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The depletion of algal beds by geese: a predictive model and test

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Abstract The short-term impact of herbivores on plant productivity has been well studied. Demonstrating long-term effects of grazing on plant populations is much more difficult, but knowledge of such long-term effects is vital in understanding plant–herbivore interactions. We address this issue in a relatively simple plant herbivore system involving the dark-bellied brent goose *Branta bernicla bernicla* and two marine macroalgae, *Enteromorpha* spp. and *Ulva lactuca*, on which the geese graze. In 3 years of sampling, goose grazing was responsible for depleting between 23% and 60% of the algae in the autumn, while wave damage caused between 15% and 70% depletion. The degree of depletion in autumn had no effect on the biomass of algae present the following summer, suggesting no long-term consequences of grazing for the population dynamics of the algae. A model simulating the change in mean algal biomass over the autumn and winter, incorporating changes due to depletion by geese, wave action and productivity, successfully described the date at which geese abandoned the algal bed in six different years. These years varied in numbers of geese, strength and timing of storms and initial biomass available. The most important factor determining the date of abandonment of the algal bed was a trade-off between the timing of storms and the numbers of geese. When storms occur early, most depletion is due to wave action and geese must abandon the bed early, regardless of the numbers grazing there. As the algae become depleted, the geese switch to feeding on saltmarsh, pastures or arable crops. The rate of depletion of algae

affects the timing of this movement, and the model presented here enables the switch to be predicted.

Keywords Brent goose · *Enteromorpha* · Herbivory · *Ulva*

Introduction

While herbivores are known to have a wide range of impacts on plant performance in terms of fecundity, growth and survival, relatively little is known about their impacts on the long-term population dynamics of plants and the consequences of these for the dynamics of the herbivore (Crawley 1997). This ideally requires an understanding of the degree of polyphagy demonstrated by the herbivore, the pattern of plant growth in the absence of the herbivore, the amount of plant material consumed by individual herbivores (the functional response), the pattern of aggregation by the herbivore in relation to the abundance of the plant (the numerical or aggregative response) together with a knowledge of the factors other than food supply that impact on the abundance of the herbivore.

Most studies of plant–herbivore dynamics are too brief to assess their impact on long-term dynamics, or are severely compromised by poor experimental design (Crawley 1997). Experimental studies focusing on the long-term dynamics of the plant typically involve the exclusion or introduction of herbivores. Some of the best documented cases of plant–herbivore dynamics following introductions come from the biological control literature (see Lonsdale 1996); the majority of these involve herbivorous insects, but the relevance of the tightly coupled dynamics of introduced weeds and pests to the understanding of plant–herbivore dynamics in native vegetation is open to question (Crawley 1997). Exclusion experiments involving insect herbivores and chemical pesticides (e.g. Louda and Potvin 1995) or fences against large vertebrate herbivores (e.g. McNaughton 1979) can dramatically illustrate the impact of herbivores on the

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abundance of native plants, but typically tell us rather little about the dynamics of the interaction and the impact of the plant on the herbivore, particularly in the case of vertebrates.

The survival, reproductive success and movements of vertebrates are strongly influenced by food availability (e.g. Drent and Prins 1987; Hubbs and Boonstra 1997; Martin 1987; Sutherland 1996). In the short term (within season), changes in food abundance are directly dependent on the overall rates of depletion and replenishment taking place. These have consequences for the movement of animals and a number of studies have now successfully predicted the distribution of grazing animals in relation to the abundance of food plants and depletion over short time scales (e.g. Percival et al. 1996; Rowcliffe et al. 1995; Sutherland and Allport 1994). However, spatial patterns of depletion within a season may also affect the long-term (between seasons) abundance of food plants. Thus predicting the distribution of grazing animals in relation to the dynamics of food plants requires an understanding of (1) the relative importance of the various factors which affect depletion and replenishment rates in the short term, and (2) the degree to which the processes acting within seasons influence long-term abundance.

We address the issue of the long-term dynamics of a plant and a herbivore in a relatively simple system involving two marine macroalgae, *Enteromorpha* spp. and *Ulva lactuca* L., and the dominant herbivore feeding upon them, the dark-bellied brent goose *Branta bernicla bernicla* L. The algae are an ephemeral food resource for brent geese (Vickery et al. 1995). Following a peak of growth and reproduction during the summer (Truscott 1978), grazing and die back of the algae occur over the autumn, and growth largely ceases over the winter (Summers 1990a). As the resource becomes depleted the geese switch to feeding on salt marsh or inland areas of arable crops and pastures (Vickery et al. 1995). The birds are thus generalist feeders but have a preference for feeding in intertidal habitats (Charman 1979; Vickery et al. 1995). We use enclosures to identify the processes that influence the abundance of the algae in both the short and long term and quantify the pattern of depletion through an examination of the consumption rate of birds (the functional response) and the number of birds feeding on the algae. The rate of depletion of algae within a season does not affect the population size of the brent geese, since the birds simply abandon the habitat and feed elsewhere. However, it does affect the timing of this abandonment. We explore the implications of the processes impacting on the abundance of the algae to determine the amount of grazing that the plants can sustain, and hence the timing of the herbivores' movements. This timing is then discussed within the context of an increasing population of brent geese over the last 40 years (Ebbinge et al. 1999), and other environmental changes currently occurring.

Materials and methods

Algal monitoring

The study was carried out at Titchwell, Norfolk (UK National Grid reference TF 753 453), where an algal bed dominated by *Enteromorpha* spp. and *Ulva lactuca* covers an area of 5 ha on the foreshore. It was not considered necessary to attempt to identify the *Enteromorpha* to the species level because the taxonomy of the genus is uncertain, identification is consequently problematic, and the essential aspects of habitat, growth and reproduction relevant to this study appear to vary very little between species (Burrows 1991). Ten enclosures were constructed at randomly chosen locations on the algal bed in October 1989. Each enclosure was 2 m × 2 m and made with two strands of fencing wire attached to corner posts with a height of 50 cm. These were sufficient to exclude grazing geese but not to shelter the enclosed algae from wave action. Algal biomass was sampled inside each of the enclosures and at adjacent points outside at 2-week intervals from October 1989 until September 1992. For each biomass sample, a 30 cm × 30 cm grid of 100 points was scored for presence/absence of algae at each point, to give an estimate of percentage algal cover. Percentage cover estimates (*c*) were then converted to biomass (*b*) in grams dry mass m⁻² using a calibration equation: $\log b = 1.92 \log c - 2.06$ ($r^2 = 0.97$, $n = 30$, $P < 0.0001$). This was obtained in October 1989 by clipping, drying at 70°C for 48 h and weighing 30 30 cm × 30 cm algal samples of known percentage cover.

Goose monitoring and behaviour

The numbers of geese grazing on the algal bed at low tide were counted at 2-week intervals in the autumns of 1989, 1990 and 1991. The mean number of geese grazing the bed in each year, from arrival to the end of grazing, could then be calculated, as well as seasonal grazing patterns. A wide variety of factors may clearly have affected the numbers of geese on the bed on any one visit (e.g. disturbance, weather, time of day), resulting in a high degree of count variability. However, by counting strictly at low tide, the sampling procedure should have avoided any obvious sources of systematic bias.

Intake rate was calculated in relation to different biomass levels by recording the mean peck rate on patches of known biomass availability (a minimum of 30 individuals observed on each patch), and multiplying this by the bite size expected on the respective algal biomass. The relationship between bite size and algal biomass could not be estimated directly, and was obtained by removing artificial bites of algae with a brent goose bill from a range of sites with different algal biomass. The bill was held closed with elastic to give a constant bite pressure, and bite samples were taken by fully opening the bill, placing it vertically onto a patch of algae, releasing the beak and removing it from the substrate. This was repeated five times in each of 50 30 cm × 30 cm random quadrats of known algal cover in both October and November 1990; the samples of algae were then dried and weighed so that the amount of algae removed per bite could be related to the amount available.

To calibrate the relationship between artificial bite size and algal biomass, a direct estimate of average bite size over the whole bed was calculated from defecation rates (*R*, measured by counting the number of droppings produced in 15-min focal observations on a sample of 36 birds), dropping weights (*W*, measured as the average of 64 randomly collected, recently produced droppings) and digestibility (*d*, defined as the proportion of ingested biomass assimilated, calculated from the relative proportions of an indigestible marker in the food and droppings) obtained from the same site by Lane (1994). Since intake rate (*I*) is given by $I = RW / (1 - d)$ (Lane and Hassall 1996a), mean bite size (*B*) can be calculated using peck rate (*P*) and proportion of time feeding (*f*) estimates by $B = RW / [Pf(1 - d)]$. Bite size estimated in this way was related to the observed mean biomass value for the period over which data were collected, and this relationship was used to calibrate the regression equations for artificial bite size against bio-

mass. The relationship between adjusted bite size and biomass was then used to predict values of bite size for the biomass values at which peck rates were recorded, yielding a functional response (intake rate in relation to available biomass).

Meteorological data

The influence of weather on the abundance of the algae during the period of goose grazing was analysed using wind data from the UK Meteorological Office European Wave Model Archive. This model provides hindcasts of the strength and direction of wind every 6 h for a grid covering European waters. The data used here were for the gridpoint 53° 25' north, 1° 14' east, a point 35 km north of the north Norfolk coast. The influence of wind and waves on rates of change of algal biomass in the absence of grazing was determined by relating mean values from these data for each interval between sampling dates to changes in biomass inside exclosures over each period.

Fig. 1a, b The seasonal and tidal patterns of geese feeding on the algal bed. **a** The peak numbers of geese counted in surveys from October to December, averaged over 3 years (1989–1991). **b** The proportion of peak numbers in relation to the tidal cycle, averaged over all surveys. *Error bars* are standard errors

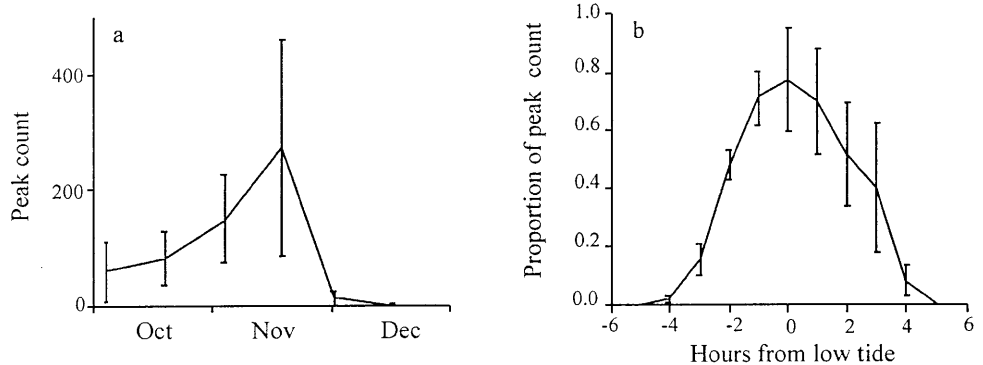
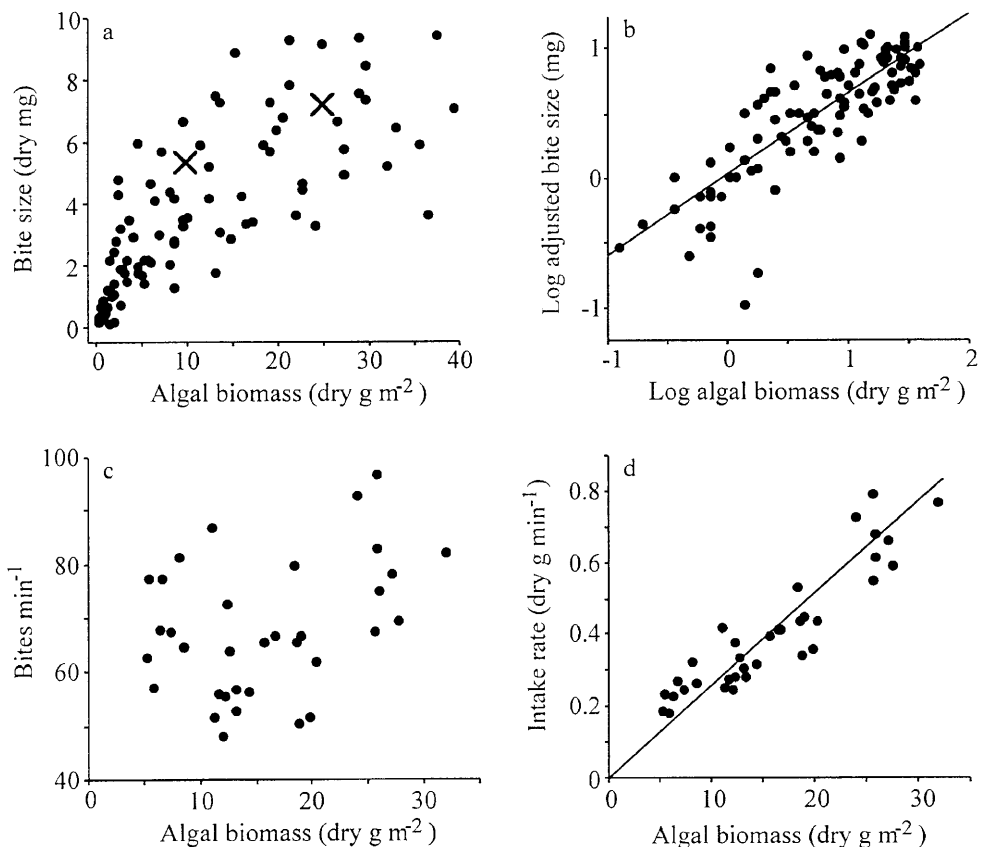


Fig. 2a–d Deriving the functional response. **a** Bite size in relation to algal biomass: *points* represent artificial bite size in relation to local biomass; *crosses* represent average bite size (estimated from dropping rates) in relation to average biomass at two different times. **b** Log of bite size, adjusted according to estimated true bite size, in relation to log algal biomass: $y=0.627x+0.029$, $r^2=0.647$, $n=95$, $P<0.0001$. **c** Bite rate in relation to algal biomass. **d** The functional response (intake rate in relation to algal biomass), calculated as the product of bite rate (c) and predicted bite size (b): $y=0.025x$, $r^2=0.97$, $P<0.0001$



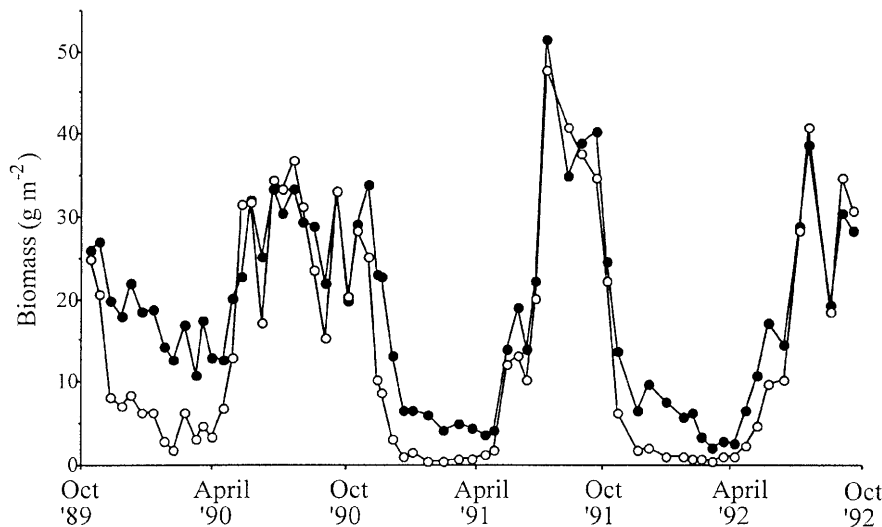
Results

Goose behaviour

Geese were recorded on the algal bed from the beginning of October, gradually increasing to a peak at around the middle of November (Fig. 1a). By early December, the algal bed was very rarely visited by geese, and none were seen there from the middle of December onwards. Geese were present on the algal bed for a period of up to 4 h either side of low tide, with peak numbers occurring at low tide (Fig. 1b).

Artificial bite sizes were similar to those expected from the direct estimates of average bite size in October and November, but on average somewhat lower (Fig. 2a). In order to correct this discrepancy, artificial

Fig. 3 Seasonal trends in algal biomass over 3 years (1989–1992) in excluded (●) and paired unexclosed (○) plots



bites were increased by 10% in October and 50% in November prior to further analysis. This discrepancy was presumably the result of measurement error. Log-transformation of both axes in the adjusted bite size response yielded a strong linear relationship (Fig. 2b). Bite rate showed maxima at both high and low algal biomass (Fig. 2c). Nevertheless, intake rate in relation to algal biomass was positive and linear (Fig. 2d). The functional response of brent geese feeding on algae is discussed in detail in Rowcliffe et al. (1999).

The effects of grazing

Goose grazing lowered algal biomass in the autumn substantially (Fig. 3). Significant differences in biomass between inside and outside the exclosures were found in all years by the end of November. Statistical testing for differences between exclosures, seasons and years indicates that all three factors have a significant effect on algal biomass (Table 1), although significant interactions indicate that these effects are uneven (Table 2). First, the exclosure-by-season interaction reflects the fact that there is a difference between excluded and unexclosed plots in winter but not in summer. Second, the season-by-year interaction reflects the fact that the levels of both summer highs and winter lows vary between years. Finally, the lack of significant exclosure-by-year and three-way interactions reflects the fact that the pattern of differences between the insides and outsides of exclosures was similar in all years.

The declining biomass in the autumn in the absence of grazing shows that there is natural die-back as well as loss to the geese. During October and November 1989, 23% of the algal biomass initially available was lost to wave action, while a further 46% was consumed by geese; in 1990 the respective figures were 15% and 60%, and in 1991 they were 70% and 23%. Despite the fact that no grazing by geese occurred after the middle of December in any year, the difference in biomass between

Table 1 Results of a randomized three-factor ANOVA with repeated measures, testing algal biomass against exclosure (inside/outside), season (winter/summer), and year (1990/1991/1992). $n=120$ [10 replicates (exclosures) per cell]. Replicates are the means of six bi-weekly measurements for each exclosure, taken from January to March for winter, and from June to August for summer

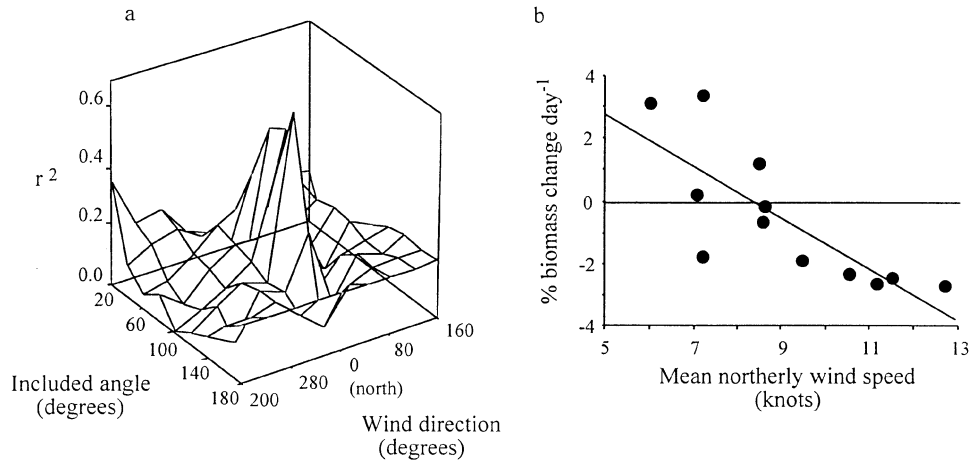
Factor	<i>F</i> ratio	<i>df</i>	<i>P</i>
Exclosure	18.3	1, 54	<0.0001
Season	945.2	1, 27	<0.00001
Year	14.1	2, 18	<0.001
Exclosure-season	7.6	1, 54	<0.01
Season-year	6.0	2, 27	<0.01
Exclosure-year	1.5	2, 54	N.S.
Exclosure-season-year	1.6	2, 54	N.S.

Table 2 Cell means \pm standard error for the ANOVA summarised in Table 1

Season	Exclosure	
	Inside	Outside
Winter		
Year 1	15.4 \pm 3.3	4.4 \pm 2.4
Year 2	5.5 \pm 0.9	0.9 \pm 0.2
Year 3	4.7 \pm 1.4	0.9 \pm 0.2
Summer		
Year 1	30.6 \pm 3.2	29.4 \pm 5.5
Year 2	30.2 \pm 1.7	28.4 \pm 1.6
Year 3	24.9 \pm 0.9	23.9 \pm 1.2

the insides and the outsides of exclosures always persisted until early summer (Fig. 3). Although this difference was considerable, there was no suggestion that biomass inside and outside exclosures differed in the summer over the 3 years (Tables 1, 2, Fig. 3). Grazing thus had no effect on the long-term abundance of algae. Mean biomass available at the beginning of October varied from 26 g m⁻² in 1989 to 30 g m⁻² in 1991. No other

Fig. 4a, b The relationship between rate of algal biomass change and mean wind strength. **a** The strength of relationship (r^2), using winds from different directions and angles of inclusion. **b** The relationship giving the strongest correlation. Mean northerly wind speed is the average of all wind data for each algal sampling period, scoring winds from directions 100° to 260° as zero. The linear regression is given by $y=7.00-0.83x$, $r^2=0.59$, $n=12$, $P<0.01$



plant species were observed to invade the algal bed, and *Enteromorpha* and *Ulva* remained the dominant species over all 3 years.

The effects of wind

Much of the natural die-back of algae in the autumn is caused by waves, and the rate of loss might therefore be expected to be related to the strength of wave action. Furthermore, wave energy and wind strength are strongly correlated, and a correlation between wind strength and the rate of algal depletion in the absence of grazing might therefore be expected. The percentage change in algal biomass per day was calculated for 14-day sampling periods in October and November in all 3 years, and the results correlated with mean wind strength for the respective periods. The hypothesis that algal biomass is affected only by winds with sufficient fetch to create significant waves was tested by examining a range of correlations using wind from different directions. For these relationships, mean wind strength was calculated by assigning winds from outside the direction to be tested a value of 0, thus combining wind strength and direction in a single index. From this it is clear that the best correlation can be obtained by including only winds 100° either side of due north (Fig. 4a). In other words, since the algal bed is on a north-facing beach, only on-shore winds have a significant depleting effect on the algae through increased wave action. The mean strength of on-shore winds over a 14-day period can thus be used to predict the depletion rate of algae in the absence of grazing (Fig. 4b).

Modelling algal depletion

We constructed a model to simulate the change in algal biomass over the winter, based on daily iterations of goose grazing depletion and change in biomass in the absence of grazing. In these simulations, the intake rate of individual geese was determined in relation to the bio-

mass available by the functional response, and this, combined with the total amount of goose grazing time on the algal bed, allowed the total depletion by geese to be calculated. Adding goose depletion to the change in algal biomass in the absence of grazing (due to growth and wave action) then determined daily biomass availability. This basic model structure was first validated by comparing predicted patterns of depletion and dates on which the geese abandoned the algal bed with those observed, and then used to explore the predicted implications of changes in environmental conditions for departure dates. Each of these applications of the model required different input to parameterize the daily grazing time and change in algal biomass in the absence of grazing, and these details are given below, together with the results of the simulations.

Validating simulated depletion by geese

The purpose of this validation was to assess how well the treatment of goose grazing could simulate the observed pattern of depletion by geese. In order to do this, the observed patterns of grazing and algal change in 1990 were used to parameterize the model. Linear interpolation between known peak counts (Fig. 1b) was used to derive the daily peak numbers, while the average pattern of relative numbers in relation to the tide (Fig. 1a) was used to derive the total daily goose minutes experienced by the algal bed from peak numbers. Although brent geese do feed at night, this takes place only on or close to the roost site (Lane and Hassall 1996b). Since the algal bed studied here was approximately 3 km from the nearest roost, it was assumed that the algal bed was available for only one low tide period per day. The proportion of the algae remaining after depletion by geese (p) within a given period was calculated from the goose minutes m^{-2} (m) and the slope parameter of the functional response (b) using: $p=(1-b)^m$. The observed changes in enclosed algal biomass between measurements (Fig. 3) were used to derive daily percentage changes in biomass in the absence of geese.

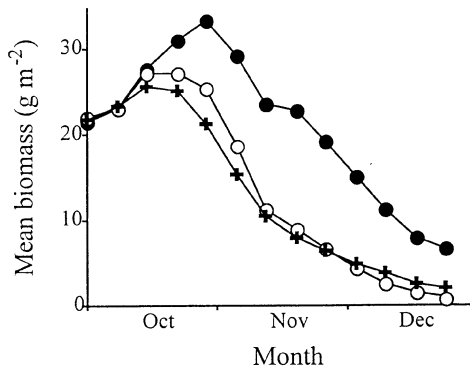


Fig. 5 The observed patterns of change in algal biomass in autumn of 1990 inside (●) and outside (○) exclosures and the predictions of the model (+)

Using the parameters defined above, together with the area and initial mean biomass available in 1990, the predicted change in algal biomass in grazed areas could be compared with the change observed in unexclosed plots over the autumn period in 1990 (Fig. 5). This indicates that the predicted pattern of algal change matches the observed pattern closely, suggesting that the essential elements of grazing depletion are captured accurately by the model.

Validating simulated dates of departure by geese

The model was also validated by comparing predicted dates on which the geese abandoned the algal bed with those observed over a number of years. Data were available to parameterize and test these predictions for 1955–1957 (Ranwell and Downing 1959), 1987–1988 (Summers 1990a) and 1989–1991 (this study). In these simulations, the pattern of relative numbers in relation to tide was used in the same way as above, but daily peak numbers were calculated using an idealized seasonal trend, as illustrated in Fig. 6. Data from Summers (1990a) and this study indicate a reasonably consistent pattern of increasing numbers of geese on the algal bed from the beginning of October as numbers in the area build up, followed by a somewhat variable plateau in numbers and eventual decline as the algae are depleted. The idealized seasonal pattern thus has an initial build-up phase, a plateau phase and a decline phase. In the first phase, the number of geese present (n) on a given day (d) can be derived from the expected peak number (p) and the number of days to the peak from the first of October (d_p) by: $n = d \cdot p / d_p$. In the second phase, the expected number is simply the peak number, while in the final phase the number is related to the biomass available. Vickery et al. (1995) found that there were changes in goose foraging efficiency and a decline in numbers below a threshold biomass of 10 g m^{-2} , and no feeding geese were recorded when algal biomass fell below 5 g m^{-2} . These thresholds were consistent in three consecutive years (1989–1991), and it was assumed that

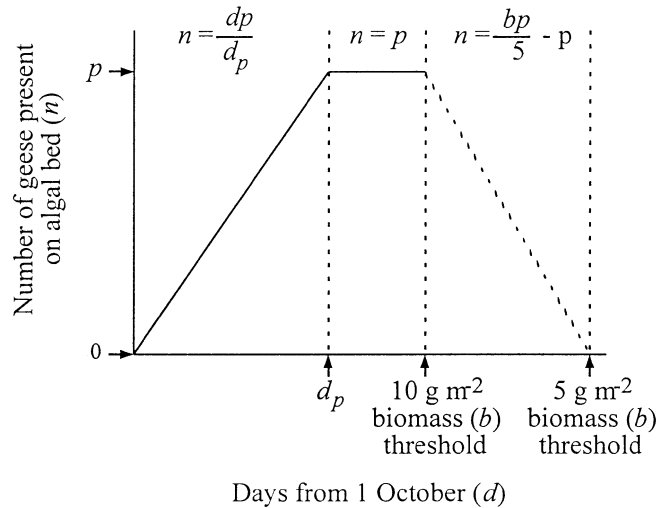


Fig. 6 The method of calculating the seasonal change in numbers of geese grazing on algae used in model simulations exploring the influence of changes in environmental conditions. Peak number (p) and date of peak (d_p) vary according to the year simulated

there was a linear decline in numbers using the algal bed, from peak numbers at 10 g m^{-2} , to none at 5 g m^{-2} . The number of geese present (n) on a given day (d) can thus be derived from the expected peak number (p) and the algal biomass available (b) by: $n = (bp/5) - p$. In all simulations, grazing depletion was calculated from daily goose usage of the bed and the functional response, as described above.

The rate of change in algal biomass in the absence of grazing was modelled in one of three ways, depending on the data available. Wind strengths and directions were available for 1989–1991, and these were used in conjunction with the relationship between wind strength and biomass change to predict daily rates of change in simulations of these years. For the years 1987 and 1988, Summers (1990a) gives seasonal patterns of biomass change in exclosures on the algal bed, from which mean daily rates of change in the absence of grazing can be calculated and applied directly to simulations of these years. Simulations for 1955–1957 also used direct daily percentage change values, but since no measurements for these values were published by Ranwell and Downing (1959) it was necessary to repeat the simulations of these years for a range of possible daily percentage changes (0.2 to $3\% \text{ day}^{-1}$). This range was defined by the minimum and maximum daily rates of change, averaged over October and November, observed in this study and in Summers (1990a).

The year-specific parameters used in simulations are summarized in Table 3, together with the observed and predicted dates on which the algal bed was abandoned in different years. This indicates a reasonably close correspondence between observed and predicted dates (Fig. 7). Note that the date of departure predicted has been heavily dependent on the timing of maximum wave damage in recent years. In 1987, for example, a very high rate of wave damage occurred in November, and

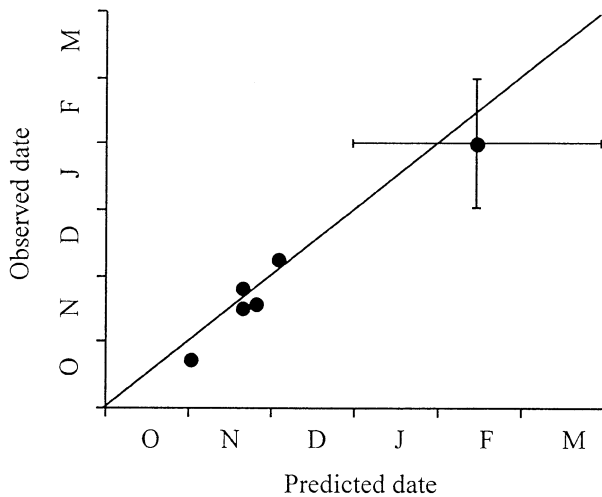


Fig. 7 The observed dates of departure from the algal bed plotted against those predicted for six different years (see Table 3). The error bars indicate the ranges observed and predicted for the years 1955–1957, for which precise data on conditions and departure dates were unavailable. Spearman rank correlation: $r_s=0.899$, $P<0.05$. The oblique line indicates observed=predicted

birds rapidly abandoned the bed in that month, while in 1991 strong northerly winds in October resulted in high wave depletion, and birds abandoned the bed much earlier that year. No data on wind strengths are available for the early years; however, the late departure dates predicted at that time are primarily due the lower numbers of geese present at that time.

The implications of changing conditions for departure date

Finally, the model was used to explore the implications of variations in a range of input parameters for the expected date of departure. The number of days required to reduce algal biomass to the $5 \text{ g}\cdot\text{m}^{-2}$ threshold in relation to the seasonal peak number of geese, wind strength, initial biomass and area of bed is illustrated in Fig. 8. October wind strength, bed area and initial biomass all have a roughly linear effect on grazing time supported, while the peak number of geese present has a strongly non-linear effect. Figure 8a illustrates the trade-off between grazing and wave loss. When there are strong northerly winds in October, most depletion is due to wave action,

Fig. 8 The predicted time for which grazing can be supported on algae in relation to **a** goose numbers and October northerly wind strength, and **b** initial biomass and area of algal bed.

a Area=5 ha, initial biomass= $40 \text{ g}\cdot\text{m}^{-2}$, mean northerly wind strength after October=8.8 knots. **b** Peak number of geese=300, mean northerly wind=9 knots throughout. When biomass is still above $5 \text{ g}\cdot\text{m}^{-2}$ at the end of March (day 182), grazing is judged to be supportable throughout the winter

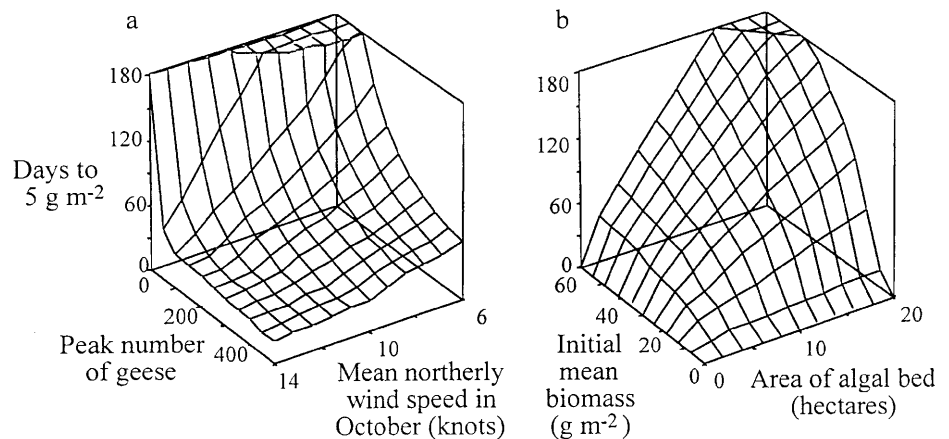


Table 3 A comparison of dates on which the algal bed was abandoned from simulation model predictions and field observation. Baseline data and observed dates of abandonment are from Ran-

well and Downing (1959) for 1955–1957, from Summers (1990a) for 1987–1988 and from this study for 1989–1991

Year	Initial biomass ($\text{g}\cdot\text{m}^{-2}$)	Peak number of geese	Date of peak number	Mean non-grazing % change in biomass day^{-1}		Date of abandonment	
				October	November	Observed	Predicted
1955–1957	40	10–40	30 Nov	–0.2 to –3		Jan/Feb	Jan/Mar
1987	60	350	2 Nov	–1.1	–4.9	24 Nov	19 Nov
1988	45	160	30 Oct	–3.1	–1.2	8 Dec	2 Dec
				Mean northerly wind strength (knots)			
1989	26	333	9 Nov	8.5	9.4	15 Nov	19 Nov
1990	20	288	17 Nov	6.7	10.8	17 Nov	24 Nov
1991	30	185	10 Oct	12.9	8.4	22 Oct	31 Oct

and the number of geese therefore has little effect on the length of time for which grazing can be supported. On the other hand, most depletion is due to geese when wind speed is low, and the grazing time supported is therefore much more responsive to goose numbers at low wind speeds.

Discussion

The results of this study show that, whilst grazing by brent geese on green algae had a short-term seasonal effect on plant biomass, there was no long-term impact of grazing on the population or community dynamics of the algae. This discussion focuses first on this result in the context of wider studies of plant herbivore interactions, and second considers the implications of results of the predictive modelling in the context of potential natural and anthropogenic changes in the system.

In three different years, grazing caused between 20% and 60% reduction in the biomass of algae in autumn but, although differences between grazed and ungrazed areas were evident throughout the winter, no differences persisted into the following summer or autumn. Moreover, there was no detectable effect of long-term grazing by geese on the algal community, which remained dominated by *Enteromorpha* spp. and *Ulva lactuca*. This result contrasts with the effects generally shown by invertebrate grazers on marine algal populations and communities (Chapman 1986; Hawkins and Hartnoll 1983; Lubchenco and Gaines 1981). In temperate regions, the most important invertebrate grazers of marine algae are gastropod molluscs, especially littorinids, although some isopod and amphipod crustaceans and dipteran larvae may also be important (Hawkins and Hartnoll 1983). Experiments excluding these grazers from algal communities on rocky shores have generally had the effect of allowing green algae (particularly *Enteromorpha* spp.) to persist where brown or red algae would otherwise dominate (Lubchenco 1978; Menge 1976; Underwood 1980). However, on soft sediments, while grazing by littorinids can prevent the establishment of green algae, it has been suggested to have a very little effect on existing algal mats (Wilhelmsen and Reise 1994).

Considering plant–herbivore interactions in all habitats, this is one of the few studies to find no long-term influence of grazing on the dynamics of a plant population, a notable exception being the interaction between cinnabar moth *Tyria jacobaea* and ragwort *Senecio jacobaea* (Dempster 1982; Van der Meijden 1979). In contrast, generalist herbivores in many other systems have been shown to have considerable impacts on both populations and communities (e.g. Kerbes et al. 1990; Kinsman and Platt 1984; Rowcliffe et al. 1998). Although it is difficult to generalize about the effects of herbivores on plant diversity, grazing typically leads to a reduction in the abundance of palatable species and an increase in unpalatable species (Crawley 1997).

The most likely explanation for the lack of any long-term effect of grazing on the population dynamics of the algae relates to the timing of grazing. Within the growing season the potential for regrowth and compensation depends critically on the timing of herbivore attack. In general, the earlier the attack in the life cycle of the plant, the greater the possibility for regrowth (Crawley 1997). Invertebrate grazers of algae frequently feed heavily on the young, sporeling stage of growth, and do so throughout the growing season (Hawkins and Hartnoll 1983). This is an important factor in the ability of invertebrates to affect algal communities; however, in the brent goose–green algae system, the period of depletion by geese overlaps very little with the main period of productivity of the plant. Although reproduction and growth in *Enteromorpha* spp. and *Ulva lactuca* can occur throughout the year in Britain (Burrows 1991), in practice there is usually little growth over winter. Geese migrate into the area just as growth and germination of the algae are slowing down, and depart before temperatures are sufficient to allow significant regeneration (Lotze et al. 1999). This means that the main period of algal growth and reproduction is unaffected by the geese, and there is consequently no effect on either the long-term population sizes or the community of green algae. This is thus a non-reactive, non-interactive system (Caughley and Lawton 1981), in which the herbivore has no influence on the rate at which its resources are renewed, and in which the number of herbivores is unrelated to plant growth.

Although the system is a non-interactive one, in which the parameters of plant growth have no effect on the herbivore population as a whole, short-term depletion of the algae does influence the movements of the brent geese. Intertidal habitats are the preferred feeding areas of brent geese (Vickery et al. 1995), but when this resource is depleted they will switch to alternative feeding habitats inland (Summers and Critchley 1990). The amount of time spent inland by geese thus depends on the length of time for which intertidal vegetation can support them. This is relevant to the issue of crop damage, since inland feeding by brent geese frequently occurs on crops, causing significant loss of yield (McKay et al. 1993; Summers 1990b; Summers and Stansfield 1991). The modelling approach adopted in this study has enabled the relationships between algal availability, wind strength, goose numbers and the potential grazing time available to be quantified. The fact that this model successfully predicted the time of abandonment of algal beds for a range of different conditions in different years suggests that the trends predicted in Fig. 8 are applicable to future changes in conditions. The model could therefore be used to help predict the likely impact of changed conditions on the amount of grazing that intertidal habitats can support, and hence the likely timing of the switch inland and potential agricultural damage that may result.

In considering future trends, account must be taken of each of the four variable components of the model:

changes in the numbers of geese, wind patterns, area of habitat and the biomass of algae available. Numbers of dark-bellied brent geese wintering in Europe have increased dramatically in the last 30 years (Ebbinge et al. 1999; Summers and Underhill 1991) and this has led to increasing inland feeding. However, current data suggest that further increases in numbers are unlikely, at least at the local level. There is some suggestion that the rate of growth in the global population has declined and is now close to zero (Ebbinge et al. 1999). However, even if a significant further increase in numbers does take place, it is likely that this will lead to an expansion of the wintering range rather than widespread local increases. This follows from evidence that most well established parts of the UK wintering range have held stable numbers over the most recent phase of global population increase, suggesting that these sites are at or close to capacity (Atkinson 1998; Rowcliffe and Mitchell 1996).

Although it has been suggested that global climate change may lead to an increased frequency of storms, this is not supported by historical records (Hammond 1990) and the predictions of climatic models are highly uncertain (Bolin 1994; Trenberth 1997). The timing and strength of winds therefore remain unpredictable elements in the depletion model. However, it can be seen from Fig. 8 that the large numbers of geese present in recent years have taken the rate of depletion into the region where grazing time which can be supported is not highly sensitive to either variation in wind strength or further increases in numbers of geese. In this region, depletion by the geese occurs early and rapidly, and the grazing time which can be supported is therefore uniformly low at between 2 and 6 weeks. In cases where high densities of geese feed on algal beds, it is therefore clear that autumn wind patterns will be of secondary importance in determining the time spent on the bed.

The area of algae available to geese is liable to change in future, but variably in time and space. The growth of *Enteromorpha* and *Ulva* depends on suitable water-retaining substrate (Nienhuis 1973), and this is influenced by local patterns of water flow and hence sediment type. Small-scale changes in patterns of flow occur naturally, but the construction of tidal barrages in estuaries has the potential to cause more widespread changes (Cadbury 1987; Rothwell 1989). In general, intertidal area is reduced by tidal barrage schemes. However, loss of algae through loss of area may be compensated to some degree by lower flow rates, resulting in finer, more stable sediments, providing a more suitable algal substrate. Reclamation of salt marsh generally leads to a narrowing of intertidal mudflats (Goss-Custard and Yates 1992) and where such development takes place, a reduction in the area of algal bed might be expected. Assuming current predictions of sea level rise related to global warming (Gregory and Oerlemans 1998), it is also likely that this factor will lead to a reduction in the availability of suitable intertidal habitat in future (Jones 1994).

The biomass of algae available on a given area in the autumn is dependent on summer growth rates. These are

generally dependent on the availability of nutrients (Björnsäter and Wheeler 1990; Lobban et al. 1985; Truscott 1978), which varies both on a predictable annual marine cycle (Falkowski and Woodhead 1992) and as a result of input from terrestrial sources such as sewage and agricultural runoff (Raffaelli et al. 1989). Acute eutrophication of coastal waters is usually localized, although there is some evidence of a long-term increase in nutrient levels in the North Sea generally (Radach et al. 1990; Riegman et al. 1992). Although increasing nutrients may result in a greater availability of algae, this should be balanced against detrimental effects on *Zostera* spp. (Burkholder et al. 1992), which are an important food resource for brent geese, both historically in this study site (Ranwell and Downing 1959) and currently in other areas (e.g. Fox 1996; Madsen 1988; Percival and Evans 1997). Indeed, changes in nutrient status may help to explain why *Zostera* was abundant in this study site in the past (Ranwell and Downing 1959) but is now almost absent, while algae are now abundant.

The approach presented here provides a simple framework by which the grazing pressure which a depleting resource can support can be predicted. Similar models have been developed for light-bellied brent geese *B. bernicla hrota* feeding on *Zostera* spp. (Percival et al. 1996) and bean geese *Anser fabilis fabilis* and wigeon *Anas penelope* on grass pasture (Sutherland and Allport 1994). However, these studies did not consider the possibility of long-term effects of grazing on the food resource, and this study is the first of its kind to demonstrate that such long-term effects may be safely discounted. In addition, because there was no overlap between the periods of depletion and productivity of the plants in this system, it was not necessary to consider the complex interaction between these factors known to be important in other plants, particularly grasses (McNaughton 1983). This greatly simplifies the modelling of the system, allowing us to predict how future scenarios might affect the birds' use of algal beds. This approach can be applied to other plant-animal interactions such as granivory and some other cases of herbivory, and may be developed to include long-term population effects or interactions between depletion and productivity. In cases where habitat switches are driven by depletion, this approach can also be used to predict the movements of animals under a range of different conditions. Finally, the method may also be a valuable tool in predicting the effects of habitat loss associated with estuarine development and long-term environmental change forecasts (Sutherland 1996).

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