British Birds

Vol. 59 No. 5

MAY 1966

The winter feeding of the Purple Sandpiper

By C. J. Feare

Wellcome Marine Laboratory, Robin Hood's Bay, Yorkshire

INTRODUCTION

IN THE PAST, studies of the feeding habits of shore birds have largely been concerned with a bird species and one prey species at a time. A series of papers by Dewar (1908, 1910, 1913) described the predation of Oystercatchers *Haematopus ostralegus* on mussels *Mytilus edulis*, dog-whelks *Thais* (=*Nucella* or *Purpura*) *lapillus* and limpets *Patella spp.* More recent studies of the Oystercatcher by Drinnan (1957, 1958) were stimulated by economic interest and centred upon its predation on cockles *Cardium edule* and mussels respectively. Drinnan noted that the subject of shore birds had had little attention from marine biologists; and, in fact, these birds have received only passing mention in works on littoral ecology (e.g. Yonge 1949, Lewis 1964).

The present paper is an attempt to study the Purple Sandpiper *Calidris maritima* as an integral part of the littoral fauna of a rocky shore. The results obtained have convinced me that this species, with several others commonly found on similar shores should, at least during the winter, be regarded as littoral organisms.

ROBIN HOOD'S BAY

The opportunity for me to study Purple Sandpipers presented itself when a party of 39 arrived in Robin Hood's Bay, North Yorkshire, on 14th November 1965. They remained in the area until 13th January 1966, after which they began to wander up and down the coast. A

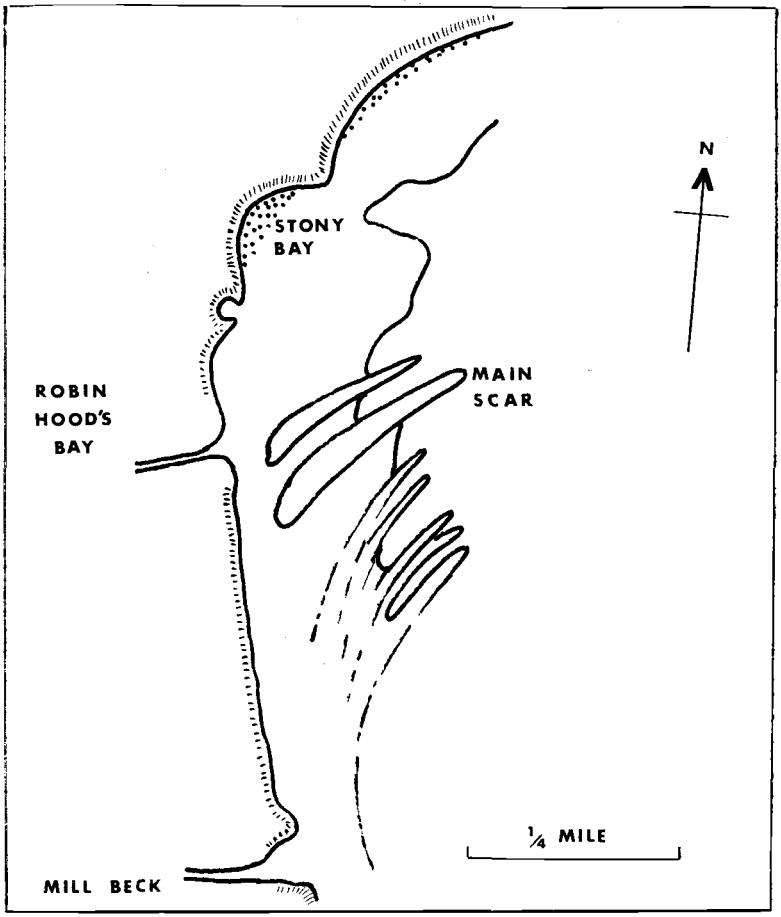

FIG. 1. Sketch map of Robin Hood's Bay, North Yorkshire

party of similar size was present on Filey Brig, East Yorkshire, during the same period and my work at Robin Hood's Bay was supplemented with information I obtained at Filey.

The shore at Robin Hood's Bay (fig. 1) is relatively sheltered, and the shale scars carry dense populations of winkles *Littorina spp.*, dogwhelks, limpets *Patella vulgata* and barnacles *Balanus balanoides*. Below mean tide level are areas of small mussels which during the study period supported very young shore crabs *Carcinus maenas*. The scars are completely covered at high water and small bays to the north of the village

then become inaccessible. These bays have narrow, sandy beaches just above the shale, which grade into a stony bank at the base of unstable mud cliffs.

METHODS

Faeces of Purple Sandpipers were collected at various states of the tide. At seven levels of the shore at least five droppings were taken and examined under a low power microscope, through which it was possible to identify and count whatever remained of animals eaten. In all, 135 droppings were examined. In order to minimise disturbance, faeces were never collected until the Purple Sandpipers had left the immediate area. The only other birds feeding in the vicinity were gulls *Larus spp.*, Oystercatchers and Rock Pipits *Anthus spinoletta*, and Purple Sandpiper droppings were readily distinguishable by their size.

Hartley (1948) and Lack (1954) regarded the examination of faeces for determining a bird's diet as a sampling technique which should be used only as a last resort. However, Purple Sandpipers take small items of food and through binoculars one cannot distinguish between the winkles and dogwhelks they pick up. Furthermore, neither of these Yorkshire flocks was large enough to enable me to take a reasonable sample of birds for gizzard examination at each level of the shore.

One Purple Sandpiper was shot; formalin was immediately syringed down the throat (see van Koersveld 1950) and the gizzard was removed and placed in formalin. From the examination of this gizzard the diet as determined by faecal examination appeared to be wholly representative of what was actually eaten. This is of course due to the nature of the diet, which will be described later.

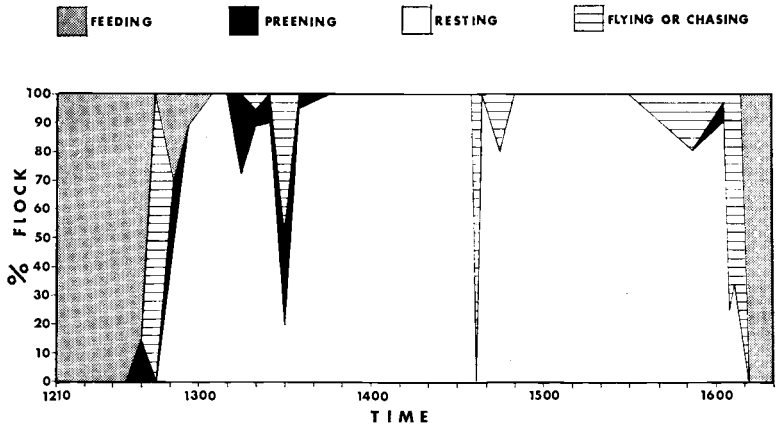

FIG. 2. Behaviour of flock of Purple Sandpipers *Calidris maritima* over high tide at Filey Brig, East Yorkshire, on 18th November 1965 (high water at 14.17 hours)

Observations were made with the aid of a stop watch on the rate of feeding and on the frequency of disturbances by waves.

FEEDING ROUTINE

The Purple Sandpipers spent the whole of the daylight period feeding when the state of the tide permitted. At high water the Filey flock was seen to rest among stones after a brief period of preening and chasing (fig. 2). It was not possible to watch the Robin Hood's Bay birds at high tide. When they were driven to the narrow zone of bladder wrack *Fucus vesiculosus* at the top of the scars they began preening. As soon as this *Fucus* zone was being regularly splashed, they flew to a stony bay which by this time was inaccessible to me and I assume that they rested there.

They appeared to rest at night, none being found feeding after dark. High tides prevented them from feeding for about three hours each day and in December this left only six daylight hours for feeding. In order to obtain sufficient food in these circumstances they must spend practically the whole of the available time feeding.

In feeding they probed in crevices and small pools amongst mussels and barnacles along the water line, and followed the tide in and out. Feeding time was reduced by waves and stormy weather, as will be described in a later section, but it was also reduced by behavioural disturbances which were seen to occur before and after a high tide, and more pronouncedly at dusk. At these times the birds were restless and, besides preening, individuals began chasing one another. At dusk the flock moved to the sand in front of their stony resting place. Even when they were not involved in chases they fed only half-heartedly, and the timed feeding rate fell considerably (see RATES OF FEEDING on page 175).

On 2nd December 1965, after a high tide, about half-a-dozen Purple Sandpipers were seen performing what Witherby *et al.* (1938-41) described as the 'wing ceremony'. Those concerned raised both wings vertically and then jumped into the air or chased other individuals with neck held low and outstretched. This was the only occasion on which this display was seen.

At dusk, and at the approach of and just after a high tide, Purple Sandpipers will have difficulty in finding food owing to bad light and a restricted feeding area respectively. The apparent scarcity of food at these times may lead to intraspecific competition for food, manifesting itself in displays and chases. Thus the evening rise in activity of these birds may be caused by this inability to find food, rather than by a direct effect of light intensity.

Apart from these periods before and after a high tide and at dusk (and presumably dawn), the whole of the daylight period was spent

feeding. This suggests that there is a diurnal rhythm of activity as described by Palmgren (1949), upon which is superimposed a tidal rhythm of lower intensity. This superimposition of rhythms will apply only during the winter, when the species is strictly coastal (Witherby *et al.* 1938-41).

DIET

Analysis of faeces showed that the diet consisted almost entirely of molluscs, gastropods being the most severely predated littoral organisms. *Littorina littorea*, *L. saxatilis* and *Thais lapillus* predominated, but *L. littoralis*, *Hydrobia ventrosa* and *Mytilus edulis* were also taken. It was not possible to produce a reliable estimate of the size of snail eaten from the fragments found in the faeces, but with the exceptions of *Littorina saxatilis* and *Hydrobia ventrosa* all snails eaten were in their first year, and the largest snail found to have been eaten was a specimen of *Thais lapillus* with a shell length of 8-10 mm.

Claws, eyes and pieces of carapace of small crabs were found in the faeces, corresponding to animals with a shell width of 5-7 mm.

Fragments of the green weeds *Enteromorpha intestinalis* and *Ulva lactuca* were frequently found.

The largely gastropod diet was confirmed by the examination of the gizzard, which contained 43 *Littorina saxatilis* and three *L. littorea*, plus

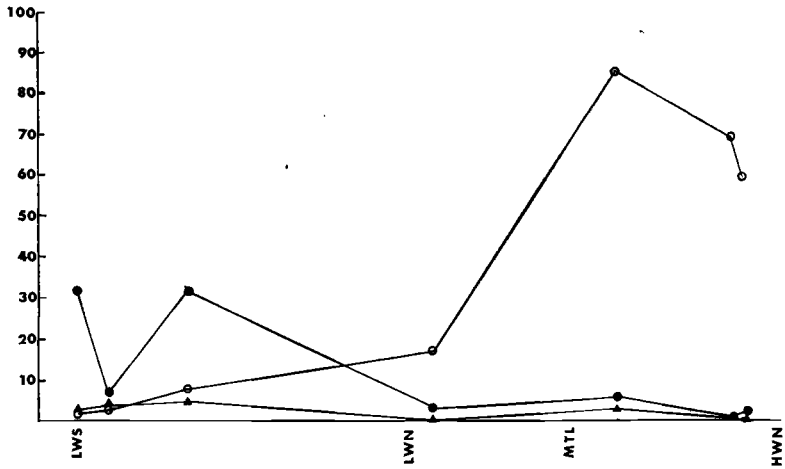

FIG. 3. Numbers of animals (● *Thais*, O *Littorina*, ▲ *Mytilus*) found in samples of five droppings from Purple Sandpipers *Calidris maritima* at each of seven levels of the main scar at Robin Hood's Bay, North Yorkshire, at spring tides. Abbreviations: LWS—Low Water of Spring Tides; LWN—Low Water of Neap Tides; MTL—Mean Tide Level; HWN—High Water of Neap Tides

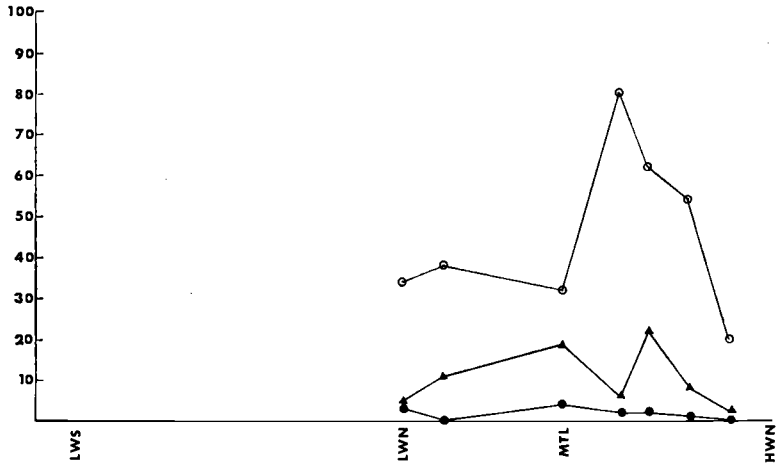

FIG. 4. Numbers of animals (● *Thais*, O *Littorina*, ▲ *Mytilus*) found in samples of five droppings from Purple Sandpipers *Calidris maritima* at each of seven levels of the main scar at Robin Hood's Bay, North Yorkshire, at neap tides. Abbreviations as in fig. 3

fragments of a further eight shells. No soft-bodied animals were found in the gizzard. During the study only two worms were seen to be picked up, both at Filey, and one of those was afterwards rejected. On the other occasion the Purple Sandpiper involved threw back its head and swallowed the worm in a series of gulps. This worm was tentatively identified through binoculars as *Eulalia viridis*, that being the only green polychaete that I have found on this shore. This behaviour was noted only on that one occasion, and it appears that worms are rarely taken by Purple Sandpipers.

By feeding at the water's edge and following the tide, Purple Sandpipers of necessity take prey species from different levels of the shore, and it follows that their diet reflects the zonation of the littoral fauna and flora. This can be seen in figs. 3 and 4, which show the numbers of the various prey species found in samples of five droppings from different levels of the shore. These do not of course indicate the food at those particular levels, owing to the unknown time taken for food to pass through the birds.

The numbers of *Thais* and *Littorina* at the different levels, presented in graphical form in fig. 3, were compared by the Spearman Rank Correlation Coefficient. This method gave a significant negative correlation coefficient, despite the smaller numbers of dogwhelks found in faeces at the lower end of the shore. It appears, therefore, that dogwhelks replace littorinids as the principal food lower down the

shore. The smaller numbers of dogwhelks perhaps indicate that, owing to the larger size of these animals, the birds are still obtaining sufficient food to fill their gizzards, whereas at higher levels of the shore many more of the smaller littorinids are needed.

DISTRIBUTION OF DOGWHELKS AND WINKLES ON THE SHORE

Fig. 5 shows the densities of *Thais* and *Littorina spp.* at six levels up the main scar at Robin Hood's Bay, determined by taking four random quarter-metre quadrats at each level. The very small littorinids under 2 mm. (chiefly *L. saxatilis*), found among the barnacles and mussels, were sampled by five-centimetre quadrats. As far as possible, sampling stations were arranged at sites where faeces had been collected on the scar, but at low tide the birds had a far greater choice of feeding areas and wandered away from the scar. Thus fig. 5 does not necessarily represent the distribution of the gastropods over the whole of the feeding area of the Purple Sandpipers.

However, the similarity between figs. 3 and 5, of frequency of appearance in the faeces and distribution on the shore respectively,

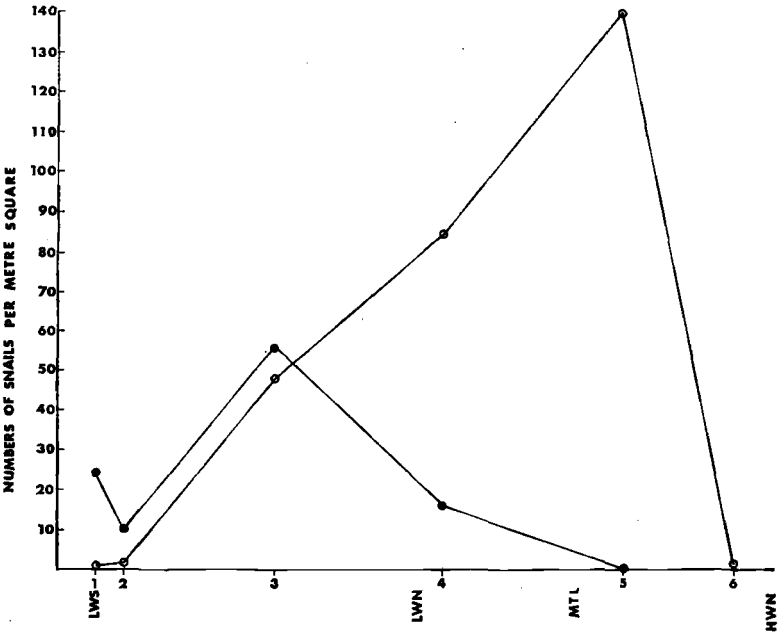

FIG. 5. Distribution of dogwhelks *Thais lapillus*(●) and winkles *Littorina spp.* (○) along a transect of six levels up the main scar at Robin Hood's Bay, North Yorkshire, the numbers of winkles having been divided by 100. Abbreviations as in fig. 3

Table 1. Proportions of winkles *Littorina spp.* to dogwhelks *Thais lapillus* in the diet of Purple Sandpipers *Calidris maritima* and on the shore at different levels of Robin Hood's Bay, North Yorkshire, mid-November 1965 to mid-January 1966

The levels, which begin with the lowest, are shown in fig. 5 and the ratios given are those of *Littorina* with *Thais* taken as unity. Level 2 is omitted because the position there was complicated by an unusual local abundance of *Hydrobia ventrosa*

Level	Diet ratio	Shore ratio
1	0.06	2.1
3	2.6	85.7
4	5.3	525
5	14.2	14,000
6	35.0	200

deserves comment. Table 1 shows the ratios of *Littorina spp.* to *Thais* in the diet and on the shore. It can be seen that this ratio in the diet is much smaller than that on the shore, and it therefore appears that Purple Sandpipers select dogwhelks. Nevertheless, it must be remembered that the vast majority of the littorinids found in the quadrats had a shell height of under 2 mm. (fig. 6) and most of these would not be taken by Purple Sandpipers. Without accurately knowing the sizes of littorinids and dogwhelks taken by Purple Sandpipers, it is therefore not possible to say definitely that they select one or the other. Amongst mussels, however, dogwhelks may be selected in preference to littorinids because their whitish shells make them conspicuous against the blue-black background of mussels.

At low water of neap tides the water receded only as far as the top of the mussel beds in this locality, and so the area available for feeding was considerably reduced. What is more, the area occupied by small dogwhelks was totally inaccessible and very few fragments of dogwhelk shells were found in the faeces. On the other hand, far greater numbers of mussels were taken during neap tides (fig. 4) than during spring tides (fig. 3). Purple Sandpipers are able, therefore, to resort to mussels when feeding conditions are not optimal. These may be taken in order to add to the diet a variety which at neap tides is not provided by other species of gastropods or by crabs.

SIZE DISTRIBUTIONS OF GASTROPODS

The dogwhelks and littorinids found in the quarter-metre quadrats mentioned above were brought back to the laboratory and measured with a calibrated low-power binocular microscope. At the time that the quadrats were sampled the larger specimens of dogwhelks and *Littorina littorea* were aggregated in crevices in the rocks, and did not

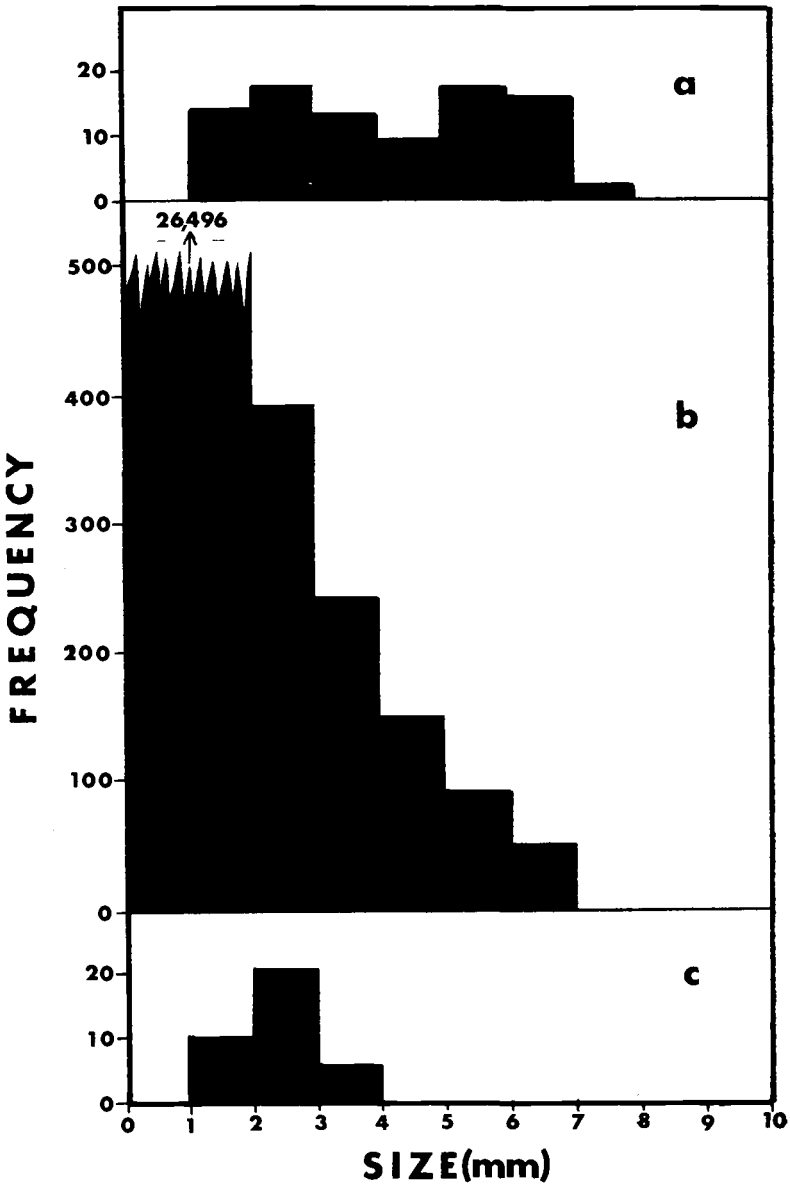

FIG. 6. Size frequency distributions of (a) dogwhelks *Thais lapillus* and (b) winkles *Littorina spp.* from six metre-square quadrats along a transect up the main scar at Robin Hood's Bay, North Yorkshire; and of (c) *Littorina spp.* in the gizzard of a Purple Sandpiper *Calidris maritima*

appear in the samples. The size distributions of the remaining small dogwhelks and littorinids are shown in fig. 6.

It was not found possible to determine the sizes of gastropods in the diet of the Purple Sandpipers from the fragments in the faeces, but by comparing these fragments with live specimens it was estimated that most of the dogwhelks eaten fell in the range of 4-7 mm. shell height. The method used by Gibb (1956) of comparing the sizes of opercula in the faeces with those of live animals was found to be inapplicable here. Few opercula of dogwhelks were found intact in the faeces and, in any case, the great variation in the shell proportions of dogwhelks even from areas only a few metres apart (Staiger 1957) rendered this method unreliable. Similarly, the presence of three species of *Littorina* on the shore, each having different shell proportions, invalidated any estimate of shell size for the group as a whole from the opercula present in the faeces.

The size range of the littorinids taken by the Purple Sandpipers thus had to be determined from the rather inadequate sample found in one gizzard (see fig. 6). The average size of these was 2.34 mm. This bird, however, had been feeding on the upper shore where the large numbers of very small *Littorina saxatilis* are found. In the faeces from this area the fragments of littorinids were generally of smaller shells than those in faeces collected elsewhere on the shore. Thus the average obtained from the gizzard sample may be somewhat lower than the true average size of the littorinids taken. This suggestion, although not backed by actual measurements, probably means that the average size of the littorinids eaten by Purple Sandpipers in Yorkshire is nearer to the figure of 2.72 mm. obtained by Gibb (1956) for this species in Cornwall.

The apparent bimodal distribution of dogwhelks on the shore must be mentioned. I have regularly sampled other areas of the shore for first-year dogwhelks, and in the larger samples have found a unimodal distribution. The bimodal distribution of size in fig. 6 may therefore be a consequence of the small sample.

It appears that, where possible, the Purple Sandpipers selected a particularly favourable size of prey. At the time of this study they were taking the larger specimens of the first-year group of dogwhelks. Personal observations have shown that these young whelks grow at the rate of approximately 1 mm. per month, so that by March the birds would presumably be feeding on the smaller members of this first-year group, assuming that the dogwhelks have a discrete breeding season, which at present appears to be the case in this area.

The Purple Sandpipers also selected a particular size range of littorinids (fig. 6), but where the larger and perhaps preferable sizes of winkles were comparatively scarce, on the upper levels of the shore

among the barnacles, they appeared to take smaller animals. To some extent, therefore, they were governed by what was available in this region.

If size is so important, why are larger size groups of dogwhelks selected than of littorinids? The answer may lie in the fact that littorinids have a fatter appearance than dogwhelks. If dogwhelks are orientated in the beak so that they are swallowed lengthways, shells of a greater height can be taken.

RATES OF FEEDING

Rates of feeding at three levels of the shore were obtained by measuring on a stop watch the time taken for individual Purple Sandpipers to pick up ten objects. The results are given in table 2, which shows that the rate of feeding was very much greater in the barnacle zone; this corresponds to an increased number of shells found in the faeces at this level. This increase was not great, however, and so the rate of defaecation must have increased, but no data were obtained for this.

The slackening in the rates of feeding lower down the shore and in the *Fucus* may result from two factors: (a) the density of the prey here is much less than amongst the barnacles, so that the birds may have to spend more time searching for food; and (b) the gastropods at the lower and higher levels of the shore are larger than those at the mid-shore level. This is particularly the case low down where dogwhelks are the principal food. Here these large shells soon filling the gizzard may contribute to the lower rate of feeding.

At dusk the feeding rate is considerably lower than at other times of the day. This is due to the birds' preoccupation with chasing and preening (mentioned under FEEDING ROUTINE on page 168).

Table 2. Time taken by individual Purple Sandpipers *Calidris maritima* to pick up ten objects on different levels of the shore at Robin Hood's Bay, North Yorkshire, and the number of objects found in the faeces at three of these levels

Level of shore	Time taken (seconds)	Average (seconds)	Number of objects in faeces
High (bladder wrack)	64, 49, 39, 60, 81, 63, 38, 88, 46, 45, 48	55	14
Mid (barnacles)	15, 16, 19, 17, 17, 18, 21, 18, 17, 15, 15	17	18
Low (mussels)	81, 43, 76, 52, 68, 67, 55, 63, 77	58	9
Sandy beach at dusk	45, 40, 86, 98, 124	79	—

OBSERVED EFFECTS OF PHYSICAL FACTORS ON FEEDING

Feeding near the water's edge frequently requires evasive action from waves and is therefore greatly influenced by weather and sea conditions. The Purple Sandpipers were watched during calm and rough seas and the frequency with which the whole flock had to fly or run out of the way of a wave was measured over hourly watches. On 23rd November 1965, a calm day, the average frequency of disturbance over three hour-long watches was six times per hour. On the other hand, similar watches on 1st December 1965, during rough seas, gave an average of 28 disturbances per hour. The average duration of these disturbances, timed with a stop watch, was 17.2 seconds. This means that on a calm day 1.7 minutes per hour were spent evading waves, whereas on a rough day 8.0 minutes were lost in this way. Thus almost five times as much time has to be devoted to wave evasion in stormy conditions as on calm days. On a December day, when the tide normally leaves the shore uncovered for only six daylight hours, storms and onshore winds may hold the tide in for a further half-an-hour or more, and a further 48 minutes are lost evading waves. This means that the normal six hours of feeding time are reduced by about a quarter.

The effect of the weather was even more pronounced on Filey Brig, where the diet normally consists of dogwhelks. During rough seas, however, the Purple Sandpipers are driven to the sheltered side of the Brig along the northern edge of Filey Bay, and the emphasis changes from dogwhelks to the small crabs which are there abundant amongst the small mussels and sand.

The other physical factor influencing feeding is of course the state of the tide, be it high or low, spring or neap, as this not only determines the diet at any moment, but also governs the extent of feeding area available. At low water spring tides there is a long water-line in Robin Hood's Bay where the Purple Sandpipers can feed, but approaching high water at every tide they are driven on to the narrow *Fucus* belt at the top of the main scar and during the winter this area must suffer particularly intense predation from them.

STRUCTURE OF THE BILL AND GIZZARD

The bill of the Purple Sandpiper that was shot was examined (fig. 7). It was short and sturdy, and slightly downcurved. Inside the upper mandible was a flexible membrane bearing pointed, backwardly-projecting teeth. Proximally there were two outer rows of large teeth and a central row of smaller teeth. More distally the rows of teeth joined until these became a single row of small teeth down the centre of the upper mandible. The distal part of the upper mandible was extremely flexible and of a rubbery nature.

The bill thus seems incapable of chewing, but is ideally adapted for

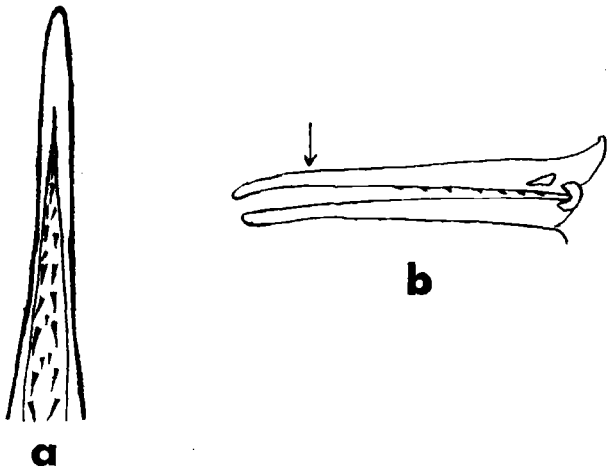

FIG. 7. Bill of Purple Sandpiper *Calidris maritima*: (a) inside of upper mandible showing rows of teeth; (b) side view showing decurvature and point of flexure on the upper mandible (marked by arrow)

grasping prey. When a Purple Sandpiper located a snail, it was seen to hold it in the tip of the bill and then throw it back up the bill until it could be swallowed. This process would doubtless be helped by the teeth, but it is thought that these may have evolved more in conjunction with its summer feeding habits when vegetable matter forms the main component of the diet (Witherby *et al.* 1938-41).

The bill modifications preclude the use of the bill for cracking shells, a process performed by the gizzard. In the gizzard of the specimen obtained, the proximal part contained unbroken shells, whereas shells further back were chipped to varying degrees and at the distal end of the gizzard only shell fragments were found. The walls of the gizzard were very thick and muscular and were lined by teeth. Small stones were found in the gizzard, and these doubtless add to the efficiency of this organ as a grinding centre.

IS THE PURPLE SANDPIPER A LITTORAL ORGANISM IN WINTER?

During the winter the Purple Sandpiper is strictly coastal (Witherby *et al.* 1938-41). It is generally found only on rocky shores and its diet consists entirely of organisms found within the littoral zone. It does not restrict itself to one prey species, but by following the tide up and down it encounters different species of potential prey owing to the zonation of these species on the shore.

The type of food and rate of feeding are governed by the state of the

tide, by the degree of shelter or exposure of the shore, and by the weather. The feeding routine is determined by the tide and by the amount of daylight. Purple Sandpipers are thus subjected to both diurnal and tidal rhythms of behaviour. That they do not apparently feed at night suggests that prey location is entirely visual.

One may ask why Purple Sandpipers have such a local distribution on the Yorkshire coast. The answer to this may lie in the availability of stony resting areas which remain uncovered by the highest spring tides. Both Robin Hood's Bay and Filey possess such areas, but the majority of the shores in the Robin Hood's Bay area do not.

Gibb (1956) calculated that one Rock Pipit may take as many as 14,300 littorinids in a day. By taking an average of the feeding rates obtained in the present study and estimating that a Purple Sandpiper spends 5½ hours feeding during a December day, it can be calculated that one Purple Sandpiper may take in the region of 4,600 snails per day. This figure is only a rough approximation, but it means that a flock of 40 would probably take in excess of 11,500,000 gastropods during a two-month stay in Robin Hood's Bay. These are taken from a restricted size range of snails, with the result that this considerable predation must impose tremendous selection pressures on species like *Thais lapillus* and *Littorina saxatilis* which have non-pelagic larvae and exist in more or less morphologically distinct populations in Robin Hood's Bay.

Purple Sandpipers are thus subjected to many of the factors which are believed to affect animals inhabiting the littoral zone, and they must play a considerable rôle in the dynamics of littoral gastropod populations. During the winter months, therefore, Purple Sandpipers are integral units of the littoral fauna.

ACKNOWLEDGEMENTS

I am indebted to Dr. E. Broadhead, of the Department of Zoology, Leeds University, and to Dr. J. R. Lewis, of the Wellcome Marine Laboratory, Robin Hood's Bay, for useful discussion, and to Dr. Lewis for reading the manuscript.

This work was carried out during the tenure of a grant from the Scientific Research Council.

SUMMARY

The winter food and feeding habits of a flock of 39 Purple Sandpipers *Calidris maritima* at Robin Hood's Bay, North Yorkshire, from mid-November 1965 to mid-January 1966 are described with supplementary observations on another flock of similar size on Filey Brig, East Yorkshire. The composition of the diet of these birds was determined by analysing faeces; owing to the nature of the food this was considered to be a reliable indicator of what they were eating. The feeding routine involved both diurnal and tidal rhythms of behaviour.

The principal food organisms were small winkles *Littorina spp.* and first-year dogwhelks *Thais lapillus*; small mussels *Mytilus edulis* and crabs *Carcinus maenas* were important reserve foods. The presence of winkles and dogwhelks in the faeces was related to the distribution of those organisms on the shore. The Purple Sandpipers took only a restricted size range of each prey species. Their bill and gizzard adaptations are described.

It is concluded that Purple Sandpipers form an integral part of the littoral fauna of Robin Hood's Bay during the winter, and probable reasons for their local distribution are given.

REFERENCES

DEWAR, J. M. (1908): 'Notes on the Oystercatcher (*Haematopus ostralegus*) with reference to its habit of feeding upon the mussel (*Mytilus edulis*)'. *Zoologist* (4), 12: 201-212.

——— (1910): 'A preliminary note on the manner in which the Oystercatcher (*Haematopus ostralegus*) attacks the purple shell (*Purpura lapillus*)'. *Zoologist* (4), 14: 109-112.

——— (1913): 'Further observations on the feeding habits of the Oystercatcher (*Haematopus ostralegus*)'. *Zoologist* (4), 17: 41-56.

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

——— (1958): 'The winter feeding of the Oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*) in the Conway Estuary, North Wales'. *Fish. Invest.*, Ser. II, 22(4): 1-15.

GIBB, J. A. (1956): 'The food, feeding habits and territory of the Rock Pipit *Anthus spinoletta*'. *Ibis*, 98: 506-530.

HARTLEY, P. H. T. (1948): 'The assessment of the food of birds'. *Ibis*, 90: 361-381.

VAN KOERSVELD, E. (1950): 'Difficulties in stomach analysis'. *Int. Orn. Congr.*, 10: 592-594.

LACK, D. (1954): *The Natural Regulation of Animal Numbers*. London.

LEWIS, J. R. (1964): *The Ecology of Rocky Shores*. London.

PALMGREN, P. (1949): 'On the diurnal rhythm of activity and rest in birds'. *Ibis*, 91: 561-576.

STAIGER, H. (1957): 'Genetical and morphological variation in *Purpura lapillus* with respect to local and regional differentiation of population groups'. *Année Biol.*, 61: 251-258.

WITHERBY, H. F., JOURDAIN, F. C. R., TICEHURST, N. F., and TUCKER, B. W. (1938-41): *The Handbook of British Birds*. London. vol. 4: 271-276.

YONGE, C. M. (1949): *The Sea Shore*. London.