Fld Stud. (1973), 3, 738–800

FEEDING PATTERNS OF WADING BIRDS ON THE GANN FLAT AND RIVER ESTUARY AT DALE

By J. M. EDINGTON, P. J. MORGAN* and R. A. MORGAN†

Department of Zoology, University College, Cardiff

In autumn large mixed-species flocks of wading birds congregate in a system of coastal habitats near Dale. Although the Gann Flat, a muddy beach, is the major feeding area for all the common species, the species are often separated, on a small scale, because they use different horizontal and vertical feeding zones. This spatial separation of species can often be correlated with their morphology and behaviour and in some cases appears to have the effect of subdividing the food resources in the habitat. Such a subdivision of food resources is likely to facilitate the coexistence of a diversity of species in the same general habitat.

INTRODUCTION

THE estuary of the River Gann and the associated beach known as the Gann Flat are situated in a north-west inlet of Milford Haven close to the village of Dale (O.S. map ref. 12/814070). They form part of a complex of coastal habitats which also includes a brackish lagoon (Pickleridge Lagoon) and an extensive salt marsh (Fig. 1a). The investigation described here concerns the feeding behaviour of some of the wading birds which congregate in the area during the autumn. Particular attention was given to the way in which different habitat zones were used by the various wader species. The observations were made in the second half of September during five annual field courses (1965–1970) run by University College, Cardiff, from Dale Fort Field Centre.

The details of the study area are shown in Fig. 1a. The Gann Flat includes a wide diversity of substrata and its physical features and invertebrate fauna have been described in detail by Bassindale and Clark (1960). At low water of spring tides a broad expanse of sand and mud is exposed on the lower part of the beach and this sand and mud area extends to the high tide level in a central strip (Fig. 1a, zones 4 and 7). On either side of this strip are areas consisting of a mosaic of bedrock, shingle, sand and mud. Fucoid seaweeds cover much of the bedrock area (Fig. 1a, zones 3, 5, 6, 8).

At the head of the beach is a shingle bank on which a series of strand lines are formed (1). Behind this shingle bank is a brackish lagoon, Pickleridge Lagoon (9) which is occasionally flooded by spring tides. The River Gann is tidal to above Mullock Bridge and runs in a muddy channel which widens at its lower end to form the Gann Pool (12, 10). An extensive salt marsh to the west of the river channel is dissected by a system of tidal creeks (11). At the northern edge of the marsh are two freshwater lagoons (13) which serve as settling ponds for a sand and gravel works.

In Table 1 a list is given of the species recorded in the area during the September periods. Seven species dominated the flocks and their relative abundance was fairly constant from year to year. Typical numbers of these species were as follows: Curlew 100–200, Oystercatcher, Redshank and Turnstone 50–150 each, Ringed

* Now at Liverpool Museum, William Brown Street, Liverpool.
† Now at the British Trust for Ornithology, Tring, Herts.

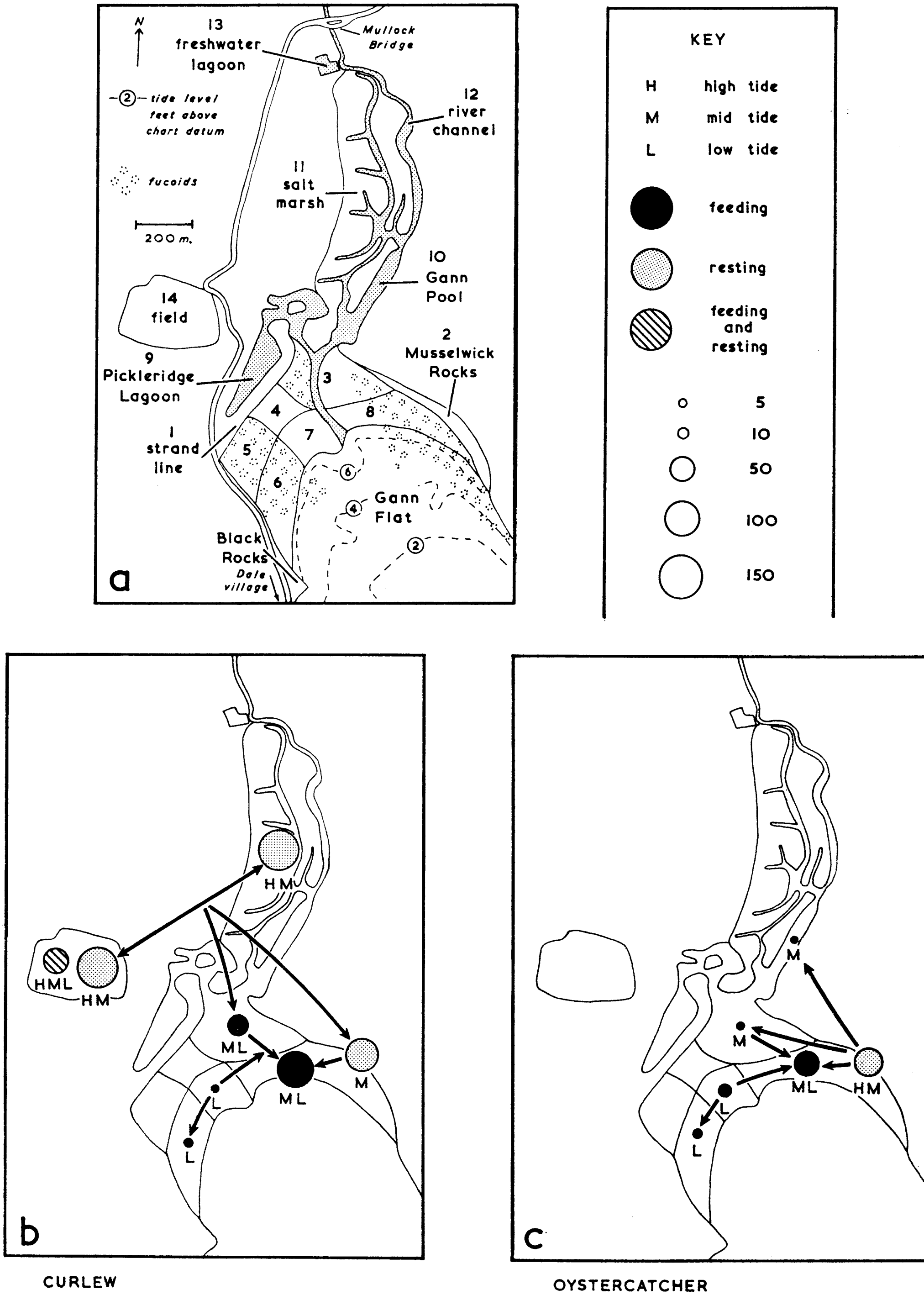

Fig. 1.

(a) Map of Study Area.

(b) (c) Movements of Curlews and Oystercatchers on the outgoing tide of 21 September 1970. The tidal range was 14·4 feet (mean tidal ranges for area were neap tides 9·1 feet, spring tides 20·8 feet).

Plover *c.* 25, Dunlin *c.* 10 and Greenshank *c.* 10. In 1969 Greenshanks were unusually abundant and 60 birds were present. Lapwings sometimes visited the beach in large numbers (e.g. 120) but they were not a regular component of the feeding flocks.

Table 1. *List of wading birds recorded from autumn flocks (1965–1970)*

Major Species		Status in Dale area		
Oystercatcher	*Haematopus ostralegus*	R	PM	WV
Ringed Plover	*Charadrius hiaticula*		PM	WV
Curlew	*Numenius arquata*		PM	WV
Redshank	*Tringa totanus*		PM	WV
Greenshank	*Tringa nebularia*		PM	WV
Turnstone	*Arenaria interpres*		PM	WV
Dunlin	*Calidris alpina*		PM	WV
Lapwing	*Vanellus vanellus*	R	PM	WV
Minor Species				
Grey Plover	*Pluvialis squatarola*		PM	WV
Golden Plover	*Pluvialis apricaria*		PM	WV
Bar-tailed Godwit	*Limosa lapponica*		PM	WV
Spotted Redshank	*Tringa erythropus*		PM	
Green Sandpiper	*Tringa ochropus*		PM	
Common Sandpiper	*Tringa hypoleucos*		PM	
Snipe	*Gallinago gallinago*		PM	WV
Knot	*Calidris canutus*		PM	WV
Sanderling	*Calidris alba*		PM	WV
Little Stint	*Calidris minuta*		PM	
Curlew Sandpiper	*Calidris ferruginea*		PM	
Ruff	*Philomachus pugnax*		PM	

R = Breeding Resident. PM = Passage Migrant. WV = Winter Visitor.

The remaining minor species (Table 1) never numbered more than 10 individuals per species in any year. The bird records for Dale compiled by Barrett (1959) suggest that most of these minor species were passage migrants which were likely to form only a transient component of the wader flocks. All the major species in addition to visiting the area as passage migrants also formed part of the winter population. By concentrating on these latter species it was hoped to gain some insight into the interactions between species which coexisted in the same area for many months of the year. Scale drawings of these species are given in Fig. 3.

Movements of Birds Between Feeding and Resting Sites

It became evident when observations were started in 1965 that the birds moved regularly with the tide from their resting places to their feeding grounds. During subsequent years the typical patterns of movement were worked out. All species rested during high tide at various sites adjacent to the shore. As the tide receded the majority of birds moved on to the beach to feed and these movements were reversed as the tide returned. The birds fed on the beach at low tide irrespective of whether low tide occurred at night or during the day.

Tidal range was the main factor which caused variations in the pattern of movements. The birds spent more time feeding in the river channel, creeks and lagoons during neap tides than during spring tides. This was probably because during neap tides only limited areas of the lower beach were exposed. The plotting of bird movements was carried out by observers (usually a team of four) stationed at suitable vantage points throughout the area. The exercise was repeated on a series of tides with different tidal ranges each year. Figs. 1 (b) and (c) and 2 show a typical plot of bird movements, in this instance relating to the outgoing tide of 21 September 1970, a tide of moderate range. The movements shown by the seven common species will now be considered in turn.

Curlew

Every year the Curlews used the saltmarsh and various fields surrounding the estuary as high tide resting places. During high tide they usually alternated between these sites according to the pattern of disturbance (Fig. 1b). Some birds, about 60 in 1970, remained in the field during the whole tidal cycle and were seen probing for food in the soil. The remainder moved during mid tide either to Musselwick Rocks or to the first fucoid areas to be exposed. At low tide the birds were generally distributed on sand, mud and fucoid areas on the lower parts of the beach. The eastern side was generally favoured (Fig. 1b). This was the case with a number of species and was probably due to the repeated disturbances of birds on the west side by holidaymakers. The Curlews, in common with the Oystercatchers, Redshanks and Greenshanks, appeared to use Musselwick Rocks as a mid tide vantage point on the outgoing tide. On the incoming tide they by-passed this site and dispersed progressively to high tide resting places.

Oystercatcher

In most years the movements of Oystercatchers were similar to those of the Curlews. They rested in the fields at high tide, moved on to Musselwick Rocks at mid tide and subsequently on to the beach. The shinglebank in Pickleridge Lagoon was an alternative high tide resting place for some birds.

The movements of Oystercatchers in 1970 (Fig. 1c) were different from those of previous years in that the birds rested at high tide on Musselwick Rocks.

Redshank and Greenshank

The Redshanks used various high tide resting places. One group was usually to be found on Musselwick Rocks and the remainder alternated between the salt marsh and the sand bars in Pickleridge Lagoon (Fig. 2b). The majority of birds moved to Musselwick Rocks at mid tide and then on to the beach to feed. During most tides another group, at least 15 per cent of the total flock, remained in the tidal creeks of the salt marsh and fed there during mid and low tide. This separation of the Redshank flock was recorded each year. During neap tides, when only a small area of the beach was exposed, a larger proportion of birds fed in the creeks and also in Pickleridge Lagoon. The Greenshanks resembled the Redshanks in their pattern of movements (Fig. 2a). In this species, too, a group of birds remained in the salt marsh creeks to feed during mid and low tides.

Ringed Plover

The Ringed Plovers made only very limited movements in relation to the tidal cycle. Typically they spent high tide and part of mid tide resting on the shingle bank in Pickleridge Lagoon, a site where their disruptive coloration was extremely effective. During mid tide they moved on to the upper part of the beach to feed and remained there until the tide returned (Fig. 2d). Occasionally they also fed on the

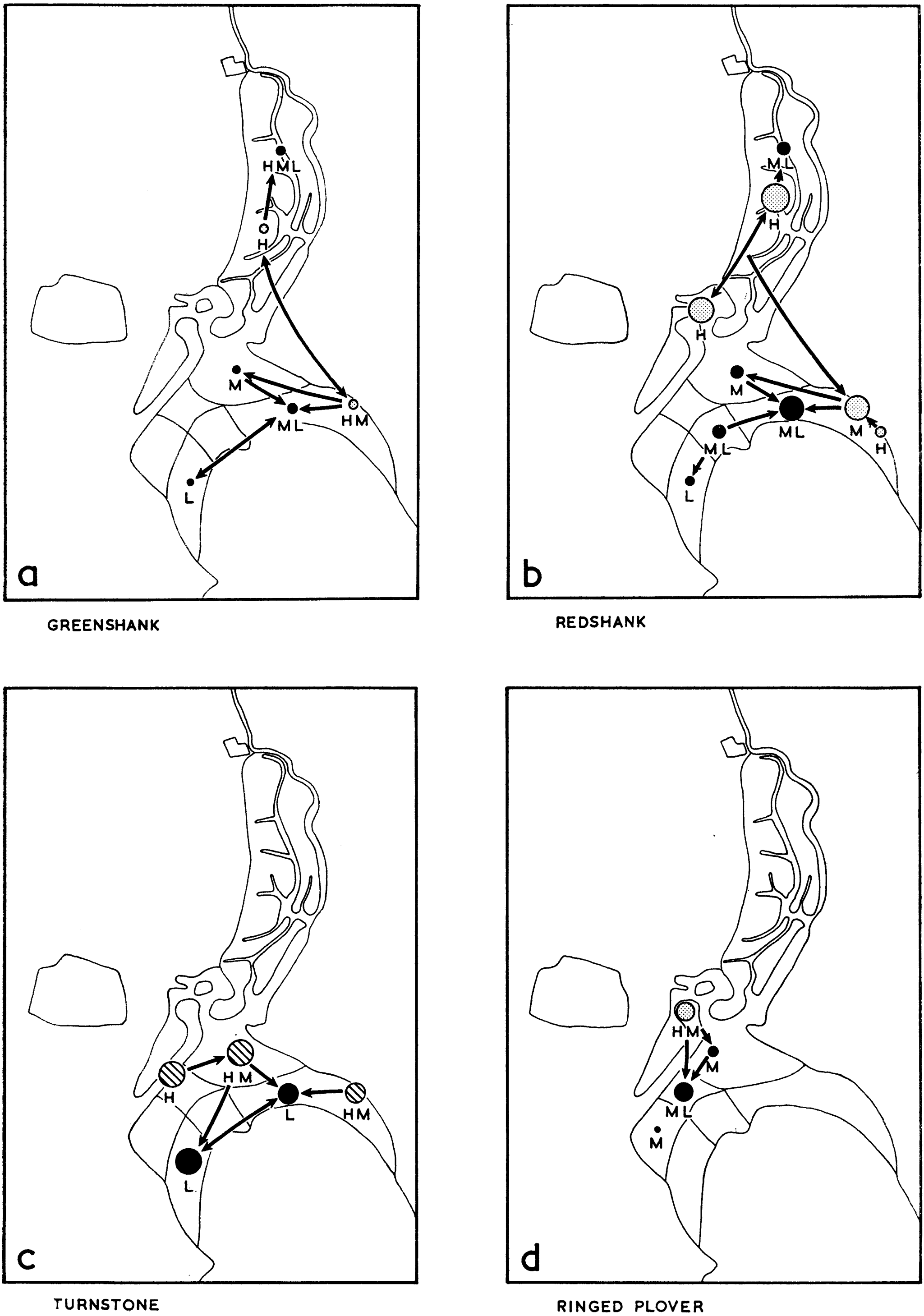

Fig. 2.

Movements of: Greenshanks (a), Redshanks (b), Turnstones (c), and Ringed Plovers (d), on the outgoing tide of 21 September 1970. Symbols as for Fig. 1.

mud at the lower end of the Gann Pool. During high water of neap tides they sometimes remained on the strand line.

Turnstone

The Turnstones spent the high tide period along the strand line and on Musselwick Rocks or Black Rocks (Fig. 2c). In contrast with the species described so far, the Turnstones did not rest continuously during high tide but showed alternating periods of rest and feeding activity. As the tide receded the birds moved progressively down the beach. They reversed their movements on the incoming tide. Variations in tidal range had little effect on the movements of either Turnstone or Ringed Plover.

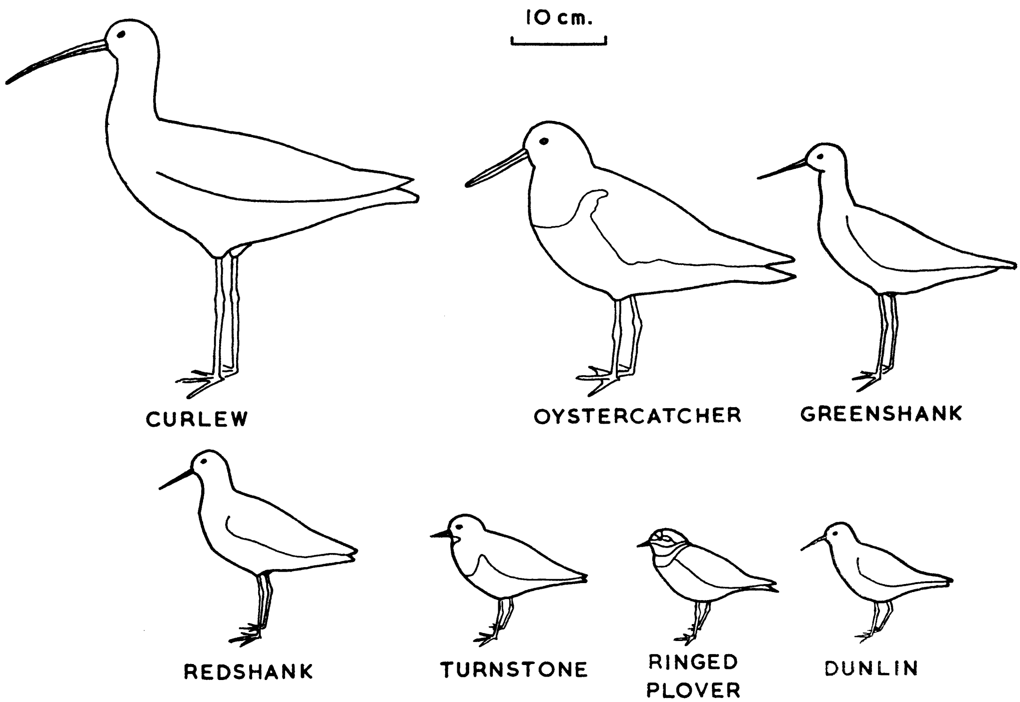

Fig. 3.
Scale drawings of the seven common wader species in the Gann System.

Dunlin

The Dunlins in the area did not all behave in the same way. Typically one group was associated with the Ringed Plovers, resting with them on the shingle bank and feeding in the same area on the upper beach. Another group associated itself initially with the Turnstones and fed with them along the strand line at high tide. As the tide receded the two species usually separated, the Dunlins remained to feed on the upper beach and the Turnstones moved on to the fucoid zone.

The feeding pattern of the Dunlins was greatly affected by tidal range. During neap tides they made much use of the salt marsh creeks and a group of four or five were usually to be found feeding in the freshwater lagoon throughout the tidal cycle.

From these observations on bird movements it was apparent that the Gann Flat was the primary feeding site for the seven major species. The river channel and salt marsh creeks provided a secondary feeding site for Redshank, Greenshank and Dunlin. This increased in importance during neap tides. Minor feeding sites included the fields adjacent to the estuary which were used by some Curlews, and the freshwater and Pickleridge Lagoons which were used by small groups of a number of species especially during neap tides. The vegetated part of the salt marsh was apparently not used by any of the major species for feeding.

Table 2 shows the maximum number of birds of each species feeding in the various sites during the September periods of 1969 and 1970. The table illustrates the importance of the Gann Flat and the river channel and creeks as feeding areas.

Table 2. *Maximum numbers of birds feeding in each site during the study periods in September 1969 and 1970*

	Freshwater Lagoon	Pickleridge Lagoon	Salt Marsh	Fields	River Channel and Creeks	Gann Flat
1969:						
Curlew	—	3	—	50	10	150
Oystercatcher	—	—	—	—	5	80
Greenshank	—	2	—	—	7	60
Redshank	2	—	—	—	30	130
Dunlin	5	3	—	—	6	12
Ringed Plover	—	—	—	—	10	20
Turnstone	—	—	—	—	3	100
1970:						
Curlew	—	—	—	50	—	140
Oystercatcher	—	—	—	—	5	75
Greenshank	—	—	—	—	5	10
Redshank	—	5	—	—	10	75
Dunlin	7	—	—	—	10	12
Ringed Plover	—	—	—	—	4	23
Turnstone	—	—	—	—	—	60

The use of the same general feeding areas by a number of species raised the question of whether each species was using the habitat in the same way. This was investigated in detail for the Gann Flat and in a more limited way for the river channel and creeks.

Distribution and Feeding Behaviour of Waders

(A) *The Gann Flat*

On the Flat there was a wide range of situations from which the birds could seek food. The substrata on the exposed parts of the beach included bare sand, mud and shingle, also areas covered by fucoid seaweed or the green seaweed *Enteromorpha*. The submerged sites included shallow pools widely distributed on the beach, deep water sites at the tide edge and areas of running water associated with the river and lagoon outflows. There was clearly the possibility that the species might use these various microhabitats to different extents or penetrate them to different depths. In order to investigate the possible separation of species on this small scale the beach was divided into a series of horizontal and vertical zones.

Eight horizontal zones were recognized (Fig. 4) and the amount of feeding taking place in each zone was estimated for the different species. The method of scoring was as follows. The period extending from 3 hours before low tide to 3 hours after low tide included the main feeding period of all species, with the possible exception of Turnstone. Every 20 minutes during this 6-hour period, the entire beach was scanned and every feeding bird was scored in the appropriate habitat category. In practice separate observers recorded for the western and eastern halves of the beach. This method seemed to work well except when the birds were repeatedly disturbed by holidaymakers, when bird movements were so extensive that there was the risk of some groups being counted twice or missed altogether.

In September 1970 four such counts were made and gave generally similar results. The most complete of these (20 September) is reproduced in Table 3 and in Fig. 4. Fig. 4 shows the use each species made of the various habitat categories.

It was apparent that there were differences in the feeding zones used by the long-legged and the short-legged species. Leg lengths are compared on the scale drawings in Fig. 3 and "tarsus" (more correctly tarso-metatarsus) lengths are given in Table 4.

Only the long-legged waders, Curlew, Oystercatcher and Redshank made use of the deep-water habitat at the tide edge. The Greenshank also came into this category but was present in only very small numbers during this count. The exposed *Enteromorpha* and shingle zones situated on the upper parts of the beach were likewise

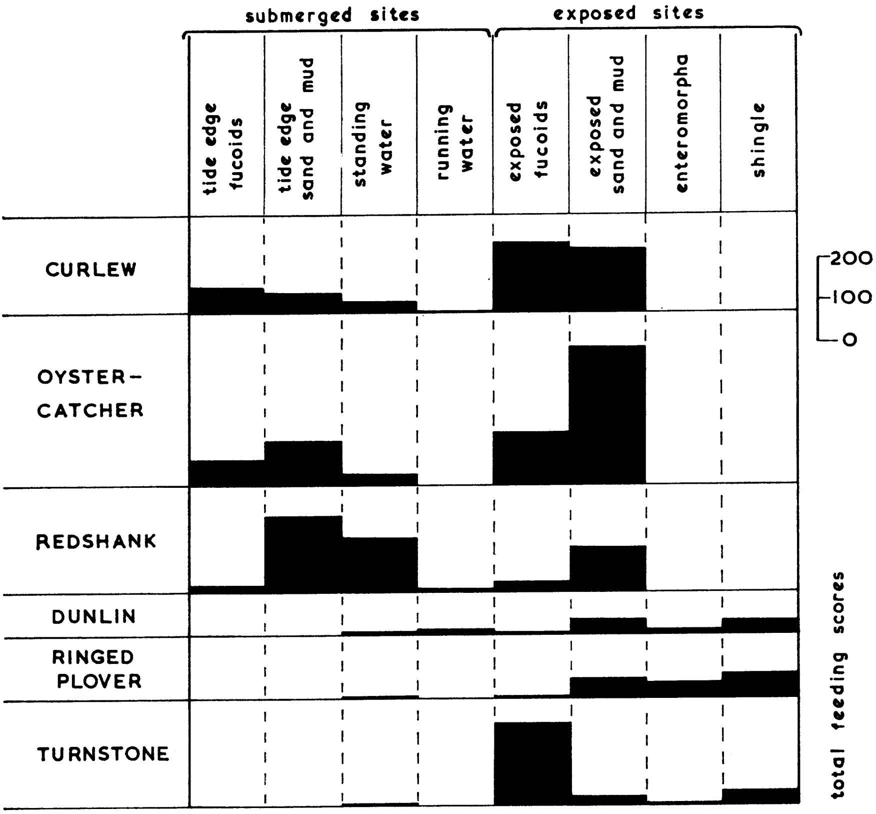

Fig. 4.
Horizontal feeding patterns, use made by each species of eight habitat categories.

Table 3. *Feeding scores of each species in eight habitat categories on 20 September 1970 (percentages in parenthesis). Low tide was 4·3 feet above chart datum*

	Submerged sites				Exposed sites				
	Tide edge fucoids	Tide edge sand and mud	Standing water	Running water	Exposed fucoids	Exposed sand and mud	Entero-morpha	Shingle	Total score
Curlew	61 (13·1)	50 (10·8)	30 (6·5)	2 (0·4)	167 (36·0)	154 (33·2)	—	—	464
Oystercatcher	59 (9·4)	100 (15·9)	26 (4·2)	—	120 (19·1)	322 (51·4)	—	—	627
Greenshank	5	8	7	—	6	—	—	—	26
Redshank	13 (2·9)	175 (38·7)	128 (28·3)	7 (1·5)	23 (5·1)	106 (23·5)	—	—	452
Dunlin	—	—	5 (5·0)	11 (11·0)	1 (1·0)	34 (34·0)	12 (12·0)	36 (36·0)	99
Ringed Plover	—	—	2 (1·3)	1 (0·6)	7 (4·4)	48 (30·2)	41 (25·8)	60 (37·7)	159
Turnstone	—	—	5 (1·8)	—	196 (72·3)	23 (8·5)	10 (3·7)	37 (13·7)	271

Table 4. *Mean bill and "tarsus" lengths (cm.). Measurements taken from specimens in the National Museum of Wales*

	Curlew	Oyster-catcher	Green-shank	Redshank	Dunlin	Ringed Plover	Turnstone
Number measured	8	12	7	21	14	5	8
Bill length	11·5	7·3	5·5	4·1	3·1	1·4	2·2
Tarsus length	8·0	4·5	5·6	4·8	2·4	2·6	2·6

used by only a limited range of species, in this case, Dunlin, Ringed Plover and Turnstone. The count for Turnstones underestimated the use of the shingle area, because the birds were also active in this area outside the 6-hour period covered by the count. Only the Dunlin used running water to any appreciable extent.

Fig. 4 shows that the remaining habitat categories: standing water, exposed fucoids and exposed sand and mud, were used to some degree by all the species although the actual amount of overlap between species was somewhat less than the diagram suggests. For example, when feeding in sand and mud, Dunlin and Ringed Plover concentrated on the upper parts of the beach, whereas the long-legged waders consistently used the lower parts of the beach (Figs. 1 and 2).

Thus although all seven waders fed on the beach, on a small scale there was some measure of horizontal separation between them. Further investigation showed that some of the species were also separated vertically.

One might expect that waders with long bills would use them to penetrate deep into sand and mud and thereby obtain food organisms which were not available to short-billed species. Certainly species feeding together on the shore often show a wide range of bill lengths (Green, 1968). However, there seems to be no quantitative information on the typical depths of probing by different species and some simple observations were made on the Gann Flat.

In order to gauge probing depths, the sand or mud was considered to be divided into a series of horizontal layers 3 cm. thick. When a bird probed, the depth of probe was scored using the bird's own bill for measurement. On the basis of its average length, the bill of each species was considered to be graduated at 3 cm. intervals starting from the tip. Thus the bill of the Curlew (average length 11·5 cm.) included four such divisions, Greenshank (average length 5·5 cm.) two divisions, Dunlin (average length 3·1 cm.) one division, and so on. It was then a relatively simple matter to record, according to the species under observation, how many divisions of the bill were buried in a probe and hence which 3 cm. layer was reached. The mean bill lengths for each species are given in Table 4.

It was not realistic to distinguish between feeding and exploratory probes, because whilst it was readily apparent when a bird secured a large food item, the capture of small organisms could not be detected with certainty.

Seven vertical feeding categories were recognized. These are listed in Table 5 and in Fig. 5. The category "surfaces" included birds pecking at any surface whether sand, mud, shingle or the surface of fucoid mounds. A distinction was made between a bird picking at the surface of a fucoid mound or shingle, an action recorded under "surfaces" and a bird penetrating into a fucoid mound or displacing shingle. In sand and mud, four depth categories were recognized each 3 cm. thick.

In many species the feeding pattern changed throughout the tidal cycle according

Table 5. *Vertical feeding patterns on Gann Flat expressed as percentage of feeding in each habitat category*

	Curlew	Oyster-catcher	Green-shank	Redshank	Dunlin	Ringed Plover	Turnstone
Total number of observations	1,620	690	541	532	1,420	1,127	2,010
All surfaces	9·5	23·6	7·7	44·3	36·8	98·7	6·0
Mud and sand:							
0–3 cm.	30·3	25·1	41·6	32·0	58·3	1·3	0·2
3–6 cm.	9·1	18·3	35·7	5·7	—	—	—
6–9 cm.	6·9	17·2	—	—	—	—	—
9–12 cm.	8·8	—	—	—	—	—	—
Overturning shingle	—	—	—	—	—	—	58·8
Probing into flucoids	35·4	15·8	15·0	18·0	4·9	—	35·0

to the parts of the beach which were exposed. For example, as the tide receded the Turnstones changed from stone-turning on the shingle areas to probing into fucoid mounds further down the beach. In view of this kind of variation in feeding behaviour the scores for each species were accumulated by recording feeding actions throughout a series of neap and spring tides in 1969 and 1970. Only a limited number of successive feeding records (about twelve) was taken from any particular bird.

Fig. 5 shows that there is a general correlation between bill length and depth of probing. Ringed Plover, the species with the shortest bill, fed almost exclusively from surfaces. Curlew, the species with the longest bill, was the only bird to use the 9–12 cm. zone. Between these two extremes, Dunlin, Redshank, Greenshank and Oystercatcher formed a series showing increasing depth penetration. It was interesting to notice that the longer-billed species did not appear to capitalize on their ability to probe deeper. For example, the 9–12 cm. zone which could be reached only by

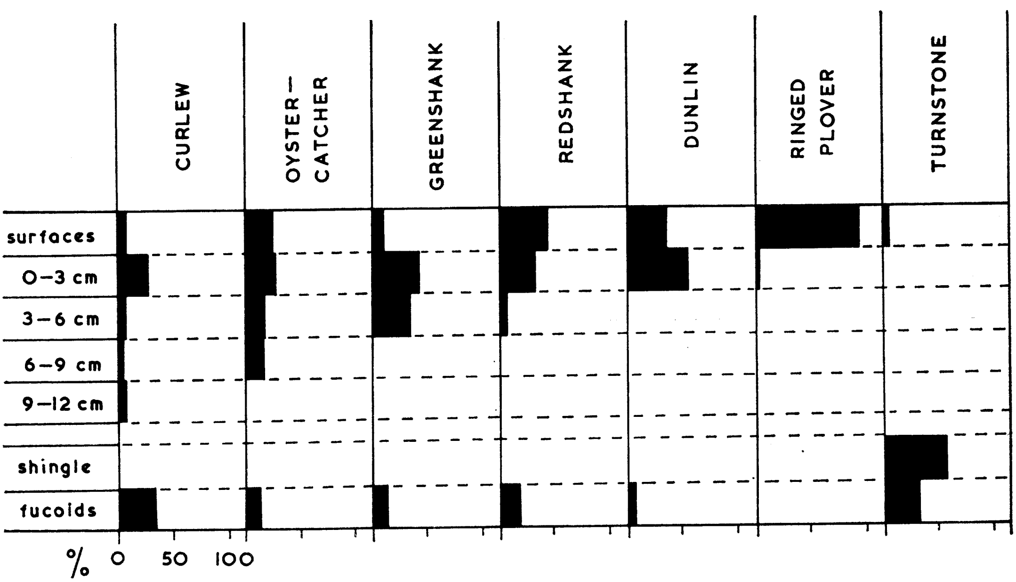

Fig. 5.

Vertical feeding patterns shown as percentage of feeding activity in each habitat category.

Curlew was not the layer most used by this species. In fact for all the five species probing frequently in sand and mud, the 0–3 cm. layer was the most important layer (Fig. 5).

In addition to probing into sand and mud, Curlew, Oystercatcher, Greenshank and Redshank also probed deep into fucoid mounds. Turnstone, too, gained access to fucoid mounds, not usually by simple probing, but by pushing back the frond layers. The Turnstone was the only species to reach organisms under stones (Fig. 5). As is well known, this is achieved by the bird pushing over stones with its bill, which is specialized for this purpose.

To some extent the vertical differences in feeding patterns seemed to separate species which had been found to overlap horizontally. For example, amongst the smaller waders frequenting the top of the beach the Ringed Plover was distinguished by being predominantly a surface picker. The Turnstone was distinguished by its stone turning and fucoid turning activities and the Dunlin by its probes into the 0–3 cm. layer of sand and mud.

(B) *The River Channel and Creeks*

Three species, Greenshank, Redshank and Dunlin, in addition to feeding on the Gann Flat also fed in the river channel and creeks (Table 2). A simple comparison was made of the feeding activities of Greenshank and Redshank in these sites (Table 6). As on the Gann Flat both species fed on exposed mud and submerged areas. When probing into exposed muds the Greenshank made more use than the Redshank of the 3–6 cm. layer. No comprehensive observations were made on Dunlin in the river channel and creeks but casual observations showed that they took food from shallow water at the edge of creeks and probed into submerged muds. They also picked material from mud surfaces and probed into the 0–3 cm. layer in exposed mud.

Table 6. *Vertical feeding patterns of Greenshank and Redshank in the river channel and creeks, expressed as a percentage of feeding in each habitat category*

	Greenshank	Redshank
Total number of observations	288	251
Water and submerged mud	33	62
Exposed mud:		
Surface	17	23
0–3 cm.	28	15
3–6 cm.	22	—

Feeding Patterns in Relation to Food Resources

It is of interest to consider whether the small-scale separation of feeding sites between the species would be likely to have the effect of sharing out the various food organisms in the habitat.

No gut content analyses were made in the present study but some information about food was obtained by the direct identification of organisms picked up by the birds and by the examination of droppings. There is some useful published information, based on gut contents, on the food of some of the species studied (Ehlert, 1964; Goss-Custard, 1969; Davidson, 1971) although it cannot always be assumed that a species will take the same foods on different shores. In our own investigation a special study was made of the distribution of invertebrate organisms in the various materials and the depth zones used by the birds.

Considering first the short-legged waders mention has been made of the surface picking of Ringed Plover, the stone and weed turning activities of Turnstone, and the mud probing of Dunlin. When the Ringed Plovers picked material from surfaces such as sand, mud, shingle and seaweeds (Figs. 4, 5), they appeared to be taking adult flies (Diptera) and beetles (Coleoptera). Their quick darting movements may be more effective in capturing rapidly moving insects than the more deliberate searching actions of other waders. They were also seen to pick up polychaete worms from the surface of the wet mud.

With the Turnstones, surface picking was of only minor importance and the main feeding action was stone turning and the turning back of matted fronds of fucoid seaweed (Fig. 5). Table 7 shows the organisms present inside and underneath fucoid mounds on the Gann Flat. Three of the organisms recorded are known from gut content analysis to be eaten by Turnstones. These are the shore crabs (*Carcinus*), the gammarid crustaceans, and the gastropod molluscs (*Littorina* spp.) (Davidson, 1971). We frequently saw Turnstones on the Gann Flat picking up gammarids after turning stones or displacing seaweed and found gammarid remains and fragments of mollusc shells in Turnstone droppings. By penetrating into fucoid mounds and turning stones it seems likely that the Turnstones were gaining access to food not available to the Ringed Plovers.

Table 7. *Distribution of invertebrate animals inside and underneath fucoid mounds (expressed as mean number/$\frac{1}{4}$ sq. metre)*

	Littorina spp.	Gammarids	*Carcinus*	*Balanus* & *Elminius*	*Clitellio*	Adult Diptera
Strand line fucoid mounds	12	1,128	—	—	10	104
Underlying sand and gravel to 3 cm. depth	2	610	—	—	50	—
Mid-beach fucoid mounds	61	21	1	—	—	—
Underlying sand and gravel to 3 cm. depth	13	8	14	220	—	—

The Dunlin may gain access to another separate food supply by its ability to penetrate into the surface layers (0–3 cm.) of sand and mud (Fig. 5). Both on the Gann Flat and in the river channel the birds were frequently seen to extract polychaete worms from the mud. The polychaete worm *Nereis diversicolor* has been recorded as important in the diet of the Dunlin (Ehlert, 1964; Bengtson and Svensson, 1968; Davidson, 1971). The birds were certainly taking this species in the river channel but probably not on the Gann Flat where it is uncommon. The exploitation of polychaete worms from below the mud surface would seem to set Dunlin apart from Turnstone and Ringed Plover. Shallow water is also more used by Dunlin than the other two species (Table 3), and it was seen picking shrimps (probably *Crangon*) from pools.

In the freshwater lagoon an interesting relationship was apparent between Dunlin and Little Stint. The two species fed together on the exposed mud of the lagoon in 1969 and in 1970. The Little Stints with their shorter bills fed entirely from the mud surface and appeared to be taking adult diptera, certainly these were the only identifiable remains in the droppings. The Dunlins fed in approximately equal amounts from the surface and the 0–3 cm. mud layer. Below the mud surface the only invertebrates present were dipterous larvae and pupae of various kinds, and by penetrating below the surface the Dunlins were apparently tapping a food resource not utilized by the little Stints.

The association of Curlew, Oystercatcher, Greenshank and Redshank with the tide edge (Fig. 4) is presumably linked with the long legs and long bills of these species which allow them to feed in deep water. However, the advantages of being adapted to feed in deep water are not entirely obvious. It might be argued that many of the invertebrates taken by the long-legged species in deep water also become available to the short-legged species as the tide recedes and so the two groups are competing for the same food.

Table 8 shows the organisms obtained by turning over cores of exposed sand with a spade in the middle sand area of the Gann Flat. The positions of the animals on the cut surface were measured from the top of the core. Some of these species are known to remain at similar depths whatever the state of the tide and their availability to birds may remain relatively unchanged. The two carnivorous worms *Nephthys* and *Glycera* have been reported to occur near the surface when submerged (Clark, 1956; Ockelmann and Vahl, 1970), the position we found them in when the tide was out (Table 8). The lugworm *Arenicola* also usually occupies the same position throughout the tidal cycle, in this case the bottom of its deep "U"-shaped burrow and beyond the reach of even the Curlew's bill (Table 8). The worm is only likely to be taken by birds when it comes to the surface to defaecate or to work on its burrow (Wells, 1945). The cockle (*Cardium*) provides an example of a species which remains in the surface layers (Table 8) but may be easier for a bird to attack when submerged because then the shell valves are open and the siphon extruded.

Table 8. *Distribution of invertebrate animals at different depths in the exposed middle sand zone of the Gann Flat*

	Nephthys	*Glycera*	*Notomastus*	*Arenicola*	*Owenia*	*Lanice*	*Cardium*
0–3 cm.	33	8	2	2	3	—	14
3–6 cm.	24	5	17	2	6	—	1
6–9 cm.	3	2	10	1	11	—	—
9–12 cm.	—	—	5	2	1	1	—
12–15 cm.	—	—	—	6	—	—	—
15–19 cm.	—	—	—	13	—	3	—
19–21 cm.	—	—	—	4	—	—	—
21–24 cm.	—	—	—	1	—	—	—

A different situation is found with tube worms such as *Lanice*, *Sabella* and *Branchiomma*, which are common on the Gann Flat although not in the places where the cores were taken. When the tide is in these worms are at the tops of their tubes with the feeding crowns extended. On the Gann Flat large numbers of these feeding crowns could be seen in the submerged areas at the tide edge. Greenshanks were seen to attack the worms by probing into the submerged mud, cutting the tube below the expanded worm and thus preventing its retreat. When the tide receded the worms retreated deep into their tubes and were difficult to extract even with a spade. This kind of situation may represent one of the advantages to be gained by a bird becoming specialized to feed in submerged habitats at the tide edge.

The relationship between the Oystercatcher and the Curlew was found to be an interesting one. The two species showed little physical separation in feeding sites, both probed into sand, mud and fucoids, whether these materials were submerged or exposed (Figs. 4, 5). However, there appeared to be some difference in the foods the birds took.

The Curlews were frequently seen with shore crabs (*Carcinus*). These were abundant amongst submerged fucoids and in exposed fucoid mounds and the birds extracted them using their curved bills like a pair of forceps. When faecal pellets were collected from the Curlews' resting sites the majority were found to contain crab fragments (Table 9). Burton (1966) has also commented on the use of crabs by Curlews in autumn. The Curlews probing into mud on the Gann Flat were sometimes seen to extract polychaete worms and chaetae were occasionally found in the pellets. Shell fragments in the pellets showed that they also swallowed whole small cockles complete with their shells. The birds were never seen to take large bivalves.

Table 9. *The number of faecal pellets of Curlew and Oystercatcher containing the listed items*

	Curlew	Oystercatcher
Number of pellets examined	30	30
Polychaetes (chaetae)	2	18
Crabs	27	3
Gammarids	3	—
Gasteropods (*Calyptraea*)	—	5
Bivalves	3	—

In the Oystercatcher the balance of food items was evidently different. On the Gann Flat this species was frequently seen to attack cockles (*Cardium*) in the sand, both in submerged and exposed situations. The methods used by the birds are well known and have been described by Drinnan (1957) and Davidson (1967). In opening the shell the Oystercatcher frequently damages the valves in a distinctive way by breaking pieces from the margin. On the Gann Flat large numbers of cockle shells were found showing this characteristic damage attributable to Oystercatchers. In the Gann Pool, empty shells of another bivalve *Scrobicularia* were found to be similarly damaged and this was probably also due to the attacks of the Oystercatchers, which are known to feed on this species in other areas (Hughes, 1970). The Oystercatchers on the Gann Flat were also seen carrying and opening mussels (*Mytilus*).

Dare (1966) in summarizing the food of the Oystercatcher in different localities has concluded that the important foods outside the breeding season are the three bivalves; the mussel, the cockle and *Macoma balthica*. The efficiency of the Oystercatcher in utilizing bivalves seems to be related to its laterally compressed blade-like bill which can be inserted between the shell valves of these organisms.

Although bivalves were evidently important to the Oystercatchers on the Gann Flat they also took other organisms. During two observation periods when the birds were concentrated on the lower sand they were seen to take 80 polychaete worms and 1 crab. The faecal pellets likewise contained numerous chaetae of polychaete worms (including the characteristic anterior hooks of the polychaete *Melinna*) (Table 9). Also identified from the pellets were shell fragments and radulae of the gastropod *Calyptraea chinensis*. In these pellets the absence of traces of bivalves was not significant, because the soft bodies of these animals are known to be digested beyond recognition (Drinnan, 1957).

A detailed comparison of the food of the Oystercatcher and the Curlew could only be achieved by the analysis of gut contents. However, on the Gann Flat in autumn the use of bivalves by the Oystercatcher could be contrasted with the use of crabs by the Curlew and this subdivision of food resources may have been important in allowing the two species to use the same range of feeding sites.

The Redshank and Greenshank showed many similarities in feeding behaviour and both species used a range of submerged and exposed sites on the Gann Flat and in the river channel and creeks. No general conclusions could be reached about the foods taken by the two species.

The study by Goss-Custard (1969) of the diet of Redshanks feeding in an estuarine area has some application to the river channel sites at Dale. He found that the birds fed mainly on the crustacean *Corophium volutator*, the polychaete *Nereis diversicolor* and the molluscs, *Hydrobia ulvae* and *Macoma balthica*. A series of invertebrate samples taken from the exposed river channel muds at Dale (Table 10) showed that the first three of these species were common and the birds probably utilized them in the same way. The greater use by the Greenshank of the 3–6 cm. layer in these muds (Table 6) would on the basis of the invertebrate samples (Table 10) be unlikely to yield food organisms which were different from those obtained by Redshank at 0–3 cm. A very different range of organisms was available to Redshanks and Greenshanks feeding on the exposed muds of the Gann Flat and our only observation from this situation was that both species were seen to take polychaete worms from the mud.

Table 10. *Distribution of invertebrate animals at different depths in the exposed mud of the river channel (expressed as mean number/$\frac{1}{4}$ sq. metre)*

	Nereis diversicolor	*Scrobicularia plana*	*Corophium volutator*	Dipterous larvae	*Hydrobia ulvae*	*Cyathura* sp.
0–3 cm.	101	21	13	18	8	14
3–6 cm.	54	3	1	1	3	12
6–9 cm.	38	1	—	—	1	4
9–12 cm.	17	1	—	—	1	2
12–15 cm.	8	2	—	—	—	1

Discussion

Species which coexist in the same general habitat frequently exploit different food supplies (Lack, 1971). There is often a correlation between the size and shape of the food a species takes and the form of its bill. Thus related species in the same habitat often have differently shaped bills which enable them to exploit separate food resources. The work of Newton (1967) on finches provides a good example of this kind of situation; he has shown how the coexistence of a number of finch species in woodlands in winter is based on specializations of this kind.

On the Gann Flat the relationship between the Curlew and the Oystercatcher seemed to be of this kind. Both species used a similar range of feeding sites but each utilized some separate food resources and its efficiency in this respect seemed to be related to the form of the bill.

However, not all species which take different foods from the same general habitat show morphological specializations which can be related directly to the shape or size of their foods. The nature of the materials containing the foods may be equally important. Thus the separation of Ringed Plover, Turnstone and Dunlin on the Gann Flat appeared to be related to the varying abilities of the three species to penetrate food-bearing materials. The Ringed Plover picked only from the surfaces, the longer-billed Dunlin was able to penetrate muds and the Turnstone, with its special ability to turn over stones and seaweed, was able to gain access to the deeper layers of shingle banks and fucoid mounds. These contrasting activities may well provide each species with a separate food supply.

The exploitation of the submerged tide-edge sites by the long-legged, long-billed waders seems to provide another example of how additional food resources become available if the surrounding material, in this case deep water, can be negotiated.

The general conclusion arising from the study is that the coexistence of mixed-species flocks of waders in coastal areas, like the Gann Flat, depends on the subdivision of the food resources between the species. This subdivision which appears to be correlated with the morphology and behaviour of the species is based either on the size and shape of food items or on the nature of food-bearing materials. Further analysis of the problem will need to combine observations on feeding behaviour with the examination of gut contents.

Acknowledgements

Our thanks are due to Dr. M. Ann Edington who helped with the work at all stages and to the many students from the University College, Cardiff, who participated in the field work over the years. Valuable assistance has been given by the staff of the Dale Fort Field Centre. The National Museum of Wales made available the specimens from which the bill and leg measurements and scale drawings were made.

References

Barrett, J. H. (1959). The birds of the parish of Dale including Skokholm. *Field Studies*, **1** (1), 1–16.

Bassindale, R., and Clark, R. B. (1960). The Gann Flat, Dale: studies on the ecology of a muddy beach. *Field Studies*, **1** (2), 1–22.

Bengtson, S. A., and Svensson, B. (1968). Feeding habits of *Calidris alpina* L. and *C. minuta* Leisl. (Aves) in relation to the distribution of marine shore invertebrates. *Oikos*, **19**, 152–157.

Burton, P. J. K. (1966). Food and feeding methods of Curlews, Golden Plover, Grey Plover and Lapwing. *Ibis*, **108**, 455.

Clark, R. B. (1956). The eyes and the photonegative behaviour of *Nephtys* (Annelida, Polychaeta). *J. exp. Biol.*, **33**, 461–477.

Dare, P. J. (1966). The breeding and wintering populations of the Oystercatcher (*Haematopus ostralegus* Linnaeus) in the British Isles. *Fishery Invest.*, *Lond.*, Ser. 2, Vol. 15, No. 5, 1–69.

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. *Fishery Invest.*, *Lond.*, Ser. 2, Vol. 15, No. 7, 1–28.

Davidson, P. E. (1971). Some foods taken by waders in Morecambe Bay, Lancashire. *Bird Study*, **18**, 177–186.

Drinnan, R. E. (1957). The winter feeding of the Oystercatcher (*Haematopus ostralegus*) on the edible cockle (*Cardium edule*). *J. Anim. Ecol.*, **26**, 441–469.

EHLERT, W. (1964). Zur Ökologie und Biologie der Ernährung einiger Limikolen-Arten. *J. Orn. Lpz.*, **105**, 1–53.

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

GREEN, J. (1968). *The Biology of Estuarine Animals*. Sidgwick and Jackson: London.

HUGHES, R. N. (1970). Population dynamics of the bivalve *Scrobicularia plana* (da Costa) on an intertidal mud-flat in North Wales. *J. Anim. Ecol.*, **39**, 333–356.

LACK, D. (1971). *Ecological Isolation in Birds*. Blackwell: Oxford.

NEWTON, I. (1967). The adaptive radiation and feeding ecology of some British finches. *Ibis*, **109**, 33–98.

OCKELMANN, K. W., and VAHL, O. (1970). On the biology of the polychaete *Glycera alba*, especially its burrowing and feeding. *Ophelia*, **8**, 275–294.

WELLS, G. P. (1945). The mode of life of *Arenicola marina* L. *J. mar. biol. Ass., U.K.*, **26**, 170–207.