DANISH REVIEW OF GAME BIOLOGY Vol. 13 No. 4

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by
JESPER MADSEN

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Abstract

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The southern part of the Danish Wadden Sea is an important autumn staging area for Brent Geese (peak numbers 6,000), Wigeon (15,000) and Teal (3,500). In autumn 1985 and 1986 their ecology and movements were studied in relation to food availability and shooting activity. In September-October the wildfowl fed in the tidal zones on a 138 ha *Zostera* bed. Due to the tide they could only feed from 3 hours before to 3 hours after low tide, and to fulfill their daily energy demands the birds also fed during nightly low water periods. During autumn the above-ground *Zostera* resources were reduced from 39 tons to 1 ton, the grazing by wildfowl accounting for the major part of the losses. In consequence, feeding efficiency of Brent Geese and Wigeon was hampered. Brent Geese switched to below-ground parts of *Zostera,* Wigeon abandoned the area. Interspecific exploitative competition became acute, with Brent Goose as the best coping species of the two.

In 1985 duck shooting on the mud flats was moderate; in 1986, however, it was intensified, displacing the ducks and geese to the southern part of the *Zostera* bed, which is part of a non-shooting zone. This zone was soon depleted for resources, and the majority of the wildfowl were forced to leave the area earlier than in 1985 even though food was still available in the shooting zone. At night the birds fed in the shooting zone. When the ducks had abandoned the area, shooting ceased, and the protected Brent Goose could remain undisturbed for the rest of the autumn.

In October a concentration of ducks built up in the non-shooting zone at the Rømø barrage. Here the ducks consumed ripening *Suaeda* and *Atriplex* seeds in the salt marshes. Ducks were actively feeding around high tide, during both day and night.

In the course of October the seed stock was heavily reduced due to ducks foraging, natural fall-off and wave action, whereupon the majority of the ducks left the area. The remaining ducks rested throughout daytime and flew into the adjacent hinterland at night to feed. The adjacent salt marshes of which parts are shooting zones were not used during daytime, and only irregularly at night.

It is concluded that the number of wildfowl was limited by the food resources, and that switching between habitats was linked to depletion of food stocks. Shooting modified movements and caused birds to leave the area prematurely.

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Contents

Introduction

The question of how many waterfowl a given foraging area along the migration route can support, i.e. the habitat capacity, has important implications for the understanding of the dynamics of the migration, as well as for the management of the key areas. Many waterfowl habitats, and especially wetlands, are today threatened by development and human disturbance. At that point when the bird numbers - or rather the number of bird-days - have reached the ceiling of the habitat capacity, human interference can be expected to have a negative impact on the status of the site.

Waterfowl movements have only recently been analysed in relation to the size of food supplies in the staging and wintering areas. For a Dutch staging area VAN EERDEN (1984) demonstrated that herbivorous wildfowl removed a considerable part of the available *Salicornia* spp. seed stock, and also that switching between food sources and areas was related to the depletion of the local food supplies. Likewise, in various goose studies, it has been demonstrated that shifts between habitats were linked to the depletion of the vegetation and impaired feeding profitability (DRENT & SWIERSTRA 1977, CHARMAN 1979, DRENT et al. 1978, LORENZEN & MADSEN 1985). Thus, there is evidence that in the absence of disturbance, foraging waterfowl make optimum use of their feeding grounds.

Substantial evidence has demonstrated the effect of disturbance, particularly shooting, on the distribution of waterfowl in potential staging and wintering areas (see review by MELTOFTE 1982, ARCTANDER et al. 1984, MADSEN 1986). However, less information exists regarding the ecological and behavioural consequences of disturbance (OWENS 1977, JOENSEN & MADSEN 1985, JAKOBSEN 1986). A central question is whether or not the birds can compensate for the lost feeding time, or whether behavioural constraints hinder exploitation of the food resources.

The Danish Wadden Sea is an important staging area for herbivorous dabbling ducks and Brent Geese *Branta bernicla.* In October-November when peak numbers are reached, up to 20,000 Dark-bellied Brent Geese *Branta b. bernicla,* 57,000 Wigeon *Anas penelope,* and 17,000 Teal *Anas crecca* can be present at one time (LAURSEN & FRIKKE in prep.). The three species feed mainly in intertidal mudflats and in saltmarshes, though at some stage in late autumn duck-flights into the hinterlands can also be observed.

The aim of this study was three-fold:

1) to describe the feeding ecology of herbivorous wildfowl and their spatial and temporal distribution in a part of the Danish Wadden Sea;

2) to analyse the impact of wildfowl grazing on food supplies, and to evaluate the extent to which bird numbers were food-limited and its possible influence on movements between habitats;

3) to analyse whether human activity, especially hunting, was modifying site usage and bird movements.

The project was part of a research programme by the Game Biology Station, evaluating the importance of the Danish Wadden Sea as a waterfowl staging area and the influence of human interference on bird numbers and distribution.

Acknowledgements

The Coast Authority (Kystinspektoratet) and the Directory of Agriculture (Jordbrugsdirektoratet) are thanked for permitting access to the Rømø Foreshore; the Royal Danish Army Air Corps (HFT) is thanked for helicopter assistance to erect the observation tower. John Frikke and Ebbe Bøgebjerg are thanked for assistance in the field. Karsten Laursen, Myrfyn Owen, John Frikke and Janice Mather kindly commented on the manuscript.

Study area

The study was carried out in the southern part of the Danish Wadden Sea (Fig. 1), part of the Nature and Wildlife Reserve Vadehavet. The study area comprised two major waterfowl feeding areas in the Danish Wadden Sea, i.e. the tidal flats at Koldby Leje, and the salt marshes along the barrage connecting Rømø with the mainland and Ballum Foreshore.

Koldby Leje, Jordsand Flak

This area is an intertidal mudflat, part of which is covered with seagrass *Zostera* spp. It is a major feeding ground for herbivorous wildfowl, especially Brent Geese and Wigeon. At high water the birds roost around the small island of Jordsand, some Brent Geese also roosting in the southern Ballum Foreshore. In 1985 and 1986, the *Zostera* bed covered 138 ha. *Zostera noltii* was the dominant species over most of the bed, showing highest densities on elevations 5-10 cm above the low water line. In shallow depressions where water was retained at low tide, however, *Z. noltii* was interspersed with *Z. marina,* though the latter never reached the densities of the former. *Z. marina* did not seem to overwinter, had an underdeveloped rhizome compared to *Z. noltii,* and was probably dependent on sexual reproduction. *Z. noltii,* on the other hand, had a well-developed rhizome, this being indicative of a high degree of vegetative reproduction.

The southern third of the flats is part of the non-shooting zone in the southern part of the Danish Wadden Sea. North of the zone, shooting of wildfowl is allowed from 16 September to 29 February.

The Rømø barrage and Ballum Foreshore

These salt marshes have been created by means of land reclamation work and are currently grazed by sheep. The marsh areas south of the barrage and most parts of Ballum Foreshore are dominated by a vegetation of *Puccinellia maritima,* and in certain regions by *Festuca rubra.* Over large areas *Atriplex litoralis* and *Suaeda maritima* occur in dense stands, *Suaeda* especially in low-lying regions. In the marsh north of the barrage, *Suaeda* occurs in extremely high densities. In the low-lying regions, especially the marsh south of the barrage, *Salicornia europaea* forms a dense vegetation. In October the salt marshes are visited by large flocks of dabbling ducks, especially Wigeon and Teal. Crop contents of collected birds demonstrated that the ducks feed primarily on seeds of *Suaeda* and *Atriplex.*

The Rømø barrage and adjoining salt marshes are non-shooting zones. In Ballum Foreshore, shooting is allowed in a zone

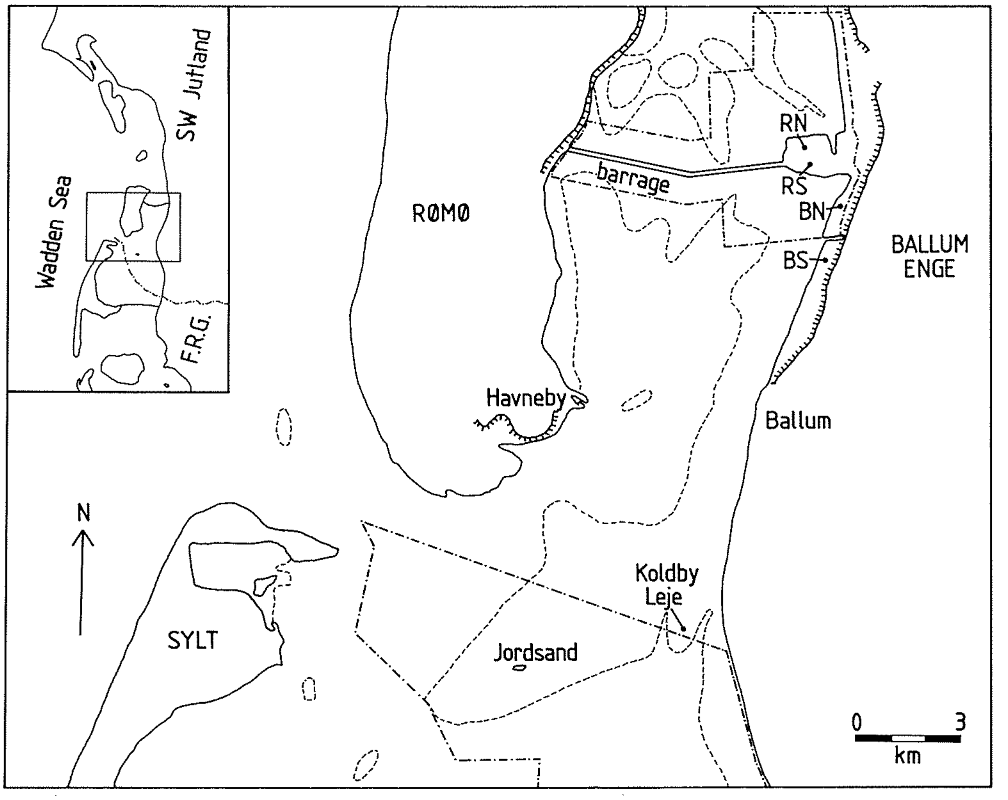

Fig. 1. Study area in the southern part of the Danish Wadden Sea. Study plots at Koldby Leje and the Rømø barrage are shown. RN: Rømø barrage north, RS: Rømø barrage south, BN: Ballum foreshore north, BS: Ballum foreshore south. Low water lines are indicated by punctuated lines, and reserve boundaries (non-shooting areas) by punctuated, dotted lines.

ranging from the dike to the edge of the old foreshore. Beyond this zone shooting is banned (Fig. 1).

Methods

Observations

The Rømø barrage and Koldby Leje were visited during the period 1 September to 20 December, 1985 and 1986, on average at intervals of six days. At each visit the number of wildfowl was counted, the distribution of flocks mapped, and their general activity (feeding, roosting) recorded. In addition, all types of human activity were noted and mapped. On the Rømø barrage, observations were carried out from the top of the barrage. At Koldby Leje, observations were made from land, and in 1986 also from a 4 m high observation tower placed in the middle of the *Zostera* bed. When observations were made from the tower, the observer entered approximately 2 hrs after high tide and left 2 hrs before the next high tide, so that disturbance was kept at a minimum. On some occasions, the observer remained in the tower during the high tide in order to continue observations during the next low water period.

Activity studies

Time expenditure of flocks of geese or ducks was recorded in relation to tidal rhythm and to time of season. At Koldby Leje, observations were carried out both during day and night, but at the Rømø barrage only during day-time.

At Koldby Leje the birds were under observation from time of arrival from the high water roost to departure from the *Zostera* bed. Every 15 minutes, the number of birds of each species engaged in various activities was recorded by 'instantaneous' scanning of the flock (after ALTMANN 1974). Recorded activities were feeding, roosting, walking, swimming, flying, aggression, and alertness. Four feeding techniques were distinguished:

1) swimming, including feeding by picking from surface, submerging head or neck, and upending;
2) paddling, only recorded in Brent Geese trampling in the sediment submerged under 5-10 cm of water. The geese took whole plants including roots and rhizomes, and left characteristic craters of roughly 20 cm diameter and 5-10 cm deep (also described by FOG (1967) and JACOBS et al. (1981));
3) grubbing, observed in geese and Wigeon, the birds taking turions and rhizomes;
4) pecking, taking leaves from the mud surface or leaves floating in shallow water.

During day-time, observations were carried out with a telescope (20-45 x). Every half hour the position of flocks was mapped and the water line drawn on a sketch map (1:10,000). In 1986, three transect lines with the observation tower in the centre were laid out over part of the *Zostera* bed, yielding 30 quadrats each of 50 m x 50 m. Corners were marked with stakes 20 cm above ground. During observations from the tower, the number of birds of each species within the quadrats was recorded at intervals of 30 minutes. Temporal and spatial overlap of two species was expressed by percentage similarity, O (HURLBERT 1978):

$$O = 1 - 1/2 \mid P_{ij} - P_{ik} \mid$$

where P_{ij} is the relative occurrence of the j'th species in square i, and P_{ik} is the relative occurrence of the k'th species in square i.

Night-time activity budgets of Wigeon and Brent Geese were recorded during three low water periods in 1986: 8-9, 9-10, and 21-22 October. Observations were carried out from the observation tower with a light-intensifying vision scope (around 8 x). The first two nights were one week prior to full moon and with overcast sky, the last night was four nights after full moon and with clear sky. During the first two observations, lights from the surrounding towns Havneby, List, and Skærbæk provided sufficient light to operate the night vision scope with success. However, during all three nights, the resolution only allowed the observer to distinguish between feeding, roosting, and flight activities.

At the Rømø barrage, observations followed the same procedure as at Koldby Leje. Ducks feeding in the salt marsh were often invisible whilst in the vegetation, but were assumed to be feeding when out of sight. Records were kept of birds flying to and from the salt marsh.

Three feeding parameters were timed by means of a stop-watch:

1) feeding bout length, i.e. the time of uninterrupted feeding with the head below the level of the shoulder;

2) pecking rate, measured as the time it took a feeding bird to make a total of 10 pecks in the vegetation. It was, however, not possible to measure pecks on the mudflats because the *Zostera* feeding birds often took turions which were chewed and swallowed in bits of varying size;
3) walking speed, measured as the time it took a feeding bird to make a total of 10 steps.

To achieve another indication of duck utilisation of the salt marshes apart from the mapping, droppings were counted within permanent plots. On the southside of the Rømø barrage 40 plots were laid out at 20 m distance; on Ballum Foreshore 20 plots. Each plot was circular with a radius of 2 m (12.6 m^2) and marked with a peg 10 cm above ground. Plots were emptied at around 10 day intervals throughout autumn. However, this method proved to be successful in 1985 only, because of too frequent flooding of the marshes in 1986.

Food and estimation of daily food consumption

Food selection of Brent Geese and Wigeon foraging on the mudflats was examined by means of microscopical identification of epidermal fragments in the droppings (for method see OWEN 1975). Samples of 25 fresh droppings were collected at low tide, and only in situations when the birds had fed in the same area for most of the low-water period.

Daily food consumption by Brent Geese and Wigeon feeding on the mudflats was estimated by the 'marker substance' method (DRENT et al. 1978). Retention rates were measured using ash content and lignin as food components not digested by gut passage. The change in concentration of the marker substance in droppings compared to food plants thus equals the retention rate. Hourly defaecation was measured in the field by keeping the abdomen of a goose under continuous observation for as long as possible, and recording the number of droppings produced in the particular period, which was timed by means of a stop-watch. Periods and numbers of droppings were summed for many individuals to achieve hourly blocks of dropping production (BÉDARD & GAUTHIER 1986). Defaecation periods were only timed from 1 hr before low tide to 3 hrs after, to ensure that defaecation rates were in equilibrium with food intake. Daily production of droppings was calculated from multiplication of average hourly defaecation and average time spent on the feeding grounds during the 24 hrs. Fresh droppings and food plants were collected for chemical analyses, and droppings for weighing. Samples of Brent Goose droppings were taken two days in October 1985, and Wigeon droppings one day in October 1986. Chemical analyses were carried out by the Central Laboratory of the National Institute of Animal Science, at Foulum. Ash content of plants and droppings was determined after removal of the silica fraction. Energetic value of the net food intake was calculated from energy content of pellets of food and droppings, measured on a Gallenkamp bomb calorimeter. All analyses were carried out in duplicate.

Standing crop and leaf cover of *Zostera*

In 1985, an exclosure experiment was set up at Koldby Leje to measure standing crop of *Zostera* throughout autumn, and to quantify wildfowl grazing impact on the vegetation.

A transect line, situated and marked as for the 1986 transect, was laid out in a part of the *Zostera* bed which visually appeared homogeneous. Four 3 m x 3 m exclosures were constructed using pegs reaching 40 cm above ground and also wires at two heights which connected the corners diagonally. The exclosures were visited weekly to clean them of material, especially algae, hanging upon the wires. At monthly intervals, samples were taken outside and inside exclosures. Outside the exclosures 15 samples were taken at 50 m distance along the transect line, and inside each exclosure two samples were taken at random. A sample consisted of a circular core of 227.6 cm². A plastic tube with sharpened edges was pressed 10 cm into the sediment, the sample was then dug out, transferred to a sieve, and the sediment superficially washed off. In the laboratory, samples were first sorted into live and dead material and also above- and below-ground biomass, then dried for 24 hrs at 80°C, cooled in an excicator, and weighed. To express biomass in ash-free dry weight, plant material was combusted for 3 hrs at 550°C. Thus, average ash content of dry weight of above-ground material and below-ground material was 14.3% and 27.1%, respectively.

To relate above-ground biomass to leaf cover, the percentage leaf cover was estimated to nearest 5% in all sample plots. In 1986, the leaf coverage was roughly estimated for the entire *Zostera* bed every three weeks from mid-September to mid-December. The map was based on permanent stations along the transect lines as well as stations at right angles to the transects. In the range from 0-90% leaf coverage, a linear correlation was found between cover and above-ground ash-free biomass: $y = 0.4x + 1.9$, where y is standing crop in g ash-free dry weight per m², and x is percentage leaf cover ($n = 61$, $r = 0.926$, $P < 0.001$). As expected, above 90% coverage, the relationship was no longer linear. For the present purpose an average value of the samples with 95% and 100% cover was used, viz. 80.2 g ash-free dwt/m² ($n = 5$).

Standing seed crop

To estimate the removal rate of *Atriplex* and *Suaeda* seeds by ducks in the salt marshes along the Rømø barrage, exclosure experiments were conducted in 1985 and 1986. In 1985, the experiments were carried out in both the southern and the northern marsh.

In each marsh area two exclosures, each 2 m × 2 m, were erected in visually homogeneous vegetation in early September. An exclosure consisted of either poles connected with wires at four heights, or sheep fence. Sample plots, i.e. areas visited by the ducks, were placed on transects 50-100 m from the exclosures. Along the transects, 40-60 plants were taken at random and individually marked with a small piece of white plastic tape just above ground. In each exclosure 20 plants were marked. The number of seeds per plant was counted repeatedly at 10-14 days intervals from September until all seeds had been removed from the plants, either due to duck foraging or natural seed fall. To follow seed ripening, plants were randomly picked on each sampling date in 1986. One hundred *Atriplex* and the same number of *Suaeda* seeds were picked and dried for 24 hrs at 80°C.

In early October 1986, the total seed crop per ha was estimated for the northern and the southern marsh along the Rømø barrage and for two sections of Ballum Foreshore. At 20 m intervals along the transects the number of seed-bearing dicotyledons was counted in 0.25 m² squares. The number of seeds per plant was counted for at least 100 plants of each species.

Results and discussion

Tidal flat feeding

Wildfowl numbers

Brent Geese and Wigeon were the most numerous waterfowl species in the tidal mudflats at Koldby Leje. In autumn 1985 the peak numbers were 4,500 and 8,000, respectively, and in autumn 1986, 6,000 and 6,500, respectively. Wigeon arrived in the middle of September (Fig. 2), peak numbers being reached from late September to early October. Thereafter, numbers dropped quickly; in 1985 a flock of 500-1,000 stayed until the end of November, whereas in 1986, no Wigeon remained after mid-October. In 1985 the Brent Geese arrived late September, and peak numbers were reached in October. In 1986, however, numbers already began to decline after the beginning of October. In 1985 the proportion of juveniles in the flocks observed throughout autumn was 35%, whilst in 1986 there were less than 1% juveniles. This difference in age structure, apparently affected neither time of arrival nor peak numbers observed. In 1985 the Brent Geese stayed until late November, whereas in 1986 they remained until mid-December.

Teal and Pintail were present in lower numbers; maxima recorded were 1,000 and 600, respectively. Both had a phenology similar to Wigeon, but numbers varied much between days.

The estimated number of bird-days spent on the mudflats in the two autumns is presented in Table 1. The number of Brent Goose-days was almost similar in the two years, whereas there was a 45% reduction in Wigeon-days in 1986 compared to 1985.

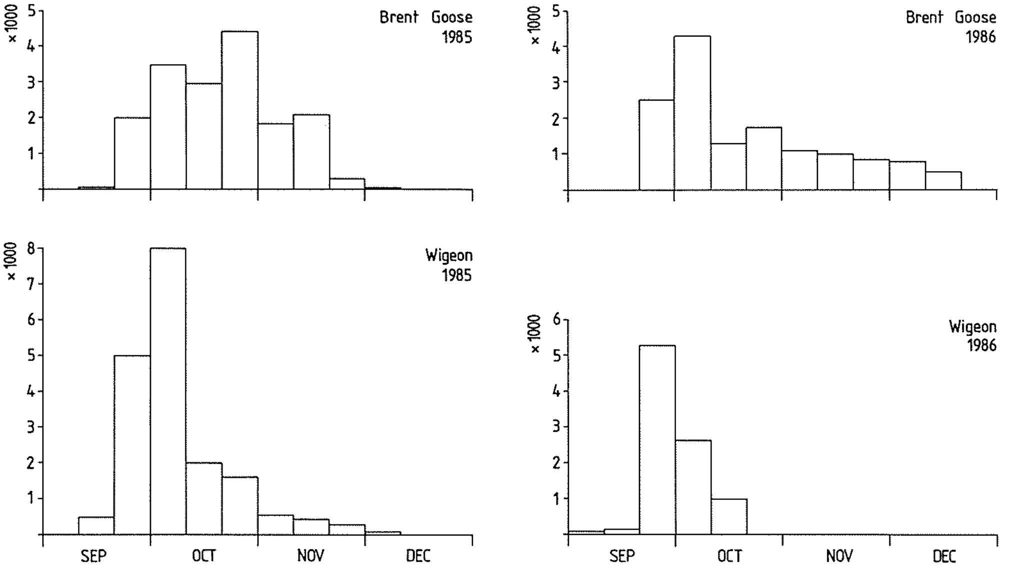

Fig. 2. Autumn occurrence of Brent Geese and Wigeon at Koldby Leje in 1985 and 1986, expressed as average numbers in 10-day periods.

Table 1. Number of bird-days spent by the most numerous wildfowl species on Koldby Leje, autumn 1985 and 1986.

	1985	1986
Brent Goose	176,200	143,400
Wigeon	176,500	96,700
Teal	19,500	23,000
Pintail	9,400	8,150

Feeding rhythm

During low water periods at day-time Brent Geese and Wigeon arrived from the high-water roost to the feeding grounds 3-4 hrs before low tide, and left 3-4 hrs after. For both species foraging was the predominant activity during low water (Fig. 3a, b). Just upon arrival and prior to departure the birds were unable to reach the flooded vegetation, and were thus roosting. As soon as they could reach the vegetation, feeding was very intense and virtually without breaks. The average active feeding period in Brent Geese and Wigeon was 6 hrs 32 minutes and 6 hrs 26 minutes, respectively.

Feeding methods changed in response to water level (Fig. 4). Brent Geese were initially swimming, and grazing *Zostera* leaves by submerging the head or neck, or by upending. When able to reach the bottom, they typically paddled in the mud for some time, but during most of the low water period they grazed by walking on the mudflats. Most of the feeding consisted of pecking leaves, and only 5-10% of the birds were grubbing. With the rising water the reverse sequence of feeding methods was observed.

Wigeon first fed by swimming, mostly submerging the head or neck, but switched to grazing by walking as soon as they could reach the bottom. The Wigeon were mainly grazing the leaves of *Zostera;* between 20-35% of the birds were judged to be grubbing, although this was sometimes difficult to ascertain.

During the three night-time observations, Brent Geese were present on all three occasions, whereas Wigeon were present only on the first two. Although the light conditions of the first two nights (overcast, dark) differed from the conditions of the third (bright, four days after full moon), activity patterns did not change in Brent Goose.

The period spent by the Brent Goose on the feeding ground did not differ from the day-time period (Fig. 3). The geese were feeding actively until low tide when feeding activity dropped, after which many birds roosted in the gullies or on the edge of the tidal flat. When the water rose the geese resumed feeding, probably triggered by the incoming water.

Wigeon started to feed approximately half an hour later than during day-time, but were feeding actively throughout the low-water period.

The nightly active feeding period of Brent Geese and Wigeon was on average 4 hrs 52 minutes and 6 hrs 16 minutes, respectively.

Combined over 24 hrs, Brent Geese and Wigeon were feeding actively for 11 hrs 24 minutes and 12 hrs 42 minutes, respectively.

Nocturnal feeding is well documented for Wigeon (OWEN 1973, CAMPREDON 1981), but virtually undocumented for Brent Geese. MAHEO (1976) did not record night-foraging Brent Geese in the *Zostera* beds in Golfe du Morbihan on the French Atlantic coast, and other authors do not mention the phenomenon (e.g., RANWELL & DOWNING 1959, CHARMAN 1979).

Overlap in distribution

The overlap of Brent Geese, Wigeon and Teal feeding in 50 m $\times$ 50 m squares was examined with regard to spatial and tem-

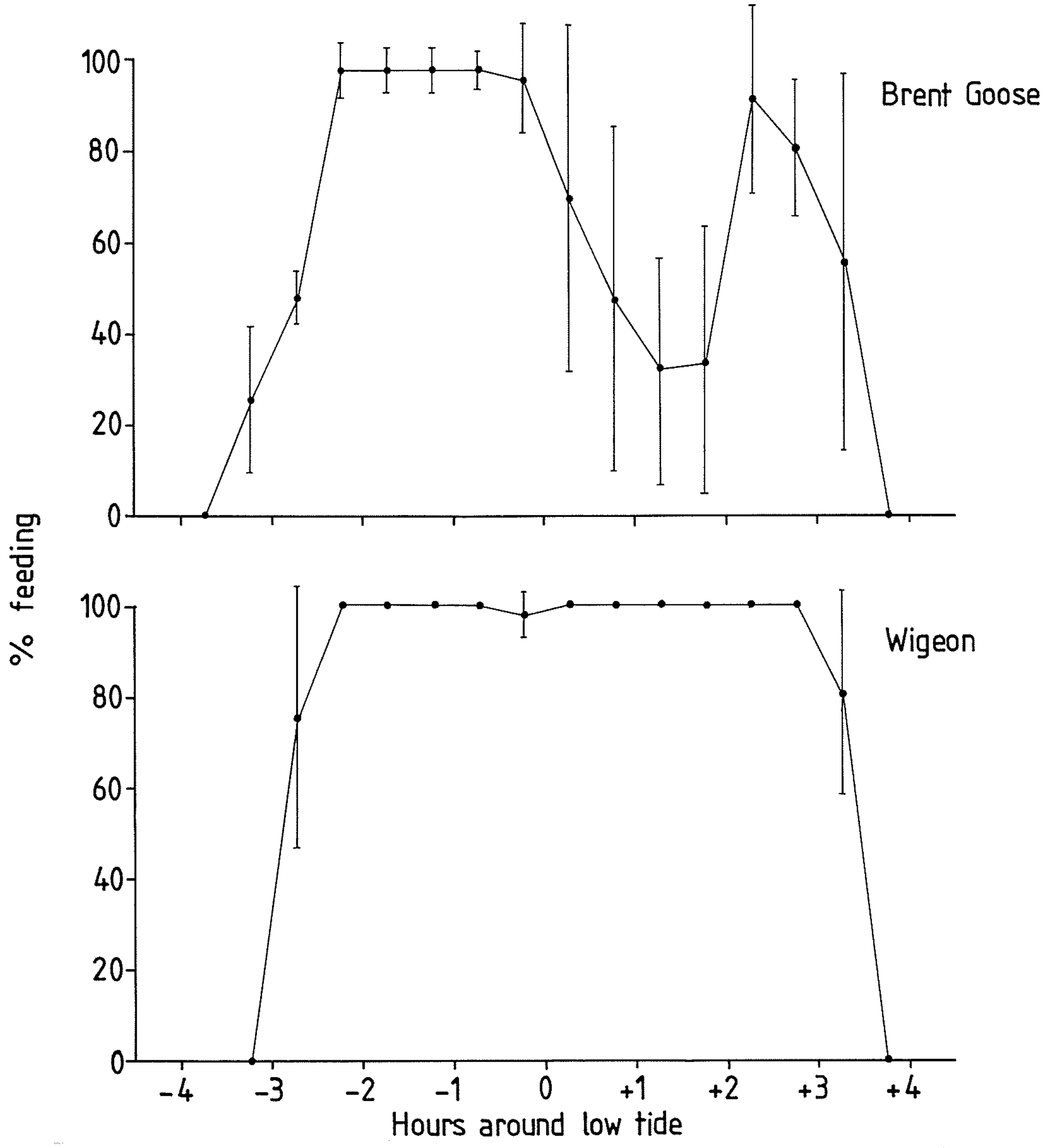

Fig. 3b. Feeding activity of Brent Geese and Wigeon at night at Koldby Leje in relation to tidal cycle (average of 3 observation periods). Bars show one standard deviation. During high water, the wildfowl roost on Jordsand Flak.

poral distribution. Temporal overlap expresses simultaneous occurrence, i.e. the degree to which particular species occur in the squares at the same time.

The southern squares were in a depression, where a depth of about 5 cm water was retained during low tide, whereas the northern squares ran dry during low water. Between the two substrates there was no difference in occurrence of the three wildfowl species, and the overall spatial overlap was high between all three species (Table 2), indicating that the birds make use of the same substrate.

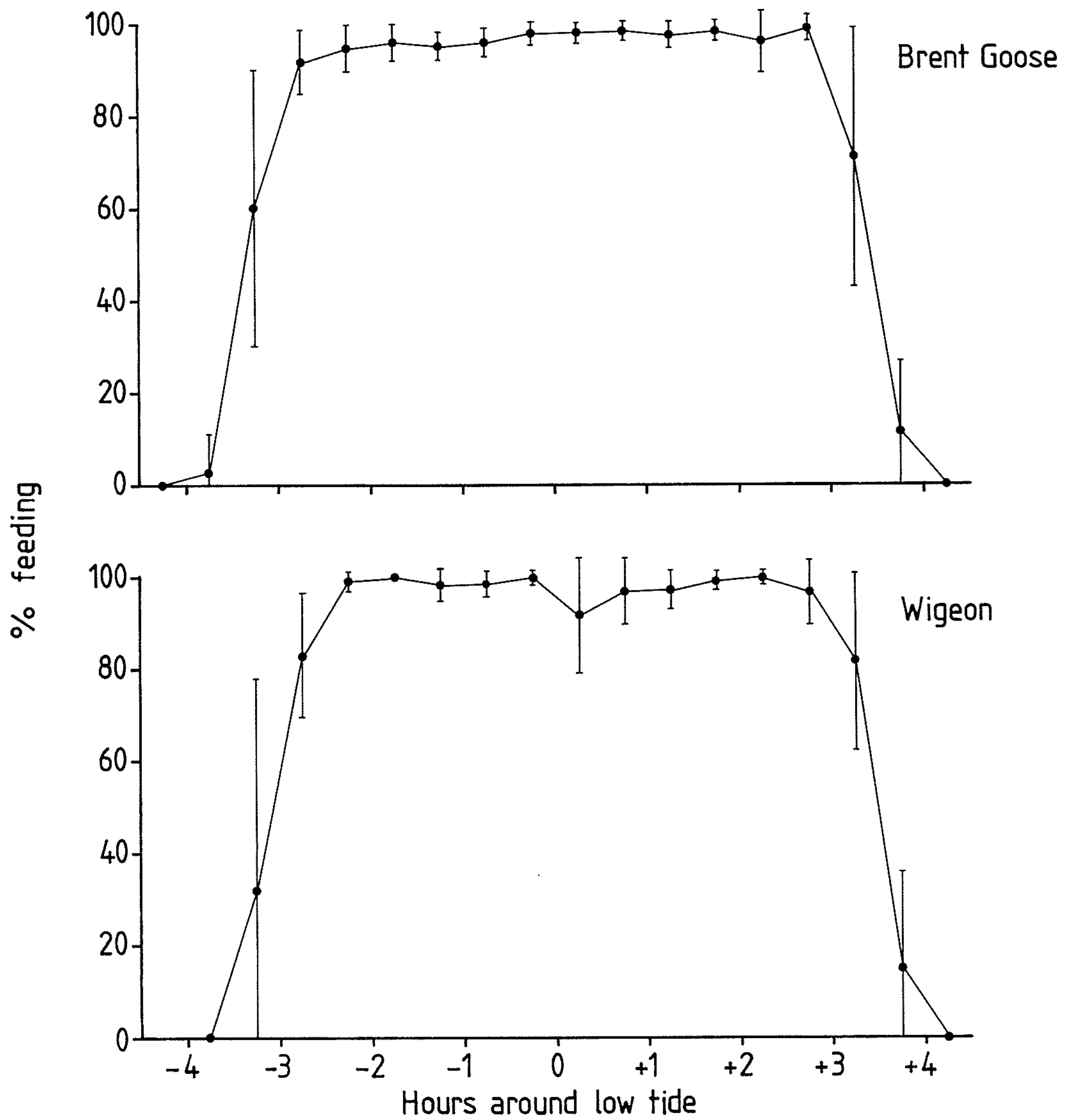

Fig. 3a. Feeding activity of Brent Geese and Wigeon during daytime at Koldby Leje (7 observation periods).

Temporal overlap of Brent Geese and Wigeon was relatively high, in that the two species often were feeding in mixed flocks, walking over the mudflats at the same speed. Teal, on the other hand, had little temporal overlap with the two other species. The three species often occurred together in flocks, but Teal walked faster over the substrate, leaving the two other species behind.

Food and food consumption

Microscopic examination of droppings

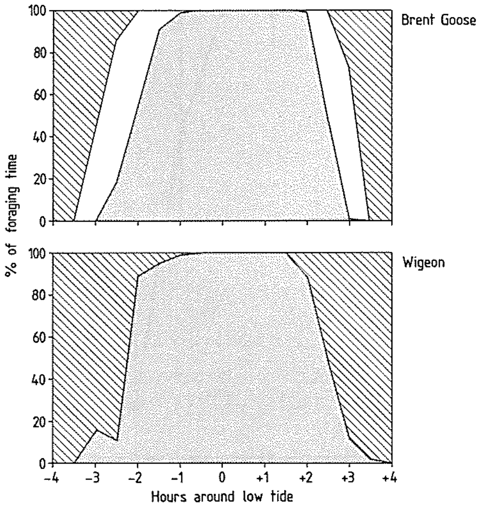

Fig. 4. Feeding techniques by Brent Geese and Wigeon at Koldby Leje in relation to tidal cycle. Hatched: feeding by swimming; open: paddling; shaded: feeding by walking. Average of two observation days in early October.

revealed that Brent Geese and Wigeon fed exclusively on *Zostera,* and that above-ground parts predominated in the diet. In three samples from October-November, leaves made up between 85 and 91% of the Brent Goose diet, and roots and rhizomes the remainder. Only in a sample from early December was the proportion of leaves lower, viz. 58%. In two samples of Wigeon droppings from October, leaves made up 98 and 92% of the diet, respectively.

Table 2. Overlap in spatial and temporal distribution of Brent Geese, Wigeon and Teal in quadrats in Zostera vegetation at Koldby Leje.

	Spatial overlap	
	Wigeon	Brent
Brent	0.781	-
Teal	0.797	0.745

	Temporal overlap	
	Wigeon	Brent
Brent	0.563	-
Teal	0.142	0.106

Food selection by Teal was not thoroughly investigated. Direct observations indicated that Teal were filtering the top layer of the muddy substrate, probably feeding on seeds of *Zostera* and also invertebrates. In a sample of Teal droppings, broken shells of *Hydrobia* snails were frequent.

An estimate of daily food and energy intake for Brent Geese and Wigeon is shown in Table 3. Computations have been conducted under the assumption that the diet consisted exclusively of *Zostera noltii* leaves. Retention rates, achieved using ash and lignin, did not differ significantly, values shown in the table being averages based upon the two tracer substances. The calculated daily net energy intake of 986 kJ for Brent Geese is somewhat higher than the estimate for Brent Geese in winter, viz. 840 kJ (DRENT et al. 1978). The difference may reflect that the geese put on weight in autumn (FOG 1967), thereby demanding more energy.

The estimated net energy intake of 592 kJ for Wigeon is somewhat lower than the daily existence energy (DEE) predicted for a 0.7 kg non-passerine by DRENT et al. (1978), viz. 2.6x Basal Metabolic Rate (BMR) (736 kJ) (formula for BMR from ASCHOFF & POHL 1970, Wigeon weight from BAUER & GLUTZ VON BLOTZHEIM 1968). It should be noted, however, that the 'marker substance' method as applied here is crude, because it only took above-ground material into account, and so the results must be regarded only as rough estimates.

Table 3. Estimates of daily food and energy intake by Brent Goose and Wigeon feeding on Zostera noltii leaves. All weights are in g ash-free dry weight.

	Brent Goose	Wigeon
Time on feeding ground (min)	684	762
Droppings per hour	17.0[a]	16.8[b]
Dropping weight (g)	0.452[c]	0.164[d]
Daily defaecation (g)	87.6	35.0
Retention rate	0.35	0.46
Daily food intake (g)	134.8	64.8
Energy content of food (kJ/g)	19.4	19.4
Energy content of droppings (kJ/g)	18.6	19.0
Daily net energy intake (kJ/)	986	592

Notes: a: n=6 block hours; b: n=3 block hours; c: n=187; d: n=99.

Zostera stock and wildfowl grazing impact

In late August 1985, the above-ground standing crop in the central part of the *Zostera* bed amounted to about 60 g ash-free dry weight (dwt) per m² (Fig. 5). From late August to early December the biomass gradually decreased, however, with a significant difference between grazed and ungrazed plots. In early December, the above-ground biomass in the exclosures was reduced by 59%, whereas in the grazed plots the reduction rate was 89%. This 30% difference represents the proportion consumed by wildfowl. Other avenues of biomass losses were: leaves dying off; leaves breaking off; and leaf consumption by invertebrates. In early December 1985, the geese abandoned the mudflats at a stage when the standing crop had been reduced to 6.6 g ash-free dwt/m², or about 10% leaf cover.

In late August 1985, below-ground biomass was on average 36 g ash-free dwt/m². During the autumn season there was an average increase of 26% in biomass in the ungrazed plots, whilst a 29% decrease in the grazed plots (Fig. 5). However, neither the increase, nor the decrease was significant at the 5% level (one-way analysis of variance). By the end of October and in early December there was, on the other hand, a significant difference in biomass in ungrazed plots (student t-test, $t=3.807$, $P<0.01$, and $t=3.424$, $P<0.01$, respectively). In December the biomass in the grazed plots was 48% lower than in the ungrazed plots. Thus, it is indicated that the wildfowl, and predominantly the grubbing Brent Geese, affected the below-ground biomass of *Zostera* as well.

Based upon both the mapping of the *Zostera* bed and the linear correlation between leaf cover and above-ground biomass established in 1985, the total above-ground standing crop of the bed was estimated at 38.8 tons ash-free dwt in early September 1986, equivalent to an average of 28.1 g ash-free dwt/m² for the whole *Zostera* bed (138 ha) (cf. Fig. 8). In mid-October, the standing crop had decreased to 25.6 tons, and in mid-December to 1.2 tons, this being 3.1% of the early September stock.

To achieve an estimate of total annual production, the value of the maximum standing stock was doubled (PETERSEN 1913). This factor is known to underestimate the production of *Zostera marina* (SAND-JENSEN 1975, JACOBS 1979, WIUM-ANDERSEN & BORUM 1984), but probably

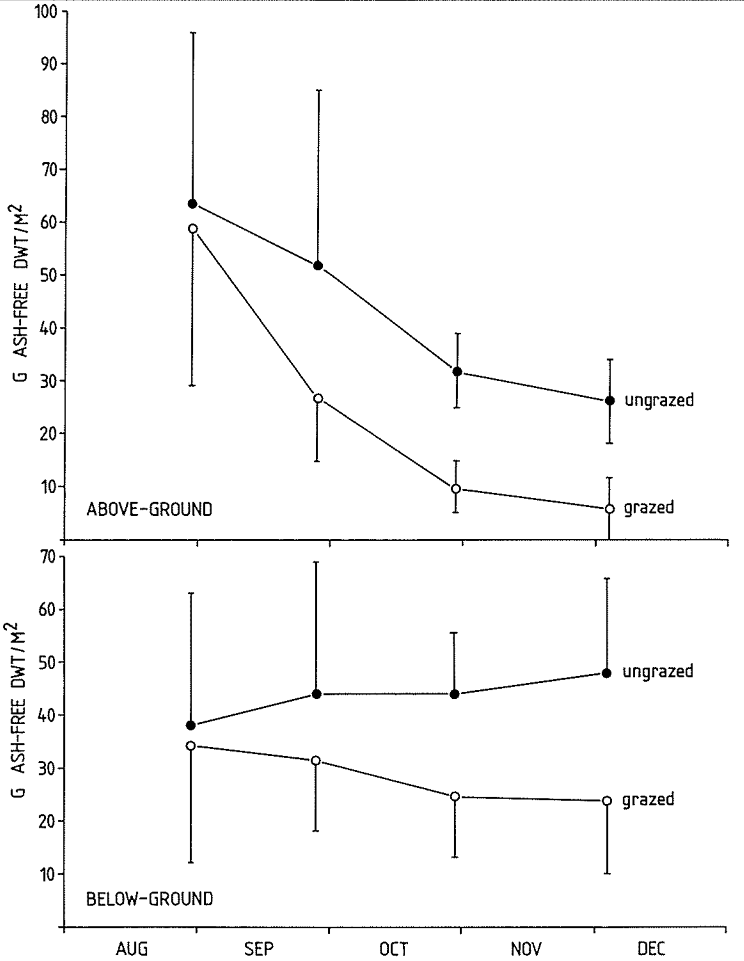

Fig. 5. Development in above-ground and below-ground standing crop of Zostera in grazed and ungrazed plots at Koldby Leje during autumn 1985. Bars represent 95% confidence limits.

gives a reasonably good estimate for *Z. noltii* (JACOBS et al. 1981). For the Dutch Wadden Sea JACOBS et al. (1983) found that the maximum standing crop of *Z. noltii* was reached in August-September. Therefore, it seems feasible to use the early September value of 38.8 tons as the maximum standing crop. Total above-ground production for the *Zostera* bed thus amounted to 77.6 tons ash-free dwt. From the estimate of the total number of Brent Goose-days and Wigeon-days spent in the area (Table 1) and their daily food consumption (Table 3), it is calculated that these wildfowl consumed a total of 35.2 tons and 25.6 tons in 1985 and 1986, respectively, of which the Brent Geese consumed 68% and 75% of the biomass, respectively. Between 1985 and 1986, there were no apparent differences in either leaf cover or *Zostera* distribution in the beginning of the autumn season, so the maximum standing crop was assumed to be similar for the two years. Thus, the consumption by wildfowl was equivalent to 45% and 33% of the total production in 1985 and 1986, respectively, or 91% and 66% of the maximum standing crop. The average grazing pressure was estimated at

25.5 and 18.6 g ash-free dwt/m^2, but was higher in the central parts of the *Zostera* bed.

Other studies have also evidenced that wildfowl grazing impact on *Zostera* can be considerable, although the values presented in literature are lower than the values from the present study.

For a *Z. noltii* bed in the Dutch Wadden Sea, JACOBS et al. (1981) found that wildfowl in autumn grazed the area down to a homogeneous stand with less than 10% leaf cover, and consumed 26% of the annual production, or 50% of the maximum standing crop.

For an estuary in southern England TUBBS & TUBBS (1983) found that grazing wildfowl, especially Brent Geese, likewise had a considerable effect on leaf cover of *Zostera* spp.

In none of the above cited studies was the consumption of below-ground biomass quantified. In the present study it was indicated that the wildfowl had an impact on this part of the biomass as well.

Impact of Zostera stock on feeding performance

Feeding efficiency as determined from feeding bout length and walking speed of Brent Goose and Wigeon at different levels of *Zostera* leaf cover, was compared (Table 4). Observations were carried out on birds feeding in areas where leaf cover had been assessed shortly before. For both species, it was found that efficiency was heavily hampered at low leaf cover. Thus, the birds had to walk faster over the substrate and the feeding bout length was reduced, indicating an increase in the distance between profitable patches of *Zostera* therefore resulting in the birds spending more time searching.

Brent Geese changed feeding method in response to the decreasing food supply, whereas Wigeon had no alternative feeding technique to which they could switch. On six days in 1986, where observations were performed over the entire low water period and leaf cover had been checked in advance, Brent Goose flocks spending the whole low water period in an area of even cover were observed. When areas of for example 10% and 90% leaf coverage were accessible, the geese selected the latter, but were sometimes forced to choose the former, due to presence of hunters in the more optimal parts of the *Zostera* bed (see next chapter).

At high leaf cover the geese spent less than 10% of the entire low water feeding period paddling (Fig. 6). As the cover be-

Table 4. Feeding parameters of Brent Goose and Wigeon at approximately 80% and 10-20% leaf cover of Zostera at Koldby Leje. Means, their standard deviations, and sample sizes are presented together with Student-t values and significance levels in two-tailed Student t-test.

	80%			10-20%				
	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	t	P
Wigeon								
Feeding bout length (sec)	34.1	22.74	41	9.4	10.42	19	5.77	<0.001
Walking speed (sec for 10 steps)	38.4	37.63	32	10.7	5.08	20	4.10	<0.001
Brent Goose								
Feeding bout length (sec)	36.0	30.14	19	9.7	6.62	32	3.75	<0.01
Walking speed (sec for 10 steps)	59.4	37.80	19	22.4	8.40	18	4.17	<0.001

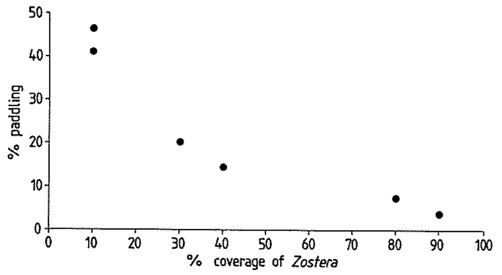

Fig. 6. Proportion of the low-water feeding period spent paddling for roots and rhizomes of Zostera by Brent Geese in relation to leaf cover.

came more sparse, the geese were paddling to a greater extent, and at 10% cover they spent almost half of the feeding period paddling for roots and rhizomes.

Due to a higher intake of below-ground parts, it was not possible to estimate food and energy intake in geese feeding at low *Zostera* cover. However, defaecation rates indicated that profitability in terms of energy intake was reduced. Thus, hourly defaecation rate at 10-20% leaf cover was estimated at 11.5 droppings/hr (3 hourly blocks), versus 17.0 at 70-90% cover (6 hourly blocks) ($Z = 5.83$, $P < 0.05$; for statistical method see BÉDARD & GAUTHIER 1986).

CHARMAN (1979) studied the energetics and performance of *Zostera noltii* feeding Brent Geese in southern England. An apparent threshold cover for *Zostera* leaf exploitation was determined as being around 15%, below which food consumption decreased markedly, and time spent feeding and also dispersion increased. In the course of the winter, the geese shifted from mudflats to salt marshes and agricultural crops, and it was demonstrated that this shift was related to the depletion of the *Zostera* resources. The data from the present study are in agreement with those results of CHARMAN (1979), and it is here added that the Brent Geese can also switch feeding technique during instances of decreasing resources.

The overlap in diet and the feeding congregation of Brent Geese and Wigeon gives rise, potentially, to interspecific competition. As the food stock at Koldby Leje was gradually depleted over the autumn, the competition probably became profound and especially critical to Wigeon which did not switch to the below-ground parts of *Zostera*. No interference was observed between the two species, and it is hypothesised that the interspecific competition is exploitative, limiting the number of birds that can utilise the food supplies.

In Golfe du Morbihan (1961-79) it was found that with the increase in the number of wintering Brent Geese, which reflected the general population increase, the number of Wigeon-days spent in the gulf decreased (CAMPREDON 1982), and this was suggested to be the result of interspecific competition for the *Zostera* resources.

However, it remains to be tested experimentally whether interspecific competition does affect bird numbers, though there are good reasons to believe that it does take place.

Effect of shooting on wildfowl distribution

Shooting in the mudflats at Koldby Leje was highly specialised. The hunters arrived around 3 hrs before low tide, and walked out on the still flooded mudflats. They placed themselves on the small hillocks and laid out duck decoys in the shallows nearby. As the water fell, the hunters lay down on the mudflat. Shooting was most intense from 3 hrs to 1 hr before low tide. Sometimes, the hunters left the mudflats around low water.

Hunting was concentrated to the period

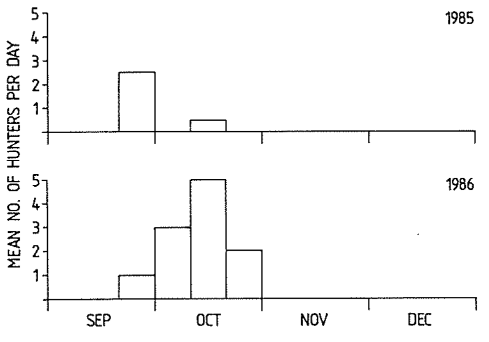

Fig. 7. Mean number of hunters present at Koldby Leje during low-water periods in autumns 1985 and 1986.

from mid-September to late October (Fig. 7), this being highly related to presence of dabbling ducks. There was, however, a big difference in the average number of hunters present between 1985 and 1986, and the estimated number of hunter-days over the seasons was 30 and 121, respectively. The peak number of hunters recorded was nine. The hunters usually placed themselves in the northern part of the *Zostera* bed. Only a few times were hunters sitting in the southern part, inside the Jordsand refuge with a complete shooting ban.

The ducks and geese reacted strongly to the presence of hunters and shooting, which was documented by a natural experiment. In Fig. 8 the size of the *Zostera* bed is depicted during the periods from mid-September to early October, and from mid- to late October 1986, respectively, and in parallel the distribution of wildfowl is shown with and without hunters present on the mudflats. Additionally, the distribution of wildfowl at night is shown. Flocks of wildfowl mapped in the field have been distributed in a 200m x 200m grid placed over the field maps. Data for Wigeon and Brent Geese have been pooled because there was neither a significant difference in the distribution pattern, nor in the reaction to hunting.

Several points emerge from Fig. 8:

1) From mid-September to late October the *Zostera* bed clearly diminished in size and biomass. Only within a 100 m radius around the observation tower was a 75-100% leaf cover of *Zostera* retained during late October.
2) When there were no hunters present, wildfowl distribution was mainly overlapping that of *Zostera,* and the birds were feeding in the zones with greatest leaf cover. However, the observation tower affected wildfowl in a radius of 150-200 m. In the second half of October the wildfowl concentrated in the northeastern part of the bed.
3) The nightly distribution of wildfowl was almost completely similar to that of day-time distribution, when the birds were undisturbed.
4) When hunters were present, the wildfowl flocks were displaced from the northern to the southern part of the *Zostera* bed, or to the western and eastern edges of the bed. From mid-September to early October, the flocks were able to withdraw to areas with good leaf cover of *Zostera.* However, during that period, hunters were present most days and the increased grazing pressure in the southern parts of the *Zostera* bed led to a fast depletion of the standing stock. During the second half of October, there was less than 25% leaf cover in those areas, to where the wildfowl were displaced due to hunting. In late October, the presence of a single hunter in the northern part was sufficient to displace the birds.

The wildfowl responded quickly to cessation of shooting. Twice it was observed that the hunters left the mudflats around low tide, and within the next hour all ducks and geese switched from the southern and eastern parts of the *Zostera* bed to the northern part with good leaf cover.

In the course of the season, shooting be-

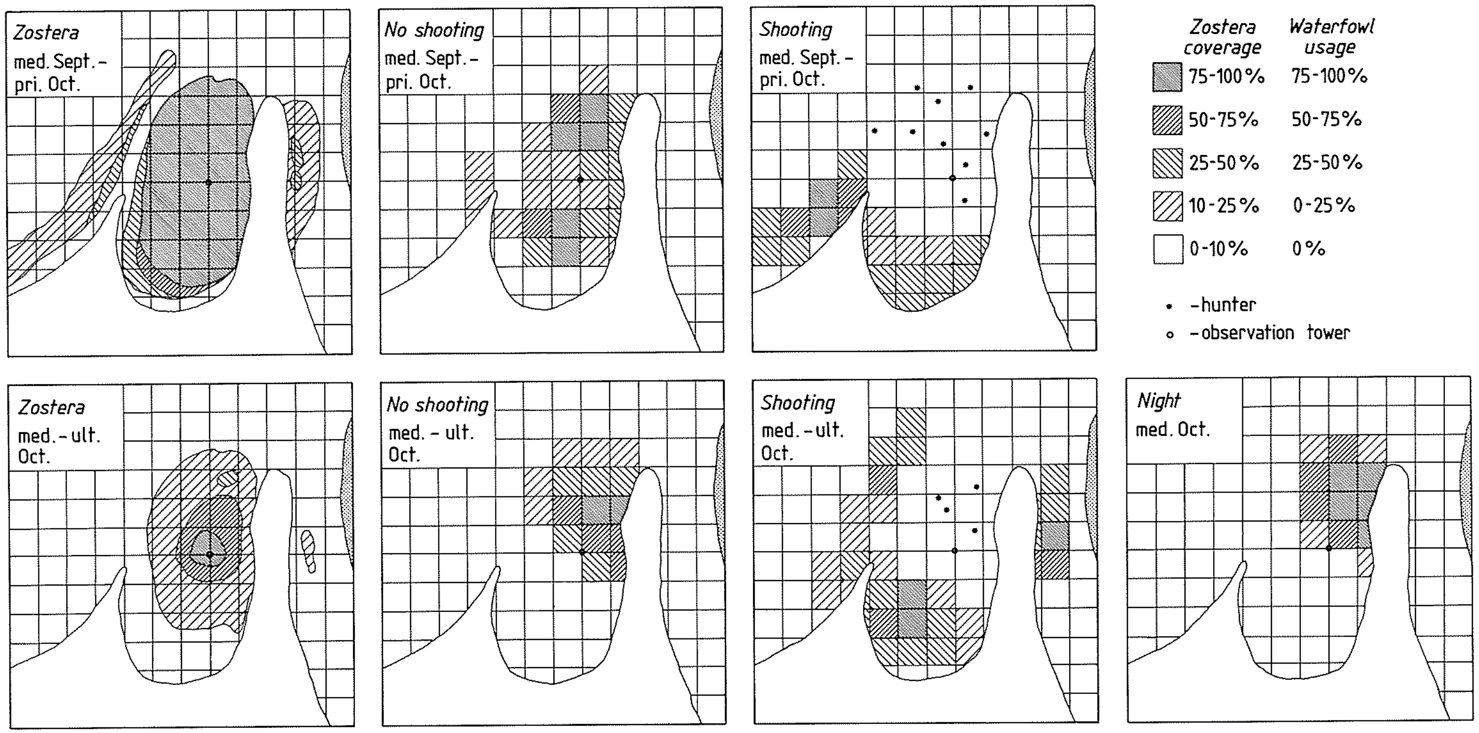

Fig. 8. Zostera resources and distribution of wildfowl (Brent Geese and Wigeon pooled) with and without hunting activity at Koldby Leje, during two stages in autumn 1986. Grid size is 200 m × 200 m. Waterfowl usage is expressed as percentage of the quadrat with the highest numbers. Each situation represents 2-3 complete low-water periods with mapping every ½ hr. The pooled numbers of hunters are shown.

came an increasingly disturbing activity, which was reflected in the flight distances of the Brent Goose flocks. The flight distance of a flock was estimated using a walking person as a standard stimulus triggering escape flight. The distance from the observer to the flock was controlled by pacing out. In late September the flight distance of a flock of 200-500 Brent Geese was on average 211 m (n = 10, S.D. = 32.4), whereas in late October it had increased to 367 m (n = 8, S.D. = 51.6), which is significantly higher (t = 7.46, P <0.001). Flight distances of Wigeon flocks were not quantified, but were comparable to those of Brent Geese.

Salt marsh feeding

Wildfowl numbers

The most numerous wildfowl around the Rømø barrage in autumn were Wigeon and Teal. In 1985 peak numbers were 10,000 and 3,500, respectively, in 1986 15,000 and 2,500, respectively. Up to 700 Pintail, 2,500 Mallard *Anas platyrhynchos,* 900 Brent Geese, and 500 Barnacle Geese *Branta leucopsis* were also present, but more irregularly. Brent Geese occurred only in autumn 1985, and it was almost exclusively family flocks, which visited the salt marshes.

Wigeon and Teal arrived from late Au-

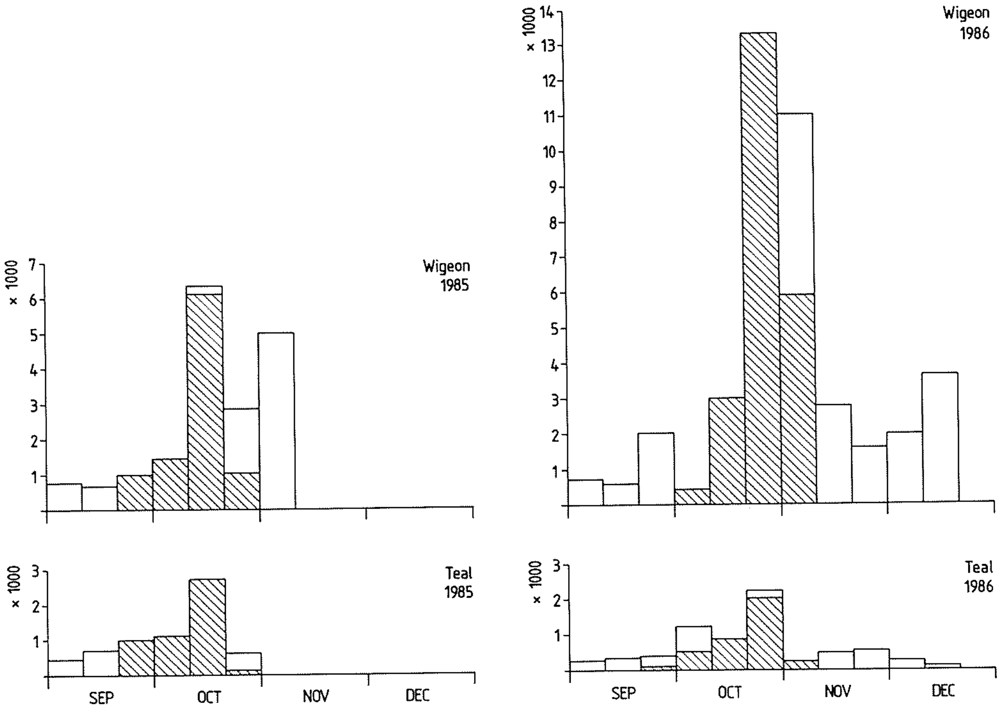

Fig. 9. Autumn occurrence of Wigeon and Teal at the Rømø barrage in 1985 and 1986, expressed as average numbers in 10-day periods. Hatched columns indicate the number of birds feeding in the salt marshes during diurnal high tides, open columns the number resting during high tide.

gust to early September (Fig. 9). For both species, peak numbers were reached in the second half of October, 2-3 weeks later than at Koldby Leje. In 1986, many ducks remained until mid-December.

In the beginning of the autumn staging period, the ducks used the barrage area as a high water roost, and fed during low water on adjacent mudflats north of the barrage. From the end of September, the ducks started salt marsh feeding. In 1985, this proceeded until late October, whereas in 1986 it continued until early November (Fig. 9). In 1985, the ducks left the area shortly after the salt marsh feeding period, whereas many stayed longer in 1986. In November, following the salt marsh feeding period, the remaining ducks roosted throughout day-time, irrespective of the tidal cycle. Evening flights of ducks into the hinterland were observed and heard on several occasions in November, though the exact feeding grounds were not identified. An indication of the Wigeon flight range comes from a bag analysis (LAURSEN 1985), which showed that Wigeon were shot up to 10 km inland from the Ballum Foreshore, i.e. into Ballum Enge. Flocks of Wigeon were also heard at night on Ballum Foreshore.

Table 5. Estimated number of bird-days spent by ducks feeding on seeds of salt marsh vegetation along the Rømø barrage, autumn 1985 and 1986. Brackets indicate that the numbers are under-estimates.

	1985	1986
Wigeon	101,000	227,000
Teal	51,000	38,000
Pintail	4,000	7,000
Mallard	(9,000)	(9,000)

The number of feeding-days spent by ducks on the salt marsh vegetation is shown in Table 5. There was a doubling in number of Wigeon-days from 1985 to 1986, while Teal and Pintail feeding-days for the 2 years did not differ significantly. The higher amount of Wigeon-days was the result of a higher feeding intensity in the northern marsh, while feeding intensity in the

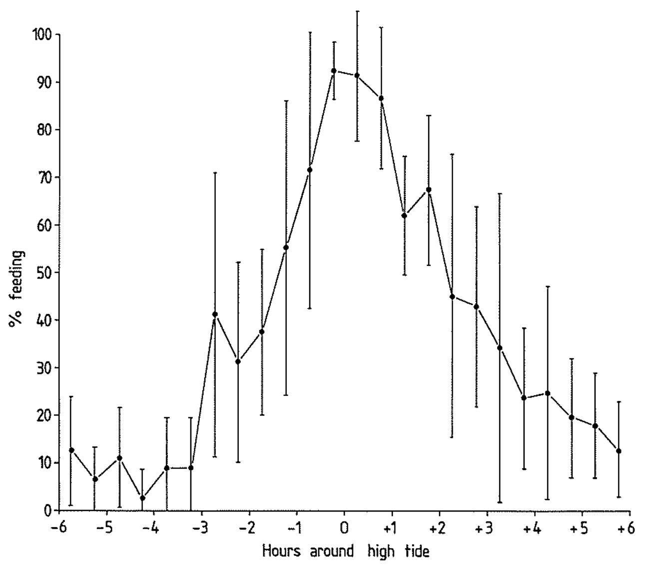

Fig. 10. Diurnal feeding activity of Wigeon at the Rømø barrage during October, in relation to the tidal cycle (average of several observation periods). Bars show one standard deviation.

southern marsh did not change noticeably. This impression is based on the mapping of the flocks during day-time. The number of Mallard-days could not be ascertained because the Mallards occurred scattered in small flocks in the ditches.

Feeding rhythm

During day-time in mid-October duck feeding in the salt marshes was most intense around high water (Fig. 10). During low water, only about 10-20% of the ducks fed, while the rest were roosting on the mudflats beyond the marshes. The feeding rhythms of Wigeon, Teal and Pintail on salt marsh were identical. Whilst feeding in the marshes the ducks concentrated in dense flocks; in October up to 8,000 ducks in a flock were observed walking over the sward. During their stay in the marshes, the ducks fed intensively. Thus, on average 97.7% were feeding while in the marsh.

Nightly feeding activity could not be quantified, but it definitely occurred. In October, Wigeon and Teal were heard in the marsh areas several nights.

Seed stock and impact of duck feeding

From early September to mid-October 1986, the weight of *Atriplex* and *Suaeda* seeds more than tripled, and the maximum average weight was reached in the second half of October. Subsequently, seed weights declined (Fig. 11).

The highest standing seed stock was found on the marsh north of the Rømø barrage, followed by the marsh to the south, and the southern Ballum Foreshore (Table 6). Seed crops of grasses and other dicotyledons were negligible, and the *Salicornia* zones were, according to mappings, little used by the ducks.

The results of the exclosure experiments in 1985 and 1986 are shown in Figs. 12 and 13, respectively. In the marsh south of the

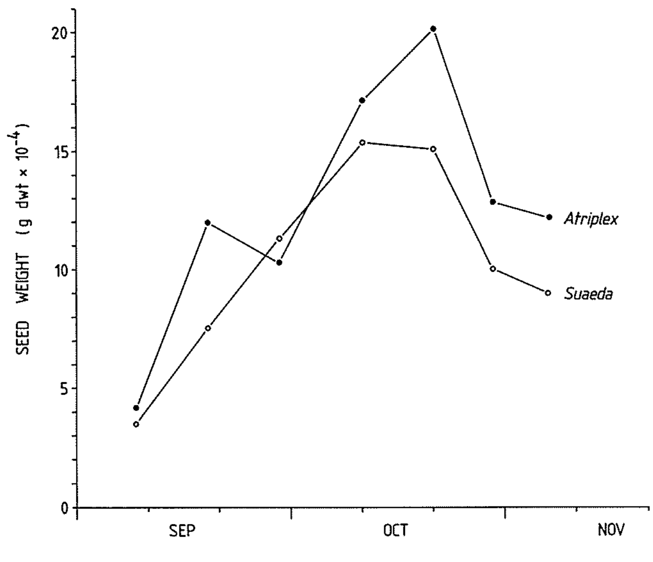

Fig. 11. Development in average seed weight of Atriplex litoralis and Suaeda maritima in autumn 1986.

Table 6. Standing seed biomass of Suaeda maritima and Atriplex litoralis on four salt marsh sections along the Rømø barrage and Ballum Foreshore, 1-10 October 1986. Mean seed weight of Suaeda and Atriplex was 0.0015 g dwt and 0.0017 g dwt, respectively, and mean number of seeds per plant 77.2 and 121.7, respectively (no significant differences between areas).

	Rømø barrage North		Rømø barrage South	
	Suaeda	*Atriplex*	*Suaeda*	*Atriplex*
Plants/m²	928.5	4.6	38.1	204.8
Seeds/m²	71680	560	2941	24924
Seed weight (g dwt)/m²	107.5	1.0	4.4	42.4
Seed biomass (kg dwt)/ha	1090		470	
	Ballum North		Ballum South	
	Suaeda	*Atriplex*	*Suaeda*	*Atriplex*
Plants/m²	0.7	13.7	362.2	7.3
Seeds/m²	54	1667	27962	888
Seed weight (g dwt)/m²	0.08	2.8	41.9	1.5
Seed biomass (kg dwt)/ha	29		434	

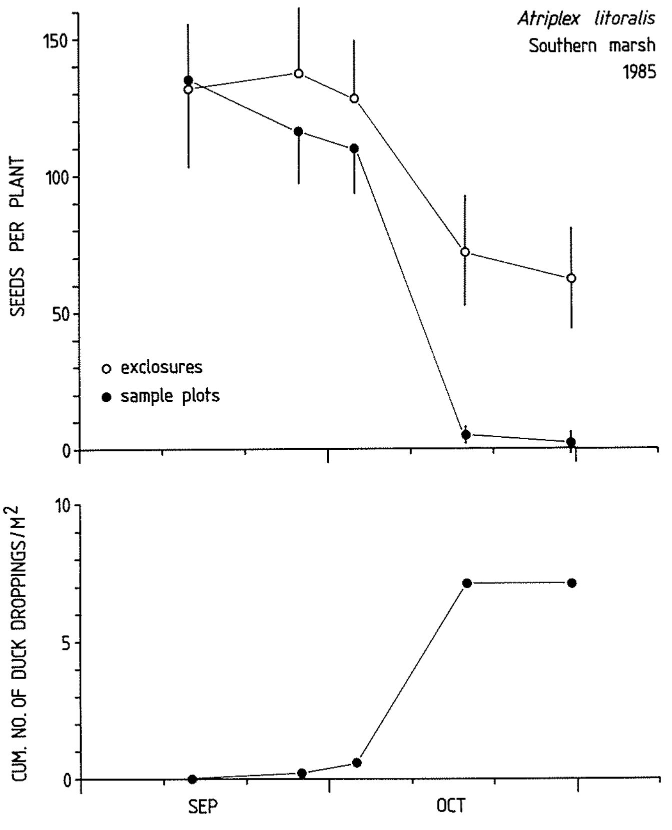

Fig. 12. Development in seed numbers per Atriplex plant (individually marked) within exclosures and duck visited plots in the southern marsh along the Rømø barrage during autumn 1985. Bars show 95% confidence limits. Below is shown the cumulative number of duck droppings counted within permanent plots in the same marsh.

Rømø barrage, for *Atriplex* seeds outside the exclosures, the reduction (representing the natural seed fall and seeds swept away during flooding) was 52% from early September to late October in both years. In other words, ducks consumed about half the standing seed stock accessible. In 1985, the *Atriplex* seed stock was depleted by the ducks in mid-October, while in 1986 this did not happen until early November. The dropping counts in 1985 showed that the substantial decline in seed stock was correlated to duck utilisation (Fig. 12). Flooding of the marshes and associated wave action was another major contributor to seed removal. After a period of flooding, a rim of seeds could be found along the barrage and the Ballum dykes. In the northern marsh dominated by *Suaeda,* the same pattern of seed removal was observed. From early September to early November 1986 the number of seeds per plant in the sample plots was reduced by 92%, and in the exclosures by 58%. Thus, the ducks consumed about 40% of the seed stock available, and the rest either fell off or was swept away during flooding. It is unknown to what extent the ducks fed on the seeds that had fallen off, but observations indicate that most ducks were picking seeds from the plants.

On the southern Ballum Foreshore seeds were counted on *Suaeda* plants on 2 October and 6 November 1986. Over that period, the average number of seeds per plant declined from 82.3 to 41.5, equivalent to a 50% reduction. This is comparable to the exclosure plots in the marsh north of the Rømø barrage, indicating that there had been no significant duck grazing.

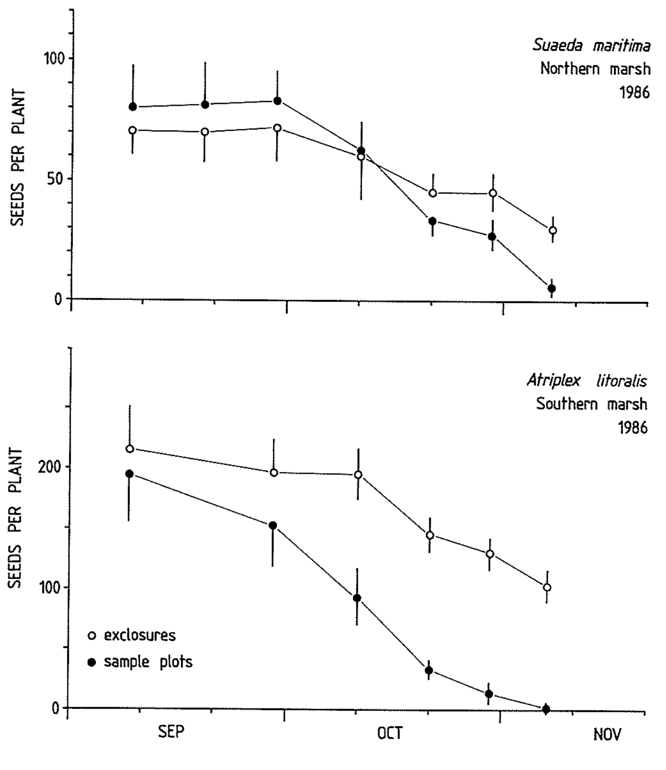

Fig. 13. Development in seed numbers for Suaeda and Atriplex plants within exclosures and duck visited plots in the marshes north and south of the Rømø barrage during autumn 1986. Bars show 95% confidence limits.

Impact of seed stock on foraging

The decreasing seed stock had a significant effect on duck foraging. This was demonstrated by the foraging parameters, walking speed and pecking rate, deployed by Wigeon feeding on *Atriplex* (Fig. 14). Unfortunately, it was not possible to relate the feeding parameters directly to seed density. However, as the curves in Fig. 13 show, date gives an approximate indication of density.

Walking speed was highly affected by the decreasing seed stock. In the start of the salt marsh feeding period the Wigeon lay down in the vegetation, stripping the seeds off the plants in the immediate surroundings. Later on in the season the ducks had to move continuously while feeding. At first, the ducks could compensate for decreasing seed density by walking faster, and pecking speed was not affected. However, by 6 November pecking speed had also decreased. This was the last date on which the ducks were seen feeding in the marshes.

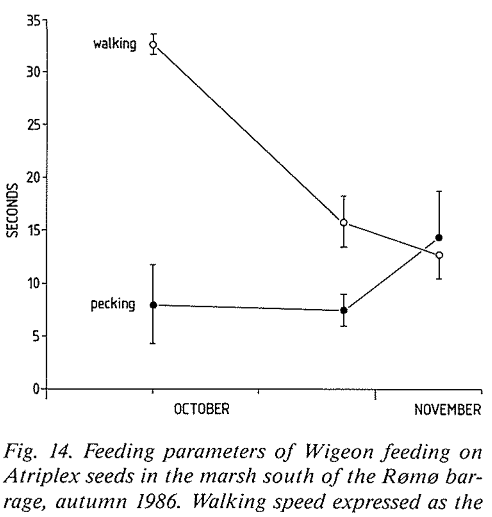

Fig. 14. Feeding parameters of Wigeon feeding on Atriplex seeds in the marsh south of the Rømø barrage, autumn 1986. Walking speed expressed as the time it took to make 10 steps, pecking speed as the time it took to make 10 pecks. Bars show 95% confidence limits.

Effect of shooting

The hunting practice and its effect on wildfowl utilisation of the Ballum Foreshore is dealt with in detail by LAURSEN, FRIKKE & BØGEBJERG (unpublished). They indicate that despite the fact that shooting closes 1 1/2 hrs after sunset (in November-December 1 hr after sunset), the ducks do not visit the marshes at night to any significant extent. Only in the outer marsh zones were duck droppings found at fair densities, but even then only infrequently over the autumn, and never at densities comparable to those found in the marshes along the Rømø barrage. Flocks of ducks were also only heard infrequently at night. These findings are supported by the seed counts in the Ballum marshes, which gave no indication of duck exploitation.

Apparently, despite the night-time being peaceful, the ducks did not feel safe enough to fly into the marshes when there was shooting during the preceding dusk. This has also been demonstrated by JAKOBSEN (1986), who made counts of dabbling ducks at night in the Skallingen salt marshes in the northern part of the Danish Wadden Sea. On nights when shooting had not occurred during the previous dusk, the number of ducks in the marshes was six times higher than compared to nights when there had been shooting during the previous evening.

Conclusions

The Danish Wadden Sea is situated in the migratory tract of the northwest European population of Wigeon numbering around 750,000 birds (RÜGER et al. 1986) and of the Siberian population of Dark-bellied Brent Goose numbering 150,000-200,000 birds (IWRB GOOSE RESEARCH GROUP unpubl.). The number of wildfowl, that can be counted at any one time in autumn, does not give a realistic picture of the total numbers passing through and making use of the food resources during autumn. Indeed, the turnover rate of birds is probably high. For the Northfriesian Wadden Sea just south of the Danish part, PROKOSCH (1984) found that the maximum staging period of Brent Geese was four weeks. Thus, over the autumn season probably double, or more, of the peak numbers present at a given time stay for a shorter or a longer period.

Within the study area, a temporal sequence of habitat shifts by wildfowl could be ascertained (Fig. 15). Wigeon first frequented the tidal mudflats, then the salt marshes, and finally the hinterland pastures. Brent Geese stayed on the mudflats throughout autumn 1986, but in 1985 part of the staging population shifted to the salt marshes. In Fig. 15, the arrows indicate that an unknown proportion of the staging population is exchanged over the season.

The wildfowl exerted heavy grazing pressure on the food supplies, both on the mudflats and on the salt marshes. By the time the birds abandoned Koldby Leje and the Rømø barrage marshes, the food resources had been exhausted to an extent where feeding efficiency was hampered, and foraging probably no longer profitable (for Brent Goose, see also CHARMAN 1979). The depletion of food supplies, in part, presents a meaningful explanation as to why wildfowl shift between habitats, and ultimately leave the area.

However, shooting actively modified movement patterns. On the mudflats hunting was a disturbing activity, displacing the ducks and geese to areas where food supplies were quickly depleted, such that feeding efficiency of the birds quickly decreased. Even if the birds were allowed to feed undisturbed at night, this was probably not sufficient to fulfil their energy demands. Wigeon, especially, were affected because they were dependent on above-ground parts of *Zostera,* whereas Brent Geese could cope better because they were able to switch to below-ground parts. However, in 1986, both the major part of the protected Brent Geese and the hunted Wigeon left the mudflats before the resources were exhausted, and this is interpreted to be a result of shooting disturbance. To the 'luck' of the Brent Geese, shooting ceased when the ducks emigrated. The remaining geese could thus stay undisturbed and utilise the rest of the *Zostera* supplies.

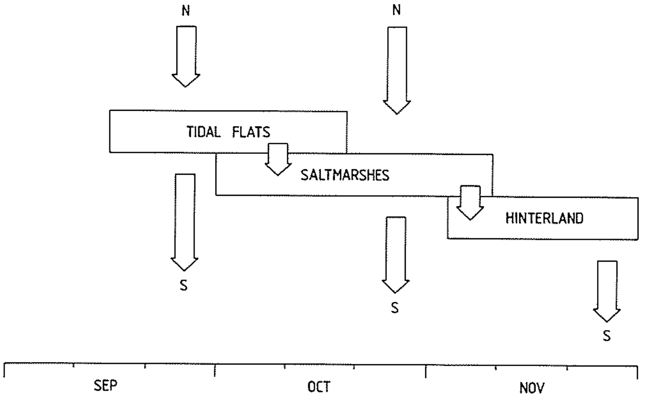

Fig. 15. A generalised outline of the movements between habitats for Wigeon over the autumn season in the Danish Wadden Sea. Arrows indicate that an unknown number moves in and out of the area.

As the *Zostera* stock decreased, exploitative competition between Wigeon and Brent Goose was another agent forcing particularly the Wigeon to leave. Shooting disturbance made the interspecific competition critical at an earlier stage in autumn than would be expected without shooting.

The Wigeon-grazing of seed in the salt marshes coincided with seed ripening. However, this time period also coincided with the time when shooting disturbance on the mudflats became critical, with the result that the ducks migrated from there. Thus, it cannot be said conclusively whether the ducks actually timed their flight to seed ripening, or whether shooting modified their movements. A combination of the two factors is feasible. Shooting in the Ballum Foreshore prevented the ducks from using those marshes in the day-time, and night-time feeding was not prevalent either. When food resources along the protected Rømø barrage were depleted, the majority of the ducks were thus forced to leave the area. The remaining ducks only fed at night and in other areas. Thus, shooting affected the activity of the ducks and also prevented them from using potential resources. In consequence, the ducks had to leave the area prematurely.

Dansk resumé

Fødeøkologi hos planteædende andefugle i Vadehavet om efteråret, og fødemængdens og jagtens effekt på flokkenes træk.

Den sydlige del af det danske Vadehav (Fig. 1) er en vigtig efterårsrasteplads for store flokke af svømmeænder og knortegæs. I september-oktober forekommer op til 6.000 knortegæs og 8.000 pibeænder på vadefladerne ved Koldby Leje, Jordsand Flak (Fig. 2), hvor de afgræsser en stor banke af ålegræs; senere i oktober-november opholder op til 15.000 pibeænder og 3.500 krikænder sig ved Rømødæmningen (Fig. 9), hvor de tager frø af marskplanterne.

Formålet med dette arbejde har været at beskrive forekomsten af andefugle og undersøge deres økologi under opholdet i Vadehavet. Det centrale spørgsmål var: hvad betinger antallet af fugle i området, og hvad forårsager træk-bevægelserne mellem delområderne? I hvor høj grad udnytter fuglene føderessourcerne, og har jagten, der drives på vadeflader og forlande, en forstyrrende effekt, så fuglene må trække bort, inden føden er brugt op?

Ved Koldby Leje kan andefuglene kun nå ålegræsset fra ca. 3 timer før til 3 timer efter lavvande. Ved lavvande i dagtimerne fouragerer fuglene næsten uden ophold (Fig. 3a). Ved hjælp af en lysforstærkende kikkert blev det påvist, at fourageringen også pågår om natten (Fig. 3b); pibeænderne fouragerer med samme intensitet som om dagen, mens knortegæssene afbryder fourageringen midt i lavvandsperioden. På det 138 ha store ålegræsbed, der primært består af dværgålegræs *(Zostera noltii)*, står der i september ca. 39 tons overjordisk biomasse (tørvægt). I løbet af efteråret falder den overjordiske biomasse drastisk (Fig. 5), så der i december kun står omkring 1 ton tilbage (3%). Andefuglene konsumerer mellem 26 og 35 tons i løbet af efteråret, svarende til 66-91% af den maksimale biomasse, eller 33-45% af årets produktion. Den øvrige reduktion skyldes naturligt henfald og planter, som knækkes af bølgeslag. Også den underjordiske biomasse af ålegræsset tages af fuglene og specielt af knortegæssene som »tramper« rødder og jordstængler frem af sedimentet. Ved sæsonens slutning var der 48% mere biomasse i ugræssede end i græssede felter (Fig. 5). Den faldende fødemængde reducerer andefuglenes effektivitet under fødesøgning (Tabel 1). På grund af den faldende fødemængde stiger fødekonkurrencen mellem knortegæssene og pibeænderne. Knortegæssene klarer sig tilsyneladende bedst, idet de gradvist skifter over til at tage rødder og jordstængler af ålegræsset, mens pibeænderne, der udelukkende tager bladene, nødsages til at forlade området.

I 1985 blev der kun drevet jagt på vaderne i få dage; i 1986 steg jagtintensiteten imidlertid kraftigt (Fig. 7). Den øgede jagt forringede fuglenes muligheder for at søge føde (Fig. 8). På dage uden jagt fordelte andefuglene sig jævnt over ålegræsbeddet. På dage med jægere fortrængtes fuglene til den sydlige zone, der er en del af Jordsand reservat med jagtforbud. Her blev ålegræsset nedgræsset i løbet af kort tid, og i midten af oktober var der kun ålegræs tilbage i jagtzonen. På dage uden jægere fouragerede fuglene, men på dage med jægere fortrængtes de igen til den fredede zone, hvor ålegræsset allerede var nedgræsset. Om natten fouragerede fuglene i jagtzonen. I 1986 forlod ænderne Koldby Leje tidligere end i 1985, hvilket kunne have været forårsaget af, at fuglene ikke kunne få dækket deres fødebehov pga. den jagtlige forstyrrelse på ålegræsbeddet i dagtimerne. Også antallet af knortegæs, der er jagtfredede, blev reduceret. Jagten ophørte imidlertid, da ænderne fortrak, og knortegæssene kunne således gå uforstyrrede på det resterende ålegræsbed resten af efteråret 1986.

På Rømødæmningens forland fouragerer ænderne især i timerne omkring højvande (Fig. 10). Deres forekomst på forlandet i oktober er sammenfaldende med frømodningen hos fødeplanterne Strandgåsefod *(Suaeda maritima)* og Strandmælde *(Atriplex litoralis)* (Fig. 11). I begyndelsen af oktober 1986 var der en frøsætning på op til 1 tons tørvægt pr. ha. Optælling af frø på hhv. planter, der blev afgræsset af ænderne, og på planter, der var indhegnede, viste at ænderne i løbet af oktober konsumerede omkring halvdelen af frøsætningen. Resten blev tabt naturligt eller skyllet bort ved oversvømmelse af forlandet. I 1985 var næsten alle frø forsvundet i midten af oktober, i 1986 først i begyndelsen af november (Fig. 12 og 13). På samme tid ophørte ænderne med at gå på forlandet. Hovedparten trak bort, mens den resterende del dagrastede på vaden ud for forlandet. De fouragerede udelukkende om natten, enten i landet bag digerne eller på Ballum Forland. På grund af jagt kunne ænderne ikke fouragere frit på Ballum Forland om dagen, og på trods af stor frøsætning viste optællinger af ande-ekskrementer, at forlandet kun blev benyttet ekstensivt om natten.

Det konkluderes, at antallet af andefugle i det sydlige Vadehav er reguleret af fødemængden, og at trækket mellem delområder og i sidste ende sydpå til overvintringsområderne forårsages af de svindende ressourcer. Jagten bevirker, at fuglene ikke kan udnytte ressourcerne maksimalt, men må trække bort tidligere end nødvendigt.

Резюме на русском языке:
Экология питания травоядных утиных на датских морских отмелях осенью, и эффект наличного количества пищи и охоты на перелеты стай.

Южная часть датских морских отмелей (Фиг. I) служит важным местом осеннего привала для больших стай водоплавающих уток и казарок. В сентябре-октябре до 6.000 казарок и 8.000 свиязей встречаются на пространствах отмелей у Кольби Лейе и мели Иордзанд Флак (Фиг. 2), где они стравливают обширную банку с водяной травой, а позднее в октябре и ноябре до I5.000 свиязей и 3.500 чирков-свистунков обитают у плотины к острову Рёмё (Фиг. 9), где они щиплют зерна растений на топи.

Целью настоящего труда было описать местонахождения утиных и исследовать их экологию во время пребывания на морских отмелях. Центральным вопросом было: от чего зависит численность птиц в этом районе, и что вызывает их перелеты из одного подрайона в другой? До какой степени используют птицы ресурсы пищи, и оказывает-ли ведущаяся на мелководных

пространствах и берегах охота какой-нибудь нарушающий покой эффект, заставляющий птиц улетать, не успев потребить всю пищу?

У Кольби Лейе утиные могут достать водяную траву только от прибл. 3 часов до отлива до прибл. 3 часов после него. Во время отлива днем птицы фуражируют почти непрерывно (Фиг. 3а). При помощи светоэффективного бинокля было выяснено, что фуражирование также происходит ночью (Фиг. 3b); свиязи фуражируют так-же интенсивно, как днем, между тем как казарки прерывают фуражирование в середине периода отлива. На обросшем водяной травой пространстве в 138 га, главным образом покрытом мелкой травой Zostera noltii, в сентябре имеется прибл. 39 тонн надземной биомассы (по сухому весу). В течение осени количество надземной биомассы резко понижается (Фиг. 5), так что в декабре остается только около 1 тонны (3%). В течение осени утиные потребляют от 26 до 35 тонн, что соответствует 66 - 91% максимального количества биомассы или 33 - 45% годовой продукции. Остальное понижение количества объясняется естественным распадом и поломкой растений волнами. Подземная биомасса из травы также потребляется птицами, в особенности казарками, "вытаптывающими" из отстоя корни и подземные части стебельков. В конце сезона на нестравленных птицами участках было на 48% больше биомассы, чем на стравленных (Фиг. 5). Уменьшающееся количество пищи понижает эффективность поисков её утиными (Табл. 1), и соревнование между казарками и свиязями обостряется. Как кажется, казарки лучше приспособляются к этому, постепенно переходя на питание корнями и подземными частями стебельков водяной травы, между тем как свиязи, питающиеся только листиками, принуждаются оставить данный район.

В 1985 г. на мелководных пространствах было только немного дней охоты; зато интенсивность охоты в 1986 г. сильно повысилась (Фиг. 7). Более интенсивная охота ухудшает возможности поиска пищи птицами (Фиг. 8). В дни без охоты, утиные равномерно распределялись по всему участку с водяной травой, а в дни с охотниками птицы вытеснялись в южный участок, составляющий часть Иордзандского заповедника, где охота запрещена. Здесь водяная трава была стравлена в течение краткого времени, и в середине октября осталась водяная трава только в зоне охоты. В дни без охотников птицы фуражировали, но при появлении охотников снова вытеснялись в зону заповедника, где водяной травы уже не было. Ночью птицы фуражировали в зоне охоты. В 1986 году птицы покинули Кольби Лейе раньше, чем в 1985-м, что могло объясняться невозможностью удовлетворения их потребности в пище вследствие нарушения их покоя на участке с водяной травой охотой во время дневного света. Понизилась также численность казарок, на которых охота запрещена. Однако, охота кончилась одновременно с отлетом уток, так что казарки до конца осени 1986 г. могли спокойно использовать оставшийся участок с водяной травой.

На прибрежном участке перед плотиной к острову Рёмё утиные в особенности фуражируют в часы около прилива (Фиг. 10). Их появление в этом участке в октябре совпадает с созреванием семян служащих им для пищи растений, прибрежной гусиной лапки (Suaeda maritima) и прибрежной крапивы (Atriplex litoralis) (Фиг. 11). В начале октября 1986 г. количество этих семян составляло до 1 тонны сухого веса на га. Подсчет семян на растениях, стравленных утиными, и на огороженных растениях показал, что утиные в течение октября потребили около половины всех семян. Остальное количество либо отпало естественным образом, либо пропало при наводнениях прибрежного участка. В 1985 г. почти все семена исчезли в середине октября, а в 1986-м только в начале ноября (Фиг. 12 и 13). Одновременно с этим утиные перестали ходить по прибрежному участку. Наибольшая часть их улетела, а остальные днем отдыхали на отмели перед прибрежным участком. Они фуражировали только ночью, либо на участках за плотинами, либо на прибрежном участке Баллум. Днем они вследствие охоты не могли спокойно фуражировать на участке Баллум, и, несмотря на изобилие созревших в этом участке семян, подсчеты испражнений уток показали, что этот участок экстенсивно использовался только ночью.

Из этого следует, что численность утиных на южной части датских морских отмелей регулируется количеством наличной пищи, и что перелеты между подрайонами и, в конце сезона, на места зимовки дальше к югу, вызываются истощением ресурсов. Эффект охоты состоит в том, что птицы не могут максимально использовать ресурсы, и принуждаются улетать раньше, чем это необходимо.

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