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Modelling water level influence on habitat choice and food availability for *Zostera* feeding brent geese *Branta bernicla* in non-tidal areas

Preben Clausen

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Brent geese *Branta bernicla* spring fattening around Agerø, Denmark, alternate between feeding on saltmarshes and submerged *Zostera* beds in Limfjorden. It appeared from field observations that these alternations depended on the water level in Limfjorden. A model was developed to assess the impact of water level fluctuations on the habitat use. A second model was developed to estimate the impact of water level on *Zostera* availability. The first model was successful in demonstrating that fluctuations in water levels had considerable influence on habitat use by the brent geese, i.e. they fed on *Zostera* at low water levels and on saltmarshes during high water levels, particularly so in early spring, and that the switch between habitats occurred within a narrow water level span of ca 30 cm. The second model demonstrated that the switch between habitats could be explained by lowered availability of *Zostera* as water levels increased. By combining the output from the two models, differences between years could partly be explained by differences in *Zostera* availability in the early spring period (21 March - 25 April), whereas a more complicated situation was detected later in spring (26 April - 31 May). The models presented may be considered as tools in investigations of habitat use and carrying capacity of seagrass beds in non-tidal areas, where birds' access to feeding areas regularly may be hindered by high water levels.

Key words: *Branta bernicla*, habitat switch, modelling, threshold, waterfowl, *Zostera*

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Waterfowl and waders feeding in intertidal areas must adapt their feeding behaviour to tidal fluctuations, which usually restrict food availability during part of the tidal cycle, because the high tides render the intertidal habitats unavailable as feeding habitat to non-diving birds. Consequently, the birds have two daily feeding periods associated with the two daily low tides. Examples include dark-bellied brent geese *Branta bernicla bernicla* and wigeon *Anas penelope* L. feed-

ing on *Zostera* spp. and *Enteromorpha* algae on intertidal mudflats (Madsen 1988, Summers 1990, Fox 1996) and waders feeding on invertebrates on intertidal mudflats (e.g. Zwarts & Drent 1981, Turpie & Hockey 1993).

Another characteristic is that the waterfowl and waders by their feeding activity deplete their intertidal food supply, and as a consequence food intake rates decline (e.g. Goss-Custard 1969, Zwarts & Drent

1981, Madsen 1988). 'Giving up' thresholds or densities of food below which the intertidal foragers abandon their feeding areas have been reported for several predator-prey relationships, and also for brent geese feeding on intertidal *Zostera noltii* and *Enteromorpha* beds (Charman 1979, Madsen 1988, Summers 1990, Vickery, Sutherland, Watkinson, Lane & Rowcliffe 1995) and oystercatchers *Haematopus ostralegus* feeding on blue mussels *Mytilus edulis* L. (Goss-Custard 1985).

Hence, by mapping densities of relevant food items over an entire estuary and rejecting areas with food densities below established thresholds, the carrying capacity of that estuary to a specific bird species can be estimated if the birds' daily intake rates of the various food items are also known (Goss-Custard, Caldow, Clark, Durell & Sutherland 1995a, Goss-Custard, Caldow, Clark & West 1995b, Percival, Sutherland & Evans 1996, 1998).

This approach is straight forward, albeit time consuming, in tidal habitats such as the British estuaries and the Wadden Sea, where the lunar tidal amplitude exceeds one metre (Huntley 1980). In such areas the birds can normally rely on two daily low tides, exposing the intertidal habitat, and the investigator can estimate available biomass by mapping food density at low tide. Superimposed on tidal fluctuations are weather induced changes in water level, whereby wind or air pressure moves additional water into or out of tidal areas and modifies the overall water table pattern (e.g. Huntley 1980, Pingree 1980). Dependent on wind strength and direction, this may increase or decrease the extent of habitat area exposed, and thereby food availability during low tide, and storm surges occasionally overrule the tidal fluctuations (Huntley 1980), with subsequent impact on the feeding performance of waders (Evans 1981) and on brent goose habitat use (Clausen & Fischer 1994). Zwarts, Hulscher, Koopman & Zegers (1996), however, made a very comprehensive analysis of oystercatchers feeding on mudflats in the Dutch Wadden Sea. They found that the feeding areas on average were exposed 11 hours per day (during 15 years of tidal level measurement), that the oystercatchers usually fed for 8½ hours per day, and that only persistent winds from W-NW with an average force above 12 m/sec (during 24 hours preceding a low tide) would be able to reduce accessibility to the tidal mudflats to less than 200 minutes per low tide (equivalent to 6½ hours per 24 hours), a situation only occurring 1.7% of days. Furthermore, they pointed out that "wind may reduce exposure time for one day, but the effect is never so long-last-

ing that it prevents the waders from feeding on the tidal flats for several days".

In contrast to these lunar tidal cycle habitats, the large virtually non-tidal areas of the inner Danish waters and the Baltic Sea, experience very little tidal amplitude, e.g. 6 cm at Lolland in southeast Denmark (Eger 1985) and 4 cm in the Szczecin Bay in Poland (Jasinska 1993). In these areas wind direction and force has a far greater effect on water table pattern than lunar tidal cycles, with water levels ranging from -75 to +140 cm at Lolland (Eger 1985) and -134 to +196 cm at Szczecin Bay (Jasinska 1993), and high (or low) water levels may prevail for weeks, if the same wind directions prevail after a storm induced high (or low) water level. In such areas estimation of available food must take the wind induced water level conditions into account.

This paper focuses on a situation where light-bellied brent geese *Branta bernicla hrota* in spring alternate between feeding on submerged *Zostera marina* beds, saltmarshes and spring-sown barley *Hordeum vulgare* fields. I present two models which can be used: 1) to test effects of wind induced changes in water levels on the habitat use of the brent geese, and 2) to model food availability in the *Zostera* beds in relation to water level. By combining results from the two models, 'giving up' thresholds can be estimated. Furthermore, it is discussed whether *Zostera* availability alone determines the observed habitat switches, and the paper is concluded by pointing out further applications of the models presented.

Material and methods

Study area

The study was conducted in March through May 1989-1993, in the Agerø area (56°43'N, 8°33'E), in the western part of Limfjorden, Denmark (Fig. 1). This site is the most important spring fattening area for the Svalbard/Greenland breeding population of light-bellied brent geese, with approximately 75% of the flyway-population being found there in spring (Clausen, Madsen, Percival, O'Connor & Anderson 1998). While spring staging in the area, the brent geese alternate between feeding on submerged *Zostera marina* beds, saltmarshes, and (rarely) spring barley fields (Clausen 1998). Both *Zostera* beds and saltmarshes are abundant habitats in the area. The shallower parts of Limfjorden used by the geese are dominated by *Zostera* beds at depths ranging within 30-300 cm, and they cover a

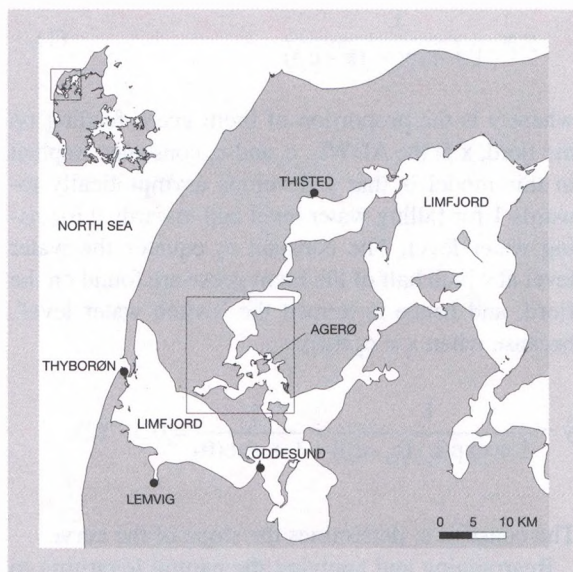


Figure 1. The western part of Limfjorden, northwest Denmark. The positions of sites mentioned in the text are given. Open areas indicate Limfjorden and the North Sea, hatched areas the surrounding land. The approximate area used by feeding flocks of brent geese, which roost communally at Agerø, is delineated by the rectangle. The small inserted map of Denmark in the top left corner gives the position of the study area.

total area of 12.0 km² (Drachmann, Mark & Clausen 1993, P. Clausen, unpubl. data). The 7.5 km² of salt-marshes are dominated by *Puccinellia maritima* (lower marsh) and *Juncus gerardi* (upper marsh) with regular presence of *Festuca rubra*, *Plantago maritima*, *Aster tripolium*, *Spergularia media* and *Triglochin maritimum*; all plant species favoured by feeding brent geese (e.g. Boudewijn 1984). An estimated 89% of the salt marshes are grazed by cattle (Clausen & Percival 1998); hence they are likely to be highly attractive to feeding brent geese (e.g. Ebbsing 1992).

Water level conditions

Data on water levels (two daily low and two daily high tides) measured from September 1988 to September 1992 were obtained from Lemvig Harbour, situated approximately 25 km southwest of Agerø (see Fig. 1). Although separated by the narrow strait of Odde-sund (see Fig. 1), water level changes recorded at Lemvig are believed to give a good estimate of water level changes at Agerø (Torben Larsen, hydraulic engineer, Department of Civil Engineering, University of Aalborg, pers. comm.). An estimate of the average daily water level (ADWL) at Lemvig was calculated as the mean water level from the four daily tides (measured relative to DNN, 'Danish Ordnance Datum'). ADWL

was calculated for September-May in 1988/89-1991/92.

As water level monitoring stopped in Lemvig in September 1992, supplementary data for September 1991 to May 1993 were obtained from Thisted Harbour, situated 30 km north of Agerø further inside Limfjorden (see Fig. 1). The average of eight daily water level measurements taken at 3-hour intervals at Thisted was used as estimates of ADWL for the periods September-May 1991/92 and 1992/93; the 1991/92 data for comparison with the Lemvig estimates of ADWL, and the 1992/93 data for use with the brent goose data.

Within-year and year-to-year variations in ADWL were tested by ANOVAs for samples with unequal numbers of observations and Duncan's multiple range tests (general linear models procedures; SAS Institute 1988).

Counts and habitat use of geese

During 1989-1990 and 1992-1993 a minimum of three counts were made each week of all brent geese found within the study area from the last 10 days of March until the end of May. In 1991 the coverage was slightly less intensive, with one to three counts per week. The positions of goose flocks were drawn on field maps (scale 1:25,000); habitat choice, behaviour (feeding/roosting/flying), and counting conditions (weather and visibility; human, mammalian or avian disturbances) were also recorded. For each count the proportion of feeding brent geese counted on the fjord (i.e. on *Zostera*) was calculated.

Throughout this paper a distinction between two periods has been used, i.e. the early spring period (21 March - 25 April) and the late spring period (26 April - 31 May), dividing the spring fattening period into two periods, each of a five week duration.

Biomass and leaf lengths of *Zostera*

The most important *Zostera* feeding site for the brent geese is situated southwest of Agerø (Jørgensen, Mad-sen & Clausen 1994). Four *Zostera* samples were taken from the shallowest part of the study area on two occasions in 1992 and on three occasions in 1993 during early April - late May. Samples were taken by placing a 0.1 m² square steel frame on the bottom; *Zostera* plants growing inside the frame, flattened when placing the frame, were gently pulled inside, and plants growing outside the frame were likewise pulled out. A square of *Zostera* turf was cut along the inside of the frame, and the whole turf was removed

to the surface in a sieve. All samples were sieved in saltwater through a 1 mm mesh and the resulting material stored in plastic bags. In the laboratory, samples were sorted into vegetative shoots, flowering shoots, rhizomes and dead material, and shoot numbers were counted; the number of leaves per shoot was counted and the length of all leaves measured from 15 or more randomly chosen vegetative shoots in each sample. All fractions were then oven-dried to constant weight at 70°C and weighed. Measured leaves were dried separately from unmeasured ones, enabling calculation of dry weight per cm leaf. As the brent geese only grazed on the above-ground plant parts, and flowering shoots were absent from the *Zostera* bed in spring (Clausen 1994), only data on vegetative shoots will be used in the present paper. All biomass data quoted hereafter refer to dry weight.

In addition, data on leaf length and dry weights per cm leaf from 100 randomly taken *Zostera* shoots which were sampled by me in early May 1991 in the northernmost end of the same *Zostera* bed are included. Additional data on *Zostera* biomass and leaf lengths were also obtained from the same area from spring 1990, collected during a study of population dynamics of *Zostera marina* (Olesen 1993, Olesen & Sand-Jensen 1994a, 1994b). Leaf lengths from that study were provided as average length of the longest leaf per shoot. The average leaf length (of all leaves) was highly significantly positively correlated with average leaf length (of the longest leaf) in the samples I collected in the springs of 1992 and 1993 (Spearman Rank Correlation: $r_s = 0.994$, $N = 8$, $P < 0.0001$), and average leaf length (all leaves) was on average 71% (range: 64-75%) of the average leaf length (longest leaf). Hence, the average leaf length (all leaves) of samples from 1990 was estimated by multiplying the average leaf length (longest leaf) with 0.71.

Modelling effects of water level on habitat use

During field work it seemed that the spring use of the *Zostera* beds coincided with periods of low water levels, induced by easterly winds. The switch from saltmarsh to fjord or *vice versa* was not a simple linear response, with flocks of brent geese gradually abandoning the saltmarshes to feed on *Zostera* as the water level fell. Instead it appeared that brent geese showed a discrete switch response within a very narrow water level range. An approximate test of this on/off response was made by use of a logistic model:

$$y = \frac{1}{1 + \exp(c_1 \cdot (x - c_2))} \quad (1),$$

where y is the proportion of brent geese feeding on the fjord, x is the ADWL, c_1 and c_2 constants. Implicit in this model is that y develops asymptotically towards 1 for falling water level and towards 0 for rising water level. The constant c_2 equates the water level at which half of the brent geese are found on the fjord, and hence is termed the 'switch water level', because when $x = c_2$ then:

$$y = \frac{1}{1 + \exp(c_1 \cdot (c_2 - c_2))} = \frac{1}{1 + \exp(0)} = 0.5 \quad (2).$$

The constant c_1 determines the slope of the curve.

Rearranging and applying the natural logarithm to equation 1 gives:

$$\ln\left(\frac{1}{y} - 1\right) = c_1 \cdot (x - c_2) = c_1 \cdot x - c_1 \cdot c_2 \quad (3),$$

which was used in an approximate test of the correlation between the ADWL and habitat choice, transforming the proportion of brent geese feeding on the fjord, y , to $\ln(1/y - 1)$.

Tests were made for each year and period. Observations of all and none of the brent geese feeding on the fjord were taken as 0.9999 and 0.0001, respectively, because of the asymptotic requirements of the model. When the ADWL and the transformed proportion of brent geese feeding on the fjord were significantly correlated, the constants c_1 and c_2 were estimated from the transformed data by simple linear regression, and used in equation 1 when fitting the curves of habitat use in relation to ADWL. Tests of equality of slopes, c_1 , and intercepts, $-c_1 \cdot c_2$, were made by multiple comparisons of linear regressions (Zar 1984).

Modelling effects of water level on availability of *Zostera*

Zostera leaves within a population on a sample date showed fairly constant widths and stood like tapes more or less vertical in the water column. This, together with leaf length measurements, allows calculation of the proportion of the *Zostera* leaves that was actually available to the brent geese at different water depths, thereby enabling the construction of availability curves in relation to water level. Measures required for modelling are length of individual leaves, l_i , and a mea-

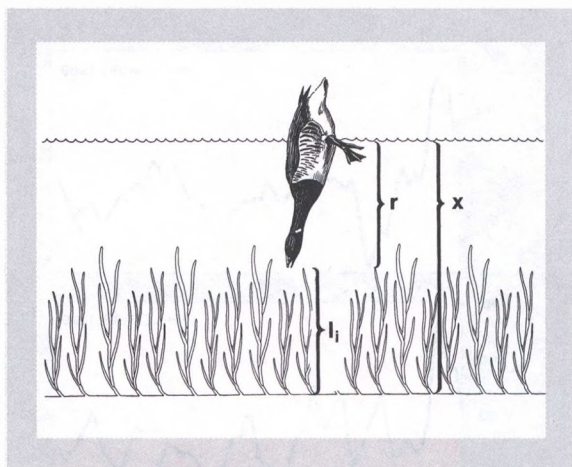


Figure 2. The basic parameters included in the modelling of effects of water level on *Zostera* availability are r : reach limit of a brent goose, l_i : the length of an individual *Zostera* leaf and x : the water depth.

sure of the depth to which a brent goose can reach by up-ending, r . Input in the model as independent variable is water depth, x (Fig. 2).

Brent geese have a total body length of 56-61 cm (measured from bill tip to tail tip on fully stretched fresh specimen; Cramp & Simmons 1977). The distance from legs to tail tip measures 17 cm (measured on a dead specimen in our department). As a few centimetres of the belly in front of the legs remain above the water when brent geese up-end (pers. obs.), it was estimated that brent geese are capable of reaching approximately 40 cm below surface when up-ending, i.e. $r = 40$.

When the water depth is less than r the total leaf biomass, T , will be available to feeding brent geese, and can be quantified by leaf measurements as:

$$T = \sum_{i=1}^n l_i \quad \text{for } x \leq r \quad (4).$$

At water depths larger than r , part of the leaf biomass becomes unavailable to feeding brent geese. Two situations will occur: one in which brent geese can reach part of the individual *Zostera* leaves, and the available leaf biomass can be quantified by leaf measurements as:

$$A_1 = \sum_{i=1}^n l_i - (x-r) \quad \text{for } x > r; l_i \geq (x-r) \quad (5a),$$

and one in which the water depth is so large that the brent geese cannot reach the individual *Zostera* leaves. In this situation, the available leaf biomass will be:

$$A_0 = 0 \quad \text{for } x > r; l_i < (x-r) \quad (5b).$$

The proportion of the total leaf biomass available will be $P = 1$ for water depths smaller than the reach limit of the birds, $x < r$; at any water depth larger than the reach limit, $x > r$, the proportion can be calculated using the following equation:

$$P = \left(\frac{A_1}{T} \right) \quad \text{for } x > r \quad (6).$$

The proportion of leaf biomass available was converted to biomass per unit area by multiplying P by unit biomass measured from the *Zostera* turves.

Modelling in relation to 'Ordnance Datum' water level measurements required a conversion factor to equate the depth in the sample area on any one date with simultaneous measurements of 'Ordnance Datum' water levels. Hence, the variable x in equations 4-6 was replaced by the variable $d = x + x'$, where x' is determined by knowledge of the depth, x , at the sample site on a given date and of the 'Ordnance Datum' water level, d , at the same date, thus $x' = (d - x)$. Average leaf length was used to calculate at which water level half of the biomass would be available to the geese, because when $P = 0.5$ then:

$$P = \left(\frac{A_1}{T} \right) = \left(\frac{n \cdot (\bar{l} - (x-r))}{n \cdot \bar{l}} \right) = 0.5 \quad (7),$$

where \bar{l} is the average leaf length, and n is the number of leaves measured. This is easily rearranged to:

$$x = 0.5 \cdot \bar{l} + r \quad (8a),$$

and as $x = d - x'$ this can be rewritten in 'Ordnance Datum' terms to:

$$d = 0.5 \cdot \bar{l} + r + x' \quad (8b).$$

The median dates of early and late spring periods, as defined above, were 7 April and 13 May, respectively. The available biomass in relation to ADWL on 7

April 1992 was assumed equal to that sampled on 9 April 1992, and those sampled on 7 April 1993, 13 May 1992, and 13 May 1993 were estimated by linear interpolation between surrounding sample dates. Availability curves derived this way were used to estimate available *Zostera* biomasses when brent geese switched habitat (when ADWL = c_2).

Results

Water level conditions

The tidal amplitude in the western part of Limfjorden is small; measurements from Lemvig during September 1989 - May 1992 (excluding June-August in all years) gave an average difference in water level between subsequent low and high tides of 21.1 ± 8.7 cm (Mean \pm S.D., $N = 3,999$). Changes in wind conditions, however, induced quite large changes in the water level even in spring, and ADWL ranged from -56.5 cm to 85.0 cm at Lemvig during 21 March - 31 May in the years 1989-1992 (Fig. 3).

Comparisons of water level fluctuations in Lemvig and Thisted showed a highly significant correlation between the water levels measured at the two harbours both in the early spring period 1992 ($R^2 = 0.978$, $t = 16.434$, $P < 0.0001$, $N = 8$) and the late spring period 1992 ($R^2 = 0.971$, $t = 32.337$, $P < 0.0001$, $N = 33$; see Fig. 3). Hence it was assumed that using the Lemvig water level measurements with the goose data for 1989-1992 and the Thisted measurements for 1993 would only introduce a negligible error to year-to-year comparisons.

Effects of water level on habitat use

Tests using the logistic model showed strong positive correlations between the ADWL and the transformed proportion of brent geese feeding on the fjord in the early spring periods of all years (1989-1993), and during the late spring periods of 1991-1993, whereas no correlation was found in the late spring periods of 1989-1990 (Fig. 4, Table 1). The interpretation of the modelling results is that geese do indeed shift habitats within a very narrow range of ADWL (see Fig. 4). Calculations from the model (equation 1), based on estimates of c_1 and c_2 , revealed that the brent geese switch from >95% feeding on the fjord to >95% feeding on land with a 22.4 (mean) cm change in ADWL (range: 14.5-29.8 cm, $N = 8$).

Multiple comparisons between the eight significant regressions showed no evidence for variance hetero-

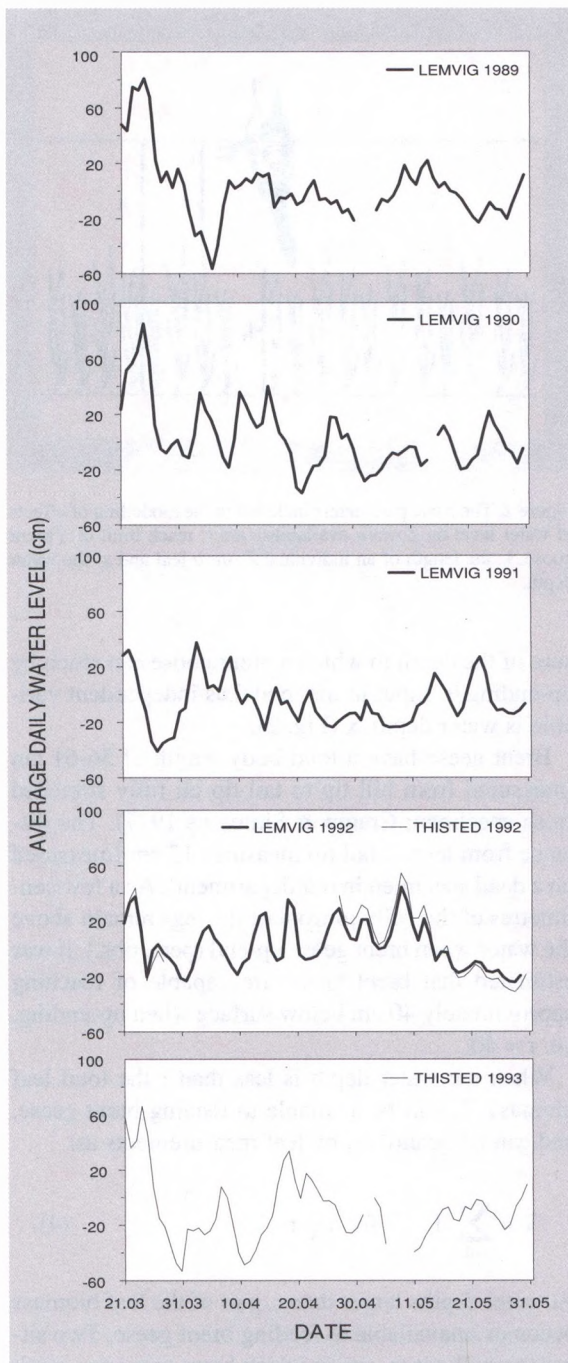


Figure 3. Fluctuations in average daily water levels at Lemvig during 1989-1992 and at Thisted during 1992-1993. Average daily water levels are given relative to DNN ('Danish Ordnance Datum').

geneity (Bartlett's test: $B_c = 6.51$, $df = 7$, $P > 0.25$), and showed that the slopes c_1 of the regressions were not significantly different ($F_{7,115} = 1.326$, $P > 0.10$), whereas the intercepts $-c_1 \cdot c_2$ were ($F_{7,122} = 9.199$, $P <$

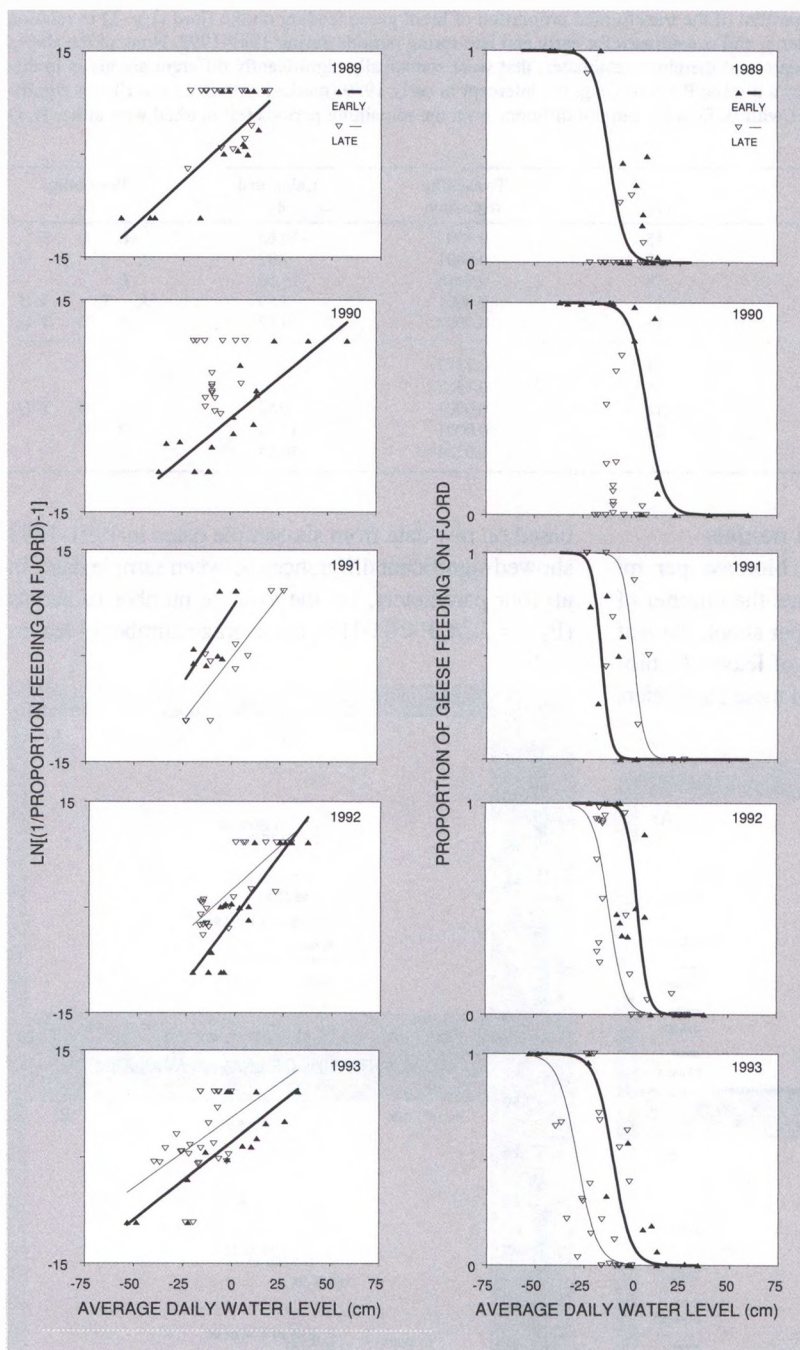


Figure 4. Linear regressions of the natural logarithm of the transformed proportion of brent geese feeding on the fjord ($1/y - 1$) in relation to the average daily water level (left), and curves of habitat choice of brent geese in relation to the average daily water level (right), fitted by estimates of constants c_1 and c_2 derived from the regressions. Only significant regressions and fits are shown. The early spring period covers 21 March - 25 April; the late spring period 26 April - 31 May.

0.0005), i.e. c_2 differed between years. Pairwise comparisons of the intercepts using Tukey q-tests gave ambiguous results with overlapping sets of similari-

ties among intercepts (see Table 1), consequently c_2 values can only be approximately ranked with the early spring period 1991 low-est, followed by late 1993, late 1992, early 1989, early 1993, late 1991 and early 1992, and the early spring period 1990 highest (see Table 1 and compare with Fig. 4).

Effects of water level on availability of *Zostera*

The comparison between water levels measured at the *Zostera* sample site and simultaneous measurements of water level at Lemvig/Thisted revealed that the value for r (40 cm for brent geese) at the sample site corresponded to a mean ADWL of -20.8 cm (range: -23.5 to -17.6 cm, $N = 4$).

The modelling of available *Zostera* based on leaf measurements showed that increases in water level above ADWL -20.8 cm had a considerable influence on *Zostera* availability (Fig. 5). An increase in mean ADWL of 9.2 cm (range: 5-15 cm, $N = 6$, 1991-1993; only 1992-1993 curves presented in Fig. 5) reduced available *Zostera* stocks by 50%, and an increase of 24.7 cm (range: 15-38 cm, $N = 6$, 1991-1993) by 95%.

Conversion of *Zostera* availability to biomass per m^2 showed an increased impact of water level on availability of *Zostera*, due to large within-year and between-year variations in the *Zostera* biomass (five sample dates in 1992-1993: $F_{4,15} = 37.66$, $P < 0.0001$; see Fig. 5). An increase in mean ADWL of 12.8 cm (range: 5-20 cm, $N = 5$) reduced available *Zostera* stocks to less than 16

g/m^2 , i.e. equivalent to 50% of the lowest initial biomass, and an increase of 22.8 cm (range: 11-41 cm, $N = 5$) to 5 g/m^2 .

Table 1. Linear regressions of the natural logarithm of the transformed proportion of brent geese feeding on the fjord ($1/y - 1$) in relation to the average daily water level, and parameter c_1 and c_2 estimates for early and late spring periods during 1989-1993. None of the slopes differed significantly from the others. Intercepts, and thereby c_2 estimates, that were statistically significantly different are given in different letters in the column to the right (Tukey's q-tests: $P > 0.05$), e.g. the intercept in early 1989 (marked with B, D and F) was significantly different from early 1990, (not marked with B, D or F), but not different from the remaining periods (all marked with either B, D or F).

Period	Slope c_1	Intercept $-c_1 \cdot c_2$	N	Probability regression	Calculated c_2	Probability c_2
Early 1989	0.27	2.83	15	0.0003	-10.65	B D F
Early 1990	0.23	-1.80	16	0.0001	7.92	A C E G
Early 1991	0.42	6.65	8	0.0418	-15.80	B
Early 1992	0.38	-1.49	17	0.0001	3.89	A C F G
Early 1993	0.22	2.10	15	0.0002	-9.62	B D F G
Late 1989			17	0.7577		
Late 1990			16	0.7527		
Late 1991	0.36	-0.29	11	0.0001	0.82	A D F G
Late 1992	0.25	2.84	24	0.0001	-11.34	B D
Late 1993	0.21	5.78	25	0.0354	-28.15	B

Combining outputs from the two models

The observed variation in *Zostera* biomass per m^2 may be caused by four parameters, i.e. the number of shoots per m^2 , the number of leaves per shoot, the leaf length, and the width and thickness of leaves (= biomass per centimetre leaf). ANOVAs of these parameters

based on raw data from six sample dates in 1991-1993 showed significant differences between sample dates in all four parameters, i.e. the average number of shoots ($F_{4,15} = 3.24$, $P < 0.0418$), the average number of leaves

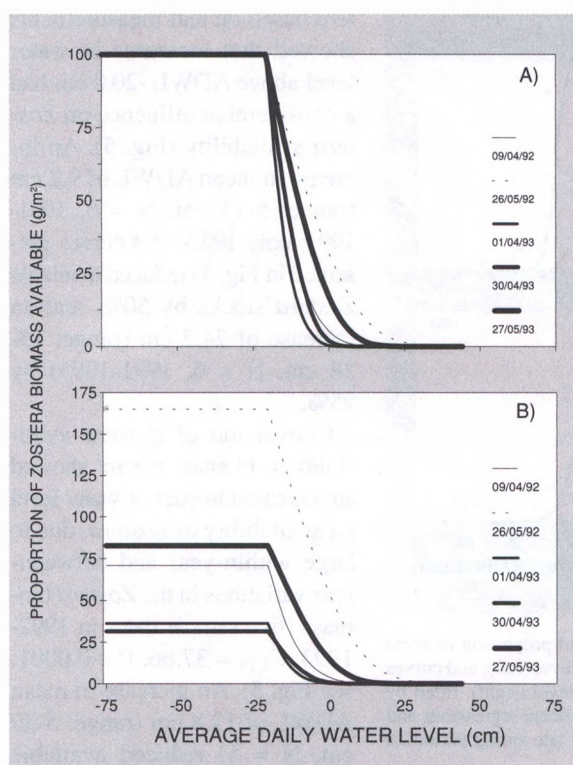


Figure 5. Availability curves of *Zostera* in relation to average daily water level on five sample dates during 1992-1993, based on the model of effects of water level on availability of *Zostera*. Both the proportional (A) and biomass specific (B) curves are shown.

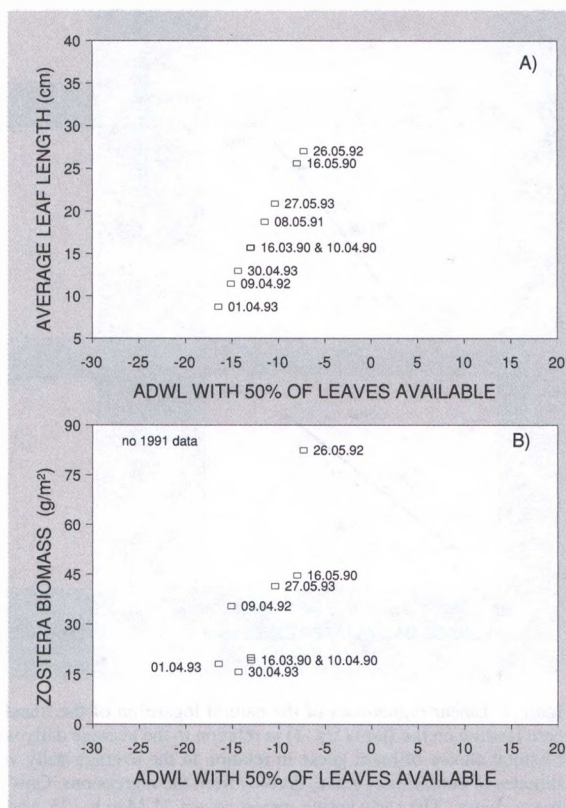


Figure 6. Relationship between the average leaf length and the average daily water level (ADWL) at which 50% of the *Zostera* leaves would be available to the brent geese (A), and the corresponding *Zostera* biomass available (B) on sample dates during 1990-1993.

per shoot ($F_{5,513} = 33.62$, $P < 0.0001$), the average leaf length ($F_{5,2373} = 260.80$, $P < 0.0001$), and the average biomass per cm leaf ($F_{4,13} = 20.94$, $P < 0.0001$).

For a feeding brent goose the most important of these parameters is believed to be the average leaf length, because this obviously has a great influence on the overall availability of the total *Zostera* biomass, whereas the other three parameters merely modify biomass density and therefore intake rates when water levels are sufficiently shallow for feeding brent geese.

The calculations of water levels at which half of the *Zostera* leaves would be available to feeding brent geese (equation 8b) on the sample dates in 1990-1993 showed that the average leaf length was longer in 1990 and 1992 than in 1993, and in 1991 perhaps similar to that of 1993 (all samples significantly different; Duncan's multiple range tests: $P < 0.05$; the 'perhaps' statement addresses the differences between years in timing of sampling dates; Fig. 6). Consequently, the brent geese might be expected to switch to feeding on the fjord at higher water levels in 1990 and 1992 than in 1993, and perhaps at intermediate water levels in 1991, and they did in fact do so in the early spring periods, but no such relation was found in the late spring periods (see Fig. 4 and Table 1).

Recalculation of the results presented in the previous paragraph to *Zostera* biomass revealed a less clear-cut pattern, due to effects of the observed variations in shoot densities, number of leaves per shoot and biomass per centimetre leaf. It turned out that in terms of biomass, 1990 was not different from 1993, whereas

1992 offered the brent geese much greater *Zostera* biomass (see Fig. 6). When the available biomass in relation to ADWL was estimated for the median dates in early and late spring 1992 and 1993 and combined with the 'switch water levels', c_2 , the biomass available at c_2 ranged from 1.7 to 5.9 g/m² in the early spring period, and from 56.3 to 79.9 g/m² in the late spring period (Fig. 7). An obvious relationship between the biomass available and the water level at which the brent geese switched habitat was consequently not found.

Discussion

Brent geese and *Zostera* use

The feeding conditions experienced by brent geese feeding on intertidal *Zostera noltii* beds are, in principle, comparable to those of oystercatchers feeding on surface-living blue mussels. Due to tidal fluctuation the entire food stock varies between complete availability and no availability, the two situations alternating every five to seven hours. In contrast, brent geese feeding on submerged *Zostera marina* in non-tidal areas may experience several days with or without access to the *Zostera* resource. This situation is more analogous to wader species feeding at low tide on mud-dwelling invertebrates such as lugworms *Arenicola marina*, ragworms *Neries* spp., or Baltic tellins *Macoma balthica*. Although abundant in the substrate, much of their food stock lies out of reach because the birds are constrained by their bill-lengths, which constrains them to feed in the upper few centimetres of the mudflat (e.g. Zwarts & Wanink 1984, 1991). Hence, to fully understand habitat use of herbivorous waterfowl feeding on submerged vegetation or estimate the carrying capacity of the submerged food resource, one must be able to account for the effects of variations in water levels on the birds habitat utilisation. The two models presented may be considered as analytical tools in this process.

The first model including equations 1-3, successfully demonstrated that water level fluctuations had a major impact on the habitat use of the brent geese in the early spring period of all five study years, and in three of the five late spring periods studied (see Fig. 4 and Table 1), and that the brent geese switched from >95% feeding on the fjord to >95% feeding on land at a mean water level increase of 22.4 cm. The curves fitted by use of estimates of c_1 and c_2 and equation 1 generally describe reality well (see Fig. 4).

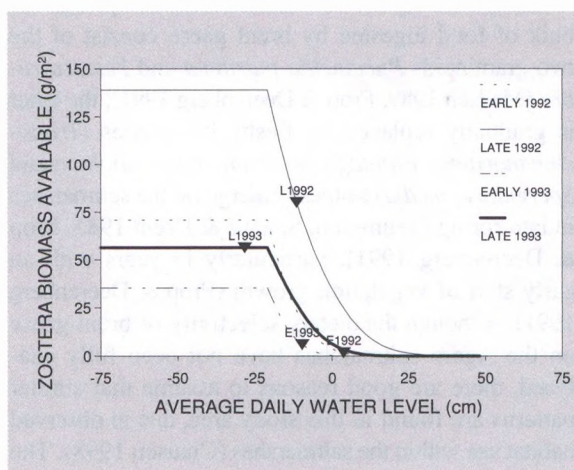


Figure 7. Availability curves of estimated *Zostera* biomass on median dates for early (7 April) and late (13 May) spring periods during 1992-1993. Triangles give the biomass at which the brent geese switched habitats, i.e. when the average daily water level was equal to c_2 for each period.

The second model including equations 4-8, clearly demonstrated that increases in water level above -20.8 cm had a substantial impact on *Zostera* availability, and that the available *Zostera* biomass would be reduced to less than 5 g/m² after an increase of 22.8 cm to a water level of 2 cm (see Fig. 5). The *Zostera* availability was modelled from samples taken in the most shallow parts of the *Zostera* bed. I did not sample *Zostera* growing in deeper areas, but this seemed even more inaccessible in spring, because there was a rather uniform leaf length throughout the *Zostera* bed on a given sample date. Hence, deeper areas would require even shallower water levels to become accessible. The second model also demonstrated relatively large within- and between-year variations in *Zostera* availability in relation to water levels, due to variations in leaf length and biomass (see Figs 5 and 6). The observed switch at higher water levels in springs 1990 and 1992 compared to 1993 (see Fig. 4) can be explained by the longer leaf lengths found in 1990 and 1992 (see Fig. 6).

The reduction in *Zostera* availability to less than 5 g/m² is interesting because several studies of brent geese feeding on intertidal *Zostera noltii* beds in autumn and winter have identified 'giving up' thresholds, i.e. densities of *Zostera* coverage or biomass below which the brent geese abandon the *Zostera* as feeding habitat, approximating 5 g/m². Charman (1979) reported that brent geese left the *Zostera* beds when coverage fell below 15%. Madsen (1988) likewise found that the geese left the *Zostera* or switched to feeding on below-ground parts of the plants when coverage reached 10-20%, equivalent to 5.9 to 9.9 g/m² and a similar result was obtained by a modelling approach to brent geese feeding on *Zostera* at Lindisfarne, England, where geese left when biomass fell below 4.5 g/m² (Percival et al. 1996). My data from early spring 1992 and 1993 suggest that a comparable threshold may be found in early spring, as the geese switched at biomasses of 1.7 g/m² in 1992 and 5.9 g/m² in 1993, but the threshold was much higher in the late spring periods (see Fig. 7).

It is reasonable to assume that the brent geese prefer to feed on *Zostera* because *Zostera* beds are generally more productive, provide higher energy intake rates and offer the geese higher protection from predators and human disturbance than do saltmarshes (Clausen 1994, 1998). One would predict that the birds should switch at a higher water level in late spring than they had done in early spring of the same year because the Danish *Zostera* stocks usually reach their

lowest biomass in February-March, followed by very rapid growth from April to June-July due to the increased radiation in spring, when most of the increase in biomass is caused by leaf elongation (e.g. Sand-Jensen 1975, Wium-Andersen & Borum 1984, Pedersen & Borum 1993). Similar increases in average leaf length and biomass were also found in the *Zostera* bed used by the brent geese (Olesen & Sand-Jensen 1994a, see Fig. 6). The expected observation of a late spring switch at a higher water level than that found in early spring of the same year was, however, only observed in 1991 (see Table 1). In 1992, the geese switched at a significantly lower water level in late spring than in early spring, whereas no significant differences were found between switches in 1993 (see Table 1).

The situation in the late spring period is puzzling if it is assumed that habitat selection should be determined by *Zostera* availability alone, but may be understood if the threshold depends on the biomass available in the alternative habitat as well, and only then if the birds on a given date choose to feed in the most profitable site and habitat in terms of nutritional intake rates. Brent geese are known to optimise their feeding in terms of energy and nutrient intake (Drent, Ebbinge & Weijand 1978/79, Prop & Loonen 1989, Prop 1991, Prop & Deerenberg 1991). This is especially important in spring when optimisation of spring fattening is considered of major importance to subsequent breeding success (Teunissen, Spaans & Drent 1985, Ebbinge 1989, Prop & Deerenberg 1991).

When feeding on the saltmarshes in spring, the bulk of food ingested by brent geese consist of the two graminoids *Puccinellia maritima* and *Festuca rubra* (Madsen 1989, Prop & Deerenberg 1991); the latter is gradually replaced by fleshy halophytes (*Triglochin maritima*, *Plantago maritima*, *Aster tripolium* and *Spergularia media*) as these emerge on the saltmarshes in late spring (Teunissen, Spaans & Drent 1985, Prop & Deerenberg 1991), particularly in years with an early start of vegetation growth (Prop & Deerenberg 1991). Although the dietary selectivity of brent geese on the Agerø saltmarshes have not been fully analysed, there are good reasons to assume that similar patterns are found in this study area, due to observed habitat use within the saltmarshes (Clausen 1998). The reason for taking a still larger proportion of the fleshy halophytes is well documented: the halophytes have higher protein content, metabolisable energy content and gross intake rate, and therefore the geese achieve higher net energy intakes by feeding on the halo-

phytes than by feeding on the graminoids (Prop & Deerenberg 1991).

In terms of net energy intake rates *Zostera marina* is a better forage than the saltmarsh graminoids, whereas it is comparable to fleshy halophytes (Clausen 1994), but the bulk of digestible energy in *Zostera* comes from soluble sugars (Buchsbaum & Valiela 1987, Clausen 1994) whereas it comes from proteins in the halophytes (Prop & Deerenberg 1991). The geese both have to build a sufficient reserve of fat (fuel for migration) and of proteins (females, to be used for egg laying in the breeding areas). Hence, in the early spring period, when graminoids are the only alternative on the saltmarshes, and still only occur there in relatively low quantity in terms of biomass (Madsen 1989, Clausen 1998), the most profitable habitat is *Zostera* and the geese respond by feeding on *Zostera* whenever it becomes available. Later in the season the balance is far less predictable; the graminoids have increased in biomass, the highly attractive halophytes begin to emerge on the marshes, and further to this, *Zostera* declines in nutritional quality due to a falling protein content (Buchsbaum & Valiela 1987, Clausen 1994). The exact timing of all these processes may be the reason behind the less clear relation between habitat use and water levels in the late spring period.

Further applications of the models

In conclusion, water level fluctuations in non-tidal areas may have a major effect on *Zostera* availability and thereby on the habitat use of brent geese. Two models were developed which can be used to predict such effects, which may be of significance for many waterfowl feeding on submerged macrophytes in non-tidal habitats. Non-tidal habitats are found for example throughout the Baltic Sea (Eger 1985, Jasinska 1993) and in the Black Sea (Verkuil, Koolhaas & van der Winden 1993), and may affect large numbers of waterfowl migrating from their wintering quarters in western and southern Europe, and Africa, towards their breeding grounds in Siberia. The models would probably also be applicable in larger coastal lagoons and lake systems, where variations in precipitation and wind directions also have large influence on water levels.

In combination, the two models can be used to determine biomass threshold values for *Zostera* feeding birds in submerged *Zostera* beds, but to fully understand the processes involved, the productivity and availability of food in alternative habitats should also be considered. This is true not only for studies of birds alternating between submerged seagrass beds and

terrestrial habitats, but also for birds alternating between different types of seagrasses. The models have been applied in a study of a moulting mute swan *Cygnus olor* population at Saltholm, Denmark, which alternate between feeding in *Ruppia* spp. dominated and *Zostera marina* dominated seagrass beds (Clausen, Kahlert, Andersen-Harild & Nilsson 1996). In addition to this, Noer, Fox, Clausen, Petersen, Christensen & Kahlert (1996) used the models, in combination with mappings of seagrass distribution, biomass samples and depth profiles, to estimate available food resources under different water level regimes in the whole moulting area.

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