum)*, the large wedge shell *(Macomona liliana)*, the ribbed venus shell *(Protothaca crassicosta)* and the dosinias *(Dosinia anus* and *D. subrosea)* all possess siphons for filter feeding at the substrate/water interface. The large wedge shell frequently occurred at a depth of 3 to 10 cm in the substrate of the Heathcote-Avon estuary, and the only indication of its presence was provided by the siphons at the surface. Oystercatchers which took these bivalves were frequently seen with their bills completely buried in the substrate, indicating they had followed the siphon canals to the buried shell.

The location of mussels attached to hard substrates in shallow water was visual. Only those shells which were gaping were attacked, suggesting that the oystercatchers distinguished suitable mussels by the presence of a gape. Not only were the birds able to see the gape, but their piercing probes were almost always orientated down the longitudinal axis of the gape, as also shown for European *H. ostralegus* (Dewar 1908; Drinnan 1958; Norton-Griffiths 1967). Freshwater mussels *(Hyridella menziesi)* were also attacked while gaping (McKenzie 1963).

The location of amphineuran and gastropod molluscs on hard substrates, and of the mudsnail *(Amphibola crenata)* in estuaries, was visual as these species occurred abundantly at the surface. The main feeding problem facing the oystercatchers on rocky shores is not one of prey location, but rather one of removing prey which are firmly affixed to the rocks.

Touch location:

On uncovered substrates the location of buried bivalves appeared to be tactile. When the feeding grounds were completely exposed, the birds explored any depression in the surface of the substrate. In soft substrates they moved slowly forward making a series of short vertical probes with the bill slightly open and beneath the surface. The regularity of this probing was occasionally interrupted to lift the bill out of the substrate, but the probing was almost immediately repeated in another area. Similar searching probes with the mandibles open have been reported for the European Oystercatcher (Hulscher 1964; Davidson 1967).

When the surface of the substrate is littered with dense concentrations of old opened shells, the location of prey becomes extremely difficult. Although some of the younger birds painstakingly investigated each shell, the majority of birds used a much faster method of differentiating between occupied and empty shells. Two or three short sharp blows were delivered to the shell with the bill held vertically. If the shell is uninhabited the valves flex beneath the applied pressure, but if inhabited the valves are rigid and immovable. A possible explanation for this behaviour is that the birds were able to detect flexibility differences in response to their hammering, and utilised it to locate live prey. Both mainland New Zealand species of oystercatcher used this type of prey location when mollusc beds were exposed by the tide.

METHODS OF TAKING PREY

Estuarine bivalves:

The methods by which New Zealand oystercatchers extract bivalve molluscs from their shells are similar for each bivalve, with small differences associated with the mode of location. Bivalves with a gape between the valves were opened by thrusting the bill into the gape so that the valves were initially parted by the minimum dimension of the bill (bill width) which is often less than 1 mm at the tip. Once the bill was deeply inserted into the shell, opening was completed by immobilising the bivalve by pressure thrusting against the substrate, and then rotating the bill (and body) through 90° so that the 9-12 mm height of the bill forced the valves wider apart and snapped or seriously weakened the adductor muscles which draw the valves together.

Rotation of the body to effect prizing of the valves apart was described for European *H. 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 New Zealand oystercatchers when prizing bivalves open was also largely to the left, but not invariably so (Table 3). This predominant sinistralism occurred with similar frequency in the three species (G = 0.532, ns.).

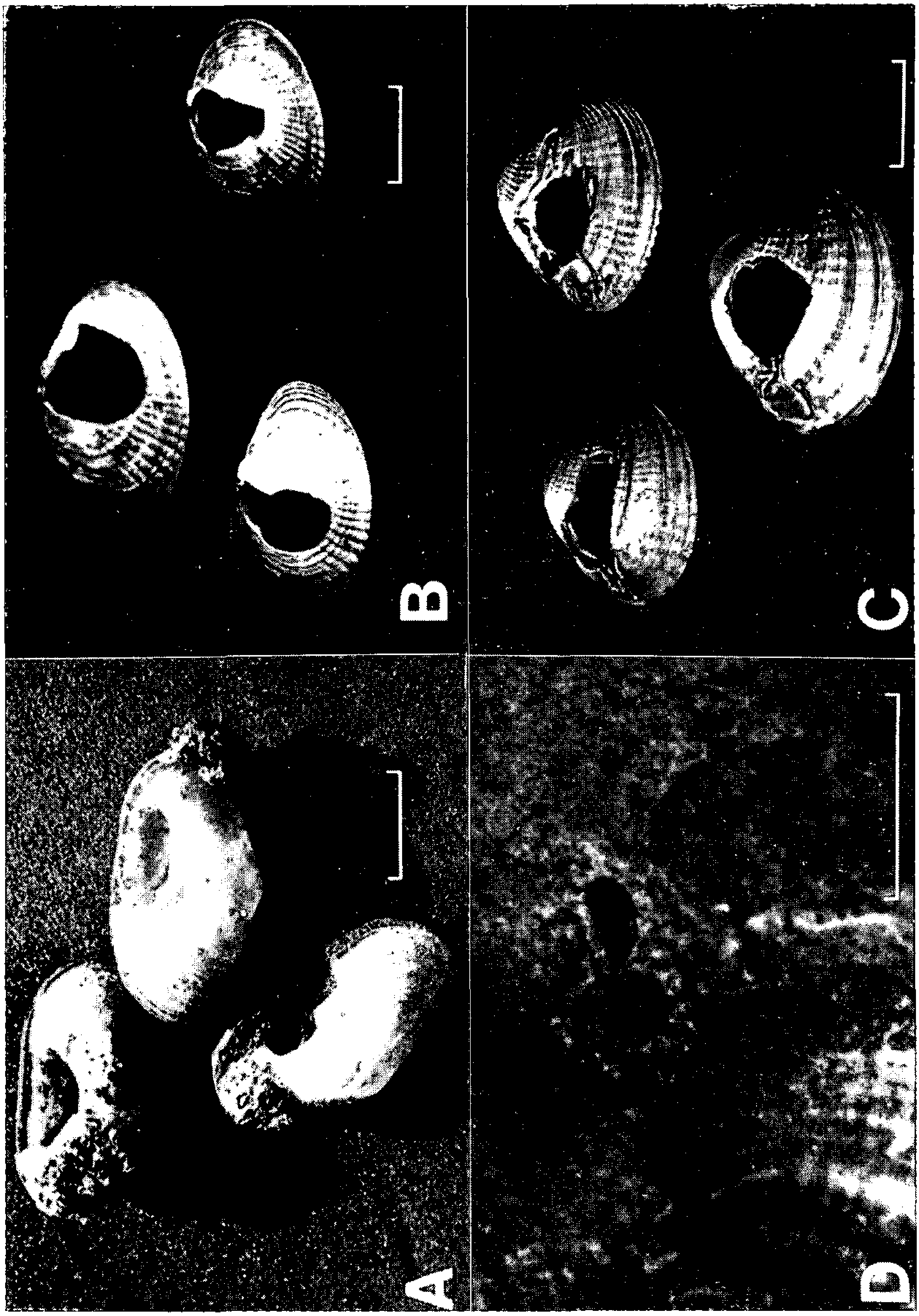

FIGURE 2 — (A) Shells of the pipi *(Paphies australe)* hammered at the ventral aspect.
(B) Shells of the cockle *(Chione stutchburyi)* hammered at the umbo.
(C) Shells of the cockle hammered at the site of borings by *Polydora ciliata.*
(D) A birds-eye view of the extended siphons of an actively feeding cockle, as seen from a height of 20 cm.

In each of the photographs the scale represents 1 cm.

Table 3. Direction of rotation by New Zealand oystercatchers when prizing open bivalves shells.

Species	Number of observations	Direction of rotation	
		to the left	to the right
South Island Pied Oystercatcher	31	28	3
Variable Oystercatcher	36	31	5
Chatham Islands Oystercatcher	24	22	2

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. I have been able to examine only seven skulls of New Zealand oystercatchers, none of which appear asymmetrical. Snyder & Snyder (1969) noted that the bill of the Limpkin *(Aramus guarauna)* was always curved to the bird's right, but found that this curvature was in the horny rhamphothecal covering rather than the underlying bones. The rhampathecae of oystercatcher bills may also be curved, but usually such curvature is very slight. In a sample of 100 bills of the South Island Pied Oystercatcher, 24 were curved to the left, 14 to the right and 62 were straight. It is therefore unlikely that sinistral rotation causes curvature of the rhamphothecae in this species. Conversely, sinistralism could not be interpreted as a behavioural adaptation to exploit a morphological peculiarity.

The location of gaping bivalves was not always followed by a successful piercing probe. Bivalves occasionally escaped the piercing probe by drawing their valves firmly together. These closed shells were 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 upward.

Firmly closed bivalves which had been dug up were dealt with by two methods: hammering and thrusting. The shell was usually opened by hammering the valves with the point of the bill. Hammering was continued until a hole was made in the shell, and this initial hole was enlarged until the body of the mollusc could be removed through it. At the Heathcote-Avon estuary, shells of both the cockle *(Chione stutchburyi)* and the pipi *(Paphies australe)* were hammered. The position at which the shell was hammered differed for cockles and pipis. The valves of the cockles were hammered in the region of the umbo, which is the thinnest part of the shell, because shell deposition occurs at the margin (see Fig. 2B). Where the valves had been bored by the marine boring worm *(Polydora ciliata)*, South Island Pied

Oystercatchers hammered at this region of weakness in preference to the umbo (see Fig. 2C). Of a sample of 100 opened shells weakened by borers, 92 were hammered at borer sites.

In contrast to cockles, the valves of pipis were 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. Hammering usually resulted in the fracture of a valve at its ventral border (see Fig. 2A). The bird's bill was then inserted through the chipped region of the shell and the body of the pipi extracted.

In sharp contrast to estuarine bivalves, the shells of bivalves on oceanic beaches do not appear to be hammered at all, but instead are opened by thrusting the point of the bill against the persistent gape at the anterio-ventral margin of a tightly closed shell. This change in feeding methods is presumably necessitated by changes in the thickness of shells in estuarine and oceanic environments. Oceanic cockle shells are noticeably thicker than estuarine ones (Baker 1969) and thus are probably too thick to hammer.

Mussels:

Variable Oystercatchers and Chatham Islands Oystercatchers were seen opening the blue mussel *(Mytilus edulis aoteanus)* and the small mussel *(Xenostrobus pulex)* during this study. When covered by shallow water, gaping mussels were pierced between the valves and pried 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 were removed from the substrate and oriented with their flatter ventral side upwards, but large mussels in excess of about 6 cm were hammered *in situ,* with both the ventral and dorsal borders being hammered depending on which aspect was presented uppermost. Norton-Griffiths (1967) has shown that the taking of closed mussels *(Mytilus edulis)* from hard substrates by European *H. ostralegus* depends upon the birds' strength in overcoming byssal attachment. Unless closed 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. As suggested by Heppleston (1971), it seems probable that oystercatchers hammer both borders of larger mussels because they are unable to remove them from the substrate and orientate them. Dense concentrations of small mussels which were less than 2 cm in length were dealt with simply by tearing shells from the substrate and swallowing them whole. Birds feeding in this manner shed faeces which were full of crushed shell fragments. South Island Pied Oystercatchers were never observed feeding on mussels during this study, but Jackson (1964) recorded birds levering them open in Manukau Harbour.

Limpets and chitons:

On rocky shores limpets and chitons form a major portion of the food of New Zealand oystercatchers. Only the Variable Oystercatcher consistently took large limpets such as *Cellana denticulata,* *C. radians,* and *C. flava,* probably because this species alone possesses a robust bill and correspondingly massive musclature (Baker 1974). Chatham Islands Oystercatchers were occasionally seen taking limpets from rocky shores on Rangatira Island, but only small shells less than 4 cm in length were attacked.

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 inspected most limpets and usually only attacked those displaying a gap. When a suitable limpet was located, the bird lowered its head, and delivered a sharp horizontal blow on the side of the shell with the bill. Small limpets were usually knocked over by this blow, but with larger limpets, several blows were required to loosen the grip of the muscular foot. Once the grip was weakened the bird then pushed against it with its bill tip until the shell was dislodged. If pushing was unsuccessful in dislodging the limpet, the bill was forced under the shell and levered against the substrate until the shell toppled over. The contents of the shell were removed by placing the upturned limpet in a suitable crevice, and paring the flesh from the shell with scissor-like movements of the bill.

All New Zealand species of oystercatchers take chitons from rocky shores. To remove chitons from rocks a sharp, angled blow was delivered on the shell plates. If the mollusc was not dislodged by this first attempt, the bird then applied lateral pressure to the margin of the foot until a small area was detached. The bill was then pushed under the chiton, flat side against the rock, and the animal cut from the rock by scissor-like movements of the bill. The flesh was removed in one piece and swallowed whole. Both the snakeskin chiton *(Sypharochiton pelliserpentis)* and the green chiton *(Amaurochiton glaucus)* were dealt with in this way.

Gastropods:

Gastropods such as the mudsnail *(Amphibola crenata)* and the common topshell *(Melagraphia aethiops)* were taken in a similar manner to that described by Dewar (1910) for the purple shell *(Purpura lapillus)*. The bill was inserted into the aperture and pressure applied against the wall of the outside whorl, resulting in a small circular hole being chipped through the shell opposite to the operculum. The shell was then rotated until the chipped hole was presented uppermost. In this position the bill was inserted into the hole and leverage applied towards the apex of the shell uisng the outside whorl as a fulcrum. Under this pressure the dorsal aspect of the shell fractured, and the exposed soft-parts were removed. 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 made them a relatively unutilised prey. During the course of this study only South Island Pied Oystercatchers were seen to take mudsnails.

Smaller gastropods such as the common mud whelk *(Cominella glandiformis)* and the small horn shell *(Zeacumantus subcarinatus)* were swallowed whole and the shells crushed in the gut. Birds feeding on these small gastropods defecated shell fragments and opercula.

Crabs:

Crabs *(Helice crassa* and *Hemigrapsis edwardsii)* were taken very efficiently by New Zealand oystercatchers. Captured prey were placed on their backs, and stabbed with the bill in the region of the supraoesophageal ganglia until immobilized. The flesh was then rapidly removed from the carapace. Similar prey-specific behaviour was noted for the European Oystercatcher when feeding on the shore crab *(Carcinus maenas)* (Tinbergen & Norton-Griffiths 1964).

FACTORS AFFECTING FEEDING BEHAVIOUR

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, when they took shelter in less exposed areas. The greatest modifying factor influencing feeding behaviour was 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 was 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 were sometimes prevented from taking prey when the exposed beach was frozen.

Physical factors:

The water content of the substrate probably determined whether bivalves were opened *in situ* or carried ashore for opening on firmer ground. As noted by Drinnan (1957) the water content of the sand, and therefore its resistance to pressure, appears to be important in opening shells. Chapman (1949) has shown experimentally that the resistance of a sandy surface to penetration increases markedly up the shore, mainly due to increased drainage.

The carrying of shells ashore for opening at the Heathcote-Avon estuary was most evident where the substrate was composed largely of sand. Although some pipis were opened at their site of capture, the majority were pierced and carried up onto the beach. The birds used two methods to locate an area of sand sufficiently firm to allow the shells to be opened:

(a) Random wandering, opening being attempted at intervals of a few metres until a suitable area was located.
(b) Flying up to the supralittoral zone of the beach where the sand was firm enough to support opening attempts.

At the Heathcote-Avon estuary cockles were carried ashore less frequently than pipis. On the feeding grounds near the upper end of the estuary, cockles were carried only short distances from the water, probably because the drainage of the mud was so poor that there were no significant differences in water content (and thus surface resistance) over the shore. The three New Zealand species of oystercatchers all carried pierced shells ashore when feeding in sandy habitats.

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 sand to form " feeding piles." Heppleston (1971) also noted the same behaviour when this species was feeding on mussels. Davidson (1967) suggested that the formation of these piles was to provide a firmer surface on which to open shells. Aggregations of predated shells were not seen during this study, indicating that New Zealand oystercatchers do not form feeding piles.

Competition:

Both interspecific and intraspecific competition influence feeding behaviour. The Red-billed Gull *(Larus novaehollandiae scopulinus)*, the Black-backed Gull *(L. dominicanus)* and the Eastern Bar-tailed Godwit *(Limosa lapponica baueri)* all compete with oystercatchers for food. The two species of gulls were " parasitic " on the oystercatchers, stealing food which the latter had located. Oystercatchers feeding in shallow water were commonly followed by both species of gulls, and when a bird located and pierced a bivalve, it was frequently harassed by two or three gulls until the bivalve was dropped or eaten. When the tide first began to expose the feeding grounds, harassment was often acute because feeding flocks were confined to small emergent areas. Oystercatchers feeding on the pipi beds of the Heathcote-Avon estuary near high water were frequently robbed of their prey. However, as the gull population was small (*ca.* 200 birds) in comparison with that of oystercatchers (*ca.* 4000 birds), competition from this source was not serious, especially at low water periods when large feeding grounds were exposed.

When harassment from gulls was temporarily severe, oystercatchers modified their feeding behaviour to reduce competitive interactions. Pierced bivalves which would normally have been carried ashore for opening were opened where they were located. In this manner, the prey could be opened and devoured before gulls were able to effectively harass them. However, localised opening of prey resulted in a higher incidence of failures at shell opening because the substrate was often too soft to support the pressure of the opening attempt.

Competitive interactions were greatest between juvenile Red-billed Gulls and South Island Pied Oystercatchers. Tinbergen & Norton-Griffiths (1964) noted a similar interaction between European Oystercatchers and juvenile Black-headed Gulls *(Larus ridibundus);*

they attributed this behaviour to the fact that the young gulls had not yet learned to fear the oystercatchers' bills. Variable Oystercatchers were rarely menaced by " parasitic " gulls, their larger body size apparently inhibiting attacks.

Godwits provide direct, but non-aggressive competition for oystercatchers as they prey on the same food species. During this study interspecific interactions with godwits were never noted even when they were feeding amongst oystercatcher flocks. At the Heathcote-Avon estuary the effects of competition from godwits were reduced by partial species segregation within the feeding habitat.

Intraspecific fighting was relatively rare, probably because food was abundant at the major wintering haunts. Densities of birds during periods of maximum feeding intensity were as high as one bird per m^2 before competitive interactions became apparent. Interactions almost always took the form of threat postures which frequently culminated in a piping display. Piping displays and fighting were most apparent at the beginning of each new feeding period as the birds were hungriest at this time and were confined to small exposed areas of the feeding grounds.

SPECIES DIFFERENCES IN FEEDING BEHAVIOUR

It is evident from the foregoing that the New Zealand species of oystercatchers differ in their feeding behaviour. Of the two mainland species, the South Island Pied Oystercatcher is behaviourally adapted to exploit estuarine bivalves, whereas the Variable Oystercatcher has strongly developed behaviour patterns for preying on limpets and chitons on rocky shores. Although both species probably possess the same repertoire of prey-specific feeding behaviour, the Variable Oystercatcher is excluded from estuarine habitats in areas of significant species overlap by its small congener (Baker 1969). Conversely, the larger Variable Oystercatcher is adaptively superior on rocky habitats where it alone, by virtue of its larger bill and associated muscles, can efficiently exploit limpets and chitons (Baker 1974). The Chatham Islands Oystercatcher seems behaviourally intermediate to the mainland species in its feeding methods which is consistent with its intermediate morphology. This species feeds in widely varying habitats ranging from sandy and gravelly beaches on Chatham Island to rocky shores on Rangatira and Mangere Island, and thus there would be considerable adaptive advantage in maintaining behavioural flexibility to exploit efficiently a range of habitats. It seems likely that the differential habitat utilization described above has been an important factor in the speciation of New Zealand oystercatchers.

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LITERATURE CITED

BAKER, A. J. 1969. The comparative biology of New Zealand oystercatchers. Unpublished M.Sc. thesis, University of Canterbury. Pp. 1-222, text-figs 1-37, tables 1-20, pls 1-68.

——— 1974. Ecological and behavioural evidence for the systematic status of New Zealand oystercatchers. Life Sciences Contributions, Royal Ontario Museum, No. 96. Pp. 1-34, text-figs 1-11, tables 1-7.

BAYNE, C. S. 1940. Feeding-habits of the Oyster-catcher and Turnstone. British Birds 34 (5): 111-112.

CHAPMAN, G. 1949. The thixotrophy and dilatancy of a marine soil. Journal of the Marine Biological Association of the United Kingdom 28 (1): 123-140, text-figs 1-6, tables 1-4.

DARE, P. J.; MERCER, A. J. 1973. Foods of the Oystercatcher in Morecambe Bay, Lancashire. Bird Study 20 (3): 173-184, text-fig 1, tables 1-3.

DAVIDSON, P. E. 1967. A study of the Oystercatcher (*Haematopus ostralegus* L.) in relation to the fishery for cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. Ministry of Agriculture, Fisheries and Food, Investigation Series II, 25 (7): 1-28, text-figs 1-6, tables 1-9, pls 1-4.

DEWAR, J. M. 1908. Notes on the Oyster-catcher *(Haematopus ostralegus)* with reference to its habit of feeding upon the mussel *(Mytilus edulis)*. Zoologist 12 (804): 201-212.

——— 1910. A preliminary note on the manner in which the Oyster-catcher *(Haematopus ostralegus)* attacks the purple-shell *(Purpura lapillus)*. Zoologist 14 (825): 109-112.

——— 1913. Further observations on the feeding habits of the Oyster-catcher *(Haematopus ostralegus)*. Zoologist 17 (860): 41-56.

——— 1915. The relation of the Oyster-catcher to its natural environment. Zoologist 19 (890): 281-291.

——— 1922. Ability of the Oyster-catcher to open oysters, and its bearing upon the history of the species. British Birds 16 (5): 118-125.

——— 1940. Identity of specialized feeding-habits of the Turnstone and Oyster-catcher. British Birds 34 (2): 26-28.

DRINNAN, R. E. 1957. The winter feeding of the Oystercatcher *(Haematopus ostralegus)* on the edible cockle *(Cardium edule)*. Journal of Animal Ecology 26 (3): 441-469, text-figs 1-7, table 1, pls 1-3.

——— 1958. The winter feeding of the Oystercatcher *(Haematopus ostralegus)* on the edible mussel *(Mytilus edulis)* in the Conway estuary, North Wales. Ministry of Agriculture, Fisheries and Food, Investigation Series II, 22 (4): 1-15, text-figs 1-6, table 1.

HEPPLESTON, P. B. 1971. Feeding techniques of the Oystercatcher. Bird Study 18 (1): 15-20, text-fig 1, table 1.

HULSCHER, J. B. 1964. Scholeksters en lamellibrachiaten in den Waddenzee. De Levende Natuur 67 (2): 80-85.

JACKSON, R. W. 1964. Notes on South Island Pied Oystercatchers. *In* New Zealand Recording Scheme, Ornithological Society of New Zealand. Pp. 4. Mimeographed.

LEGG, K. 1954. Nesting and feeding of the Black Oystercatcher near Monterey, California. Condor 56 (6): 359-360, table 1.

McKENZIE, H. R. 1963. Notes on South Island Pied Oystercatchers. *In* New Zealand Recording Scheme, Ornithological Society of New Zealand. Pp. 3. Mimeographed.

NORTON-GRIFFITHS, M. 1967. Some ecological aspects of the feeding behaviour of the Oystercatcher *(Haematopus ostralegus)* on the edible mussel *(Mytilus edulis)*. Ibis 109 (3): 412-424, text-figs 1-9, tables 1-4.

OLIVER, W. R. B. 1955. New Zealand birds. 2nd ed., rev. and enlarged. Pp. 1-661, text-illus., 12 unnumb. col. pls. Wellington: A. H. & A. W. Reed.

SNYDER, N. F. R.; SNYDER, H. A. 1969. A compartive study of mollusc predation by Limpkins, Everglade Kites and Boat-tailed Grackles. The Living Bird No. 8: 177-223, text-figs 1-39.

SOKAL, R. R.; ROHLF, F. J. 1969. Biometry. The principles and practice of statistics in biological research. Pp. 1-776, text-figs 1-89, tables 1-58. San Francisco: W. H. Freeman & Co.

STRESEMANN, E. 1929. Aves. *in:* Handbuch der Zoologie 7 (2): 438-439, text-illus. Berlin: De Gruyter.

TINBERGEN, N.; NORTON-GRIFFITHS, M. 1964. Oystercatchers and mussels. British Birds 57 (2): 64-70, pls. 9-12.

TOMPKINS, I. R. 1947. The Oystercatcher of the Atlantic coast of North America and its relation to oysters. Wilson Bulletin 59 (4): 204-208.

WEBSTER, J. D. 1941. The feeding habits of the Black Oystercatcher. Condor 43 (4): 175-180.

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