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Depletion models can predict shorebird distribution at different spatial scales

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Predicting the impact of habitat change on populations requires an understanding of the number of animals that a given area can support. Depletion models enable predictions of the numbers of individuals an area can support from prey density and predator searching efficiency and handling time. Depletion models have been successfully employed to predict patterns of abundance over small spatial scales, but most environmental change occurs over large spatial scales. We test the ability of depletion models to predict abundance at a range of scales with black-tailed godwits, *Limosa limosa islandica*. From the type II functional response of godwits to their prey, we calculated the handling time and searching efficiency associated with these prey. These were incorporated in a depletion model, together with the density of available prey determined from surveys, in order to predict godwit abundance. Tests of these predictions with Wetland Bird Survey data from the British Trust for Ornithology showed significant correlations between predicted and observed densities at three scales: within mudflats, within estuaries and between estuaries. Depletion models can thus be powerful tools for predicting the population size that can be supported on sites at a range of scales. This greatly enhances our confidence in predictions of the consequences of environmental change.

Keywords: functional response; prey selection; waders

1. INTRODUCTION

The degradation and loss of suitable habitat resulting from human activities is one of the most important processes currently driving species' declines. These processes are so widespread and affect so many species that the challenge for ecologists is not just to identify the factors causing the declines but also to focus efforts on the most important processes. To do this, we need to be able to predict the likely impact on species of different types of habitat change. Such predictions require an understanding of the factors that determine the size of a population that can be supported in a given area. Models of resource depletion have provided a conceptual framework for understanding the distribution of individuals across patches varying in resource density (Royama 1971; Bernstein *et al.* 1988; Sutherland & Anderson 1993; Rohani *et al.* 1994; Goss-Custard *et al.* 1995; Sutherland 1996). These are based on components of the functional response: the relationship between the intake rate of a predator and the density of its prey (Holling 1959).

Depletion models have been used previously to predict patterns of abundance across small spatial scales (Sutherland & Allport 1994; Percival *et al.* 1996, 1998). These models can then be used to predict the effect of habitat changes on the number of animals that can be supported within these patches by altering the resource abundance parameters. There is a clear need to test the predictions from such models. Furthermore, many of the most important types of environmental change, such as sea-level rise resulting from global warming, agricultural intensification, industrial development and pollution, take

place over very large spatial scales. To determine the potential impact of these large-scale processes, we need therefore to assess the ability of current models to predict patterns of abundance at a range of spatial scales.

Sutherland & Anderson (1993) described a theoretical depletion model which uses the searching efficiency and prey handling time parameters derived from functional response curves to estimate the number of predators per unit area (P) required to deplete a given amount of available resources:

$$P = T_h \sum_{d_c}^{M} (j - d_c)f_j + 1/a' \sum_{d_c}^{M} f_j \log(j/d_c), \qquad (1)$$

where j is the density of available prey at the start of the season over the area f, M is the maximum value of j, a' is the searching efficiency, T_h is the prey handling time and d_c is the threshold prey density at which the predators no longer feed in the site. If it is possible to predict predator densities from such a model, it will then be possible to predict the consequences of habitat loss (which reduces the area and thus the f_j values) or any change in habitat quality, such as pollution, sediment changes or sea level rise, which results in a change in prey density (expressed as changing the areas of each prey density). It is likely that these models will apply more readily at some scales than others due to, for example, the problems of sampling at large spatial scales or to other factors unrelated to prey density becoming increasingly important at larger scales. We therefore tested the ability of depletion models to predict predator density at a range of spatial scales.

Black-tailed godwits *Limosa limosa* are a common wading bird species in Europe. The *islandica* subspecies, which breeds in Iceland and winters mainly in Britain,

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Ireland, France and Portugal, spends the majority of the non-breeding season on estuaries feeding on benthic invertebrates. The aim of this study was to describe the small-scale functional response of black-tailed godwits to spatial variation in resource densities. This response was then used in conjunction with the Sutherland & Anderson (1993) depletion model to make and test predictions of the spatial distribution of the birds at different scales.

2. METHODS

(a) *Large-scale invertebrate survey*

The study took place on six estuaries on the south-east coast of England: the Alde, Deben, Orwell, Stour, Colne and Blackwater estuaries. These estuaries were chosen because they provide a range of faunal types and densities and support large populations of wintering black-tailed godwits. A survey of the abundance and size distribution of benthic invertebrates was carried out during September and October 1994 on five of the estuaries (the Alde, Deben, Orwell, Colne and Blackwater) and during October 1996 on the Stour estuary. These estuaries were selected in these winters to coincide with the British Trust for Ornithology (BTO) Low Tide Count Scheme (Waters *et al.* 1996). Sites within the estuaries were selected using a 1 km × 0.5 km grid on a 1:50 000 map of the estuary and sampling at each intersection. In cases where the intersection lay just adjacent to the mudflat, samples were taken from as near as possible to the intersection. At each of the 126 sampling points, four replicate cores of 10 cm diameter and 15 cm depth were collected. The maximum depth to which a godwit could potentially reach determined this depth of core. These samples were then sieved in tap water through a 1 mm sieve and all invertebrates were identified, measured and preserved in alcohol. Each species of bivalve was separated into maximum shell length categories (< 2.5, 2.6–3.9, 4.0–5.5, 5.6–9.5, 9.6–14.5, 14.6–19.5, 19.6–29.5, 29.6–39.5 and > 40 mm) to make the data comparable with previous studies. This sampling procedure was repeated during the following March.

(b) *Black-tailed godwit foraging behaviour*

The foraging behaviour of black-tailed godwits was measured at a range of sites throughout the winters of 1995–1996 and 1996–1997. Intake rates were measured by observing one individual for the time taken for ten paces while foraging. Within this time, the number of successful and unsuccessful pecks made was recorded, as was the identity of the prey (as bivalve or polychaete), where possible. Black-tailed godwits in these sites fed almost exclusively on bivalves and polychaetes. It is possible to identify the prey being consumed as it can usually be seen in the bill, and as the birds use slightly different foraging techniques for bivalves and polychaetes. Over 95% of prey could be identified. From this, intake rates were calculated as the number of successful pecks per second of foraging time (excluding time spent vigilant) and all observations from a flock were averaged to give a mean intake rate at that site and time (one observation period).

The number of black-tailed godwits in each observed flock was counted and the area they covered was recorded using 1:25 000 maps. After each observation period, the prey were sampled from the area where the godwits had been feeding by taking six replicate cores of 6.4 cm diameter and 15 cm depth. These smaller cores were used to maximize the number of

replicates that could subsequently be processed in the available time. These samples were then sorted, identified and measured as described above.

(c) *Black-tailed godwit site selection and use*

During the winter of 1996/1997, detailed studies were carried out on 20 sites on six estuaries (mean area = 7.5 ha ± 1.6 s.e.), chosen to represent a range of prey densities and godwit presence or absence. Each site was visited once in every two-week period between 16 October 1996 and 20 March 1997. At each visit, one hour was spent at the site, during which counts were made of all waterfowl on the site and the prey selection and intake rate of any black-tailed godwits were measured. From these count data, the number of godwit-days was calculated as the sum of the number of godwits present on every count multiplied by the number of days between that and the subsequent count. After each hour-long survey, the prey density was sampled within the site by taking six replicate cores of 6.4 cm diameter and 15 cm depth, as described above.

(d) *Large-scale waterfowl censuses*

The number of waterfowl occurring on British estuaries is counted monthly by volunteers as part of the BTO Wetland Bird Survey (WeBS; Waters *et al.* 1996). These counts generally take place at high tide when birds are roosting. They give estimates of the total number of bird-days on an estuary by a given species by multiplying the number of that species recorded in each month by the number of days in the month and summing these values over the winter (October to March). These monthly volunteer counts (or in two cases, counts carried out by us) were used to calculate the number of godwit-days for six estuaries: the Alde, Deben, Orwell, Colne and Blackwater in 1994/1995 and the Stour in 1996/1997 (the years in which the invertebrate surveys took place; mean estuary intertidal area = 1591 ha ± 410 s.e.).

The distribution of waterfowl on British estuaries is counted monthly from November to February by volunteers as part of the BTO Low Tide Count Scheme (Waters *et al.* 1996). In this scheme, the distribution of birds is recorded by counting the number of foraging and roosting birds on individual mudflats. As the invertebrate sampling takes place from October to March, but low tide counts are only available from November to February, it was necessary to estimate the numbers of godwits present in October and March. This was done by assuming the number on each mudflat in October to be the same as that recorded in November and the number in March to be the same as that in February. This was tested using the regular counts of godwits on 20 smaller sites carried out in 1996/1997. Although movement of birds between patches within a mudflat is likely to make numbers on these smaller patches more variable, the counts show significant correlations in these pairs of months, with coefficients not significantly different from one and intercepts not significantly different from zero (Oct/Nov, $r = 0.57$, $p < 0.01$, coefficient = 0.89, 95% CI 0.25−1.53, intercept = −3.89, 95% CI −23.02−+15.25; Feb/Mar, $r = 0.65$, $p < 0.01$, coefficient = 0.83, 95% CI 0.35−1.31, intercept = 0.9, 95% CI −0.61−+2.41). Low tide counts take place on each estuary in Britain approximately once every five years. During the course of this study, three of the study estuaries were counted in this manner; the Colne and Blackwater in 1994/1995 and the Stour in 1996/1997. The mean area of the mudflats counted on these three estuaries was 62.8 ± 4.9 ha.
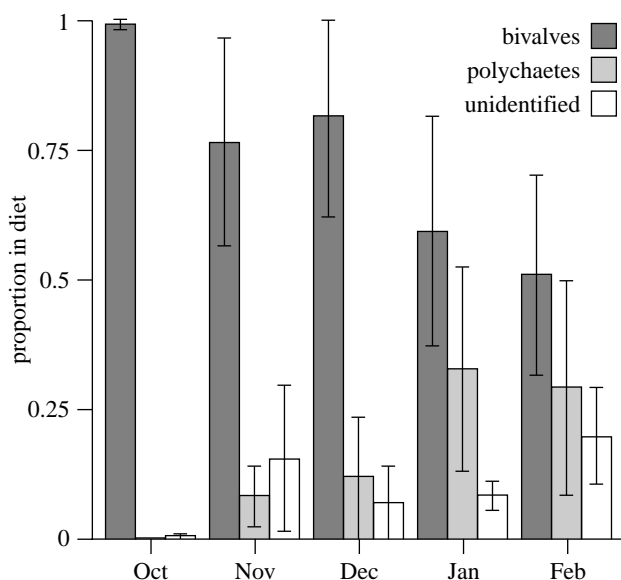
Figure 1. The mean ($\pm$ s.e.) proportion of bivalves, polychaetes and unidentified prey in the diet of black-tailed godwit flocks over the winter of 1995/1996.

3. RESULTS

(a) *Prey selection*

The only prey types that black-tailed godwits were observed consuming were bivalves and polychaetes. Figure 1 shows the seasonal change in the proportion of polychaetes and bivalves in the diet during the winter 1995–1996. Bivalves were the most abundant food source in the diet throughout the winter and polychaetes were only included in the diet in significant proportions towards the end of the winter. The change in diet from bivalves to polychaetes could arise either by individuals switching at different times (with some never making the transition) or by all individuals increasing the proportion of polychaetes in their diet over the winter. The mean proportion of observations per flock in which individuals took more than one prey type was 0.02 ± 0.006 s.e. ($n = 71$); thus within foraging bouts individuals have extremely consistent prey selection. It was therefore possible to separate the intake rates of godwits feeding on bivalves and polychaetes. In 1995–1996, 74% of observations were of godwits selecting bivalves. In the areas in which the godwits fed, three species of bivalve (*Scrobicularia plana*, *Macoma balthica* and *Mya arenaria*) comprised, on average, 88% ($n = 30$) of the bivalve population and one species of polychaete, *Nereis diversicolor*, comprised on average 86% ($n = 25$) of the polychaete population.

Studies elsewhere (Goss-Custard *et al.* 1991; Moreira 1994) have shown that black-tailed godwits select bivalves of between *ca.* 5 and 20 mm shell width. In this study, the fraction of the bivalve population considered as available to the godwits was therefore restricted to *Scrobicularia plana*, *Macoma balthica* and *Mya arenaria* of size classes 3 to 6 (4.0–19.5 mm), which comprised on average 55% ($\pm 8\%$ s.e.) of the bivalves in areas where godwits selected bivalves. In all further analyses, the term 'available bivalves' refers to these four size classes of the three species.

(b) *Functional response*

The average intake rate of black-tailed godwits that were feeding only on bivalves is strongly related to the density of available bivalves (figure 2). This relationship follows a type II functional response (Holling 1959), indicating that at low prey densities, intake rate declines rapidly but that at high prey densities, intake rate is constrained by the time taken to consume the prey rather than the time taken to find prey. The parameters from this response gives estimates of prey handling time ($T_h = 4.095$) and searching efficiency ($a' = 0.00033$).

(c) *Threshold prey density*

Across the 20 sites studied intensively in 1996/97, black-tailed godwits showed a strong aggregative response, with the total number of godwit-days per hectare over the winter period (for godwits consuming bivalves only) being significantly, positively related to the initial density of available bivalves ($r^2 = 0.45$, $p < 0.002$). Sites containing less than 150 available bivalves per square metre were not used by godwits feeding on bivalves and this was thus used as the value of d_c, the threshold density at which they stop feeding on bivalves.

(d) *Predicting black-tailed godwit densities within and between estuaries*

The resource depletion model presented in Sutherland & Anderson (1993) calculates the number of predators supported by a given resource density from the parameters determining prey intake rates (equation (1)). To make comparisons between predicted and observed bird densities possible, the predicted values need to be presented as the number of bird-days per unit area, hence it is also necessary to incorporate the number of hours per day spent feeding. The predicted number of godwit-days per hectare can thus be calculated from equation (1), using the searching efficiency and prey handling time parameters estimated from the functional response (figure 2) and dividing the number of predators (P) by the number of hours per day spent feeding. The potential amount of time that the birds can spend feeding is restricted by the tidal regime to between *ca.* 8 and 14 h day^{-1}. This value was therefore initially set at 10 h day^{-1} and later varied between these extremes. The daily energy requirement of black-tailed godwits is given by Moreira (1994) as 447 kJ day^{-1}. Assuming an average bivalve ash-free dry mass of 0.003 g (this study; J. A. Gill, unpublished data; Zwarts & Wanink 1989) and an energetic content of these bivalves of 22 kJ g^{-1} (Zwarts & Wanink 1993), at prey densities of 4000 bivalves m^{-2}, the godwits would have to feed for 9 h day^{-1} to achieve 447 kJ day^{-1}. At a density of 2000 bivalves m^{-2}, they would have to feed for 10.5 h day^{-1} and at 1000 bivalves m^{-2}, 13.5 h day^{-1} of feeding would be required. Below these densities, intake rate drops rapidly and the birds will clearly need to either move to better patches, feed on larger bivalves or switch prey in order to achieve the daily requirement. At the patch scale, the number of godwit-days ha^{-1} predicted by the depletion model can be compared with the actual number of godwit-days ha^{-1} over the winter (for godwits feeding on bivalves only). Figure 3*a* shows a strong correlation between these observed and predicted densities.
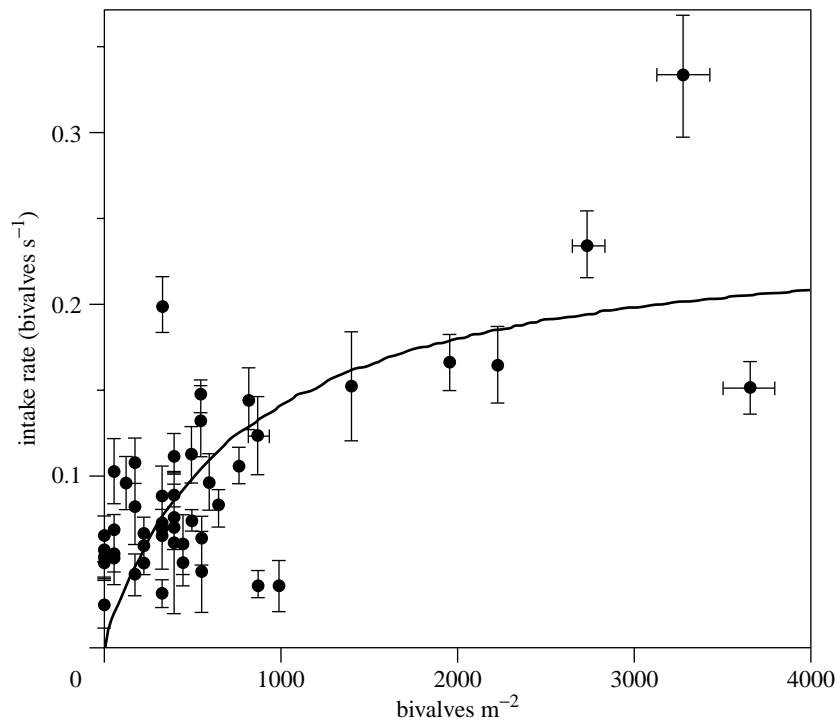
Figure 2. The relationship between the mean ($\pm$ s.e.) intake rate of black-tailed godwits feeding on bivalves (bivalves consumed per second of foraging time) and the mean ($\pm$ s.e.) density of available bivalves measured on each site immediately following the observations of foraging birds. The function is Holling's (1959) disc equation: $y = a'N/1 + a'NT_h$ ($r^2 = 0.35$, $n = 47$, $p < 0.001$), where $a' = 0.000\,33 \pm 0.000\,07$ s.e. ($\chi^2 = 1.08$, n.s.) and $a'T_h = 0.001\,33 \pm 0.000\,47$ s.e. ($\chi^2 = 3.41$, $p < 0.07$).

At the mudflat scale, precise available bivalve densities at the point where godwits abandoned the mudflats could not be ascertained. The spring prey densities were therefore used as the threshold densities (d_c) and were also given a lower threshold value of $150\,\mathrm{m}^{-2}$. The number of black-tailed godwits on individual mudflats was counted once a month in the same year as the invertebrate survey on three of the estuaries (Colne and Blackwater, 1994/1995; Stour, 1996/1997) as part of the BTO Low Tide Count Scheme. Low tide counts and invertebrate samples coincided on 22 mudflats on these three estuaries. Figure 3*b* shows that observed and predicted godwit densities across these mudflats are also strongly correlated. Thus, despite the small number of prey samples collected per mudflat ($n = 4$), the effect of bivalve density on godwit distribution is strong enough to provide quite accurate predictions of bird density.

At the estuary scale, the autumn (j) and spring (d_c, again with a lower limit of $150\,\mathrm{m}^{-2}$) densities of available bivalves could then be estimated for six estuaries as the mean of the estimates for individual mudflats within each estuary (excluding those with autumn densities lower than 150 available bivalves m^{-2}, approximately half of the mudflats). The predicted number of godwit-days ha^{-1} could then be related to the number of godwit-days ha^{-1} counted at high tide on these estuaries in these years. Figure 3*c* shows that the predicted and observed godwit densities are also strongly correlated across entire estuaries.

The predicted bird-days for each estuary are based on a relatively small number of sample sites at which prey densities were measured (between 15 and 28 sites per estuary). Prey densities vary spatially within each estuary,

so to examine the effect of this variation on the precision of our model predictions for each estuary, we employed a bootstrapping procedure. For each estuary, we sampled, with replacement, prey densities from the distribution of observed prey densities, a number of times that corresponded to the number of prey samples actually taken. For example, 17 sites were sampled on the Alde, so we sampled, with replacement, from this distribution 17 times. This resampling procedure was undertaken for the October and March samples for each estuary, allowing us to calculate predicted bird-days for each estuary. We then compared observed and predicted bird-days using linear regression, to calculate model parameters (regression coefficient and intercept) and goodness-of-fit (r^2). We then repeated this entire process 99 times, to generate distributions of regression coefficient, intercept and r^2-values that reflect the underlying variation in prey densities recorded in each estuary. We then calculated the mean for each of these distributions and the 95% confidence interval, as a measure of how variation in prey densities affected our degree of precision in predicting bird-days. The results (table 1) show that the 95% confidence interval for the goodness-of-fit values only varied by 3% of the mean r^2, so, although prey densities varied between sampling sites within an estuary and only a small number of sampling sites per estuary were used, this had little direct impact on the number of bird-days predicted by the model.

(e) *Sensitivity analyses*

Within these calculations, the parameter for which there is greatest uncertainty is the number of hours per
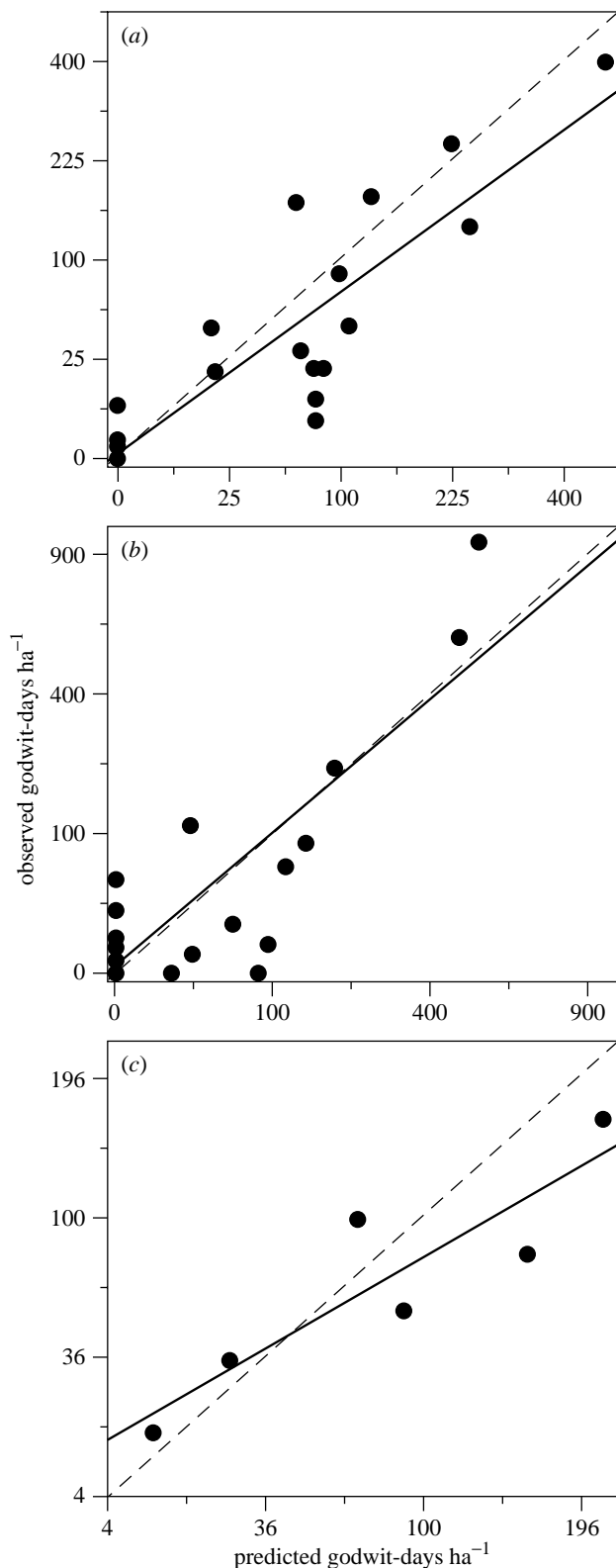
Table 1. *A comparison of the actual regression coefficient, intercept and goodness-of-fit of the relationship between observed and predicted black-tailed godwit densities across estuaries (figure 3c) and the mean (±confidence interval) regression coefficient, intercept and goodness-of-fit of this relationship generated by resampling of the prey density data*

(See § 3(d) for details.)

	mean	95% CI	actual value
coefficient	0.657	0.632 − 0.680	0.64
intercept	2.314	2.121 − 2.508	2.33
r^2	0.768	0.744 − 0.793	0.79

day spent feeding. The amount of time spent feeding at night by this species is not known. However, during daylight, black-tailed godwits tend to roost for 4–6 h over high tide and often also roost for 1–2 h at low tide (J. A. Gill, personal observation). If it is assumed that nocturnal foraging follows the same pattern, then the godwits have *ca.* 8–14 h day^{-1} available for feeding. At all three scales, varying the time spent feeding between 8 and 14 h day^{-1} altered the resulting predicted godwit densities but did not result in a relationship that varied significantly from unity (table 2).

The handling and searching time parameters must be estimated from the functional response. To investigate the sensitivity of the predictions to these estimates of a' and T_h, each was varied by 5%, 10% and by the standard error of the mean. The effects on the regression coefficient of the relationships between predicted and observed godwit densities are summarized in table 3. At all three scales, altering the handling and searching time parameters within likely levels of inaccuracy has very little impact on the relationships between observed and predicted densities.

At the mudflat and estuary scales, the consequences of altering the threshold spring bivalve density of 150 available bivalves m^{-2} can also be assessed. Table 3 shows that altering this value by ±10% has a negligible impact on the predicted godwit densities. The consequences of altering the range of bivalve sizes that is available to the godwits can also be examined in this way. The upper size limit is determined by the size of the gape and is therefore fixed. However, the lower size limit (4 mm) could potentially be flexible. The predicted density of godwits at all three scales was therefore recalculated using the autumn and spring density of all *S. plana*, *M. balthica* and *M. arenaria* of < 20 mm shell width. This results in the predicted densities overestimating the actual densities by a mean (±s.e.) of 72.3 ± 32.8 godwit-days ha^{-1} (patch scale), 54.4 ± 33.6 godwit-days ha^{-1} (mudflat scale) and 53.2 ± 25.4 godwit-days ha^{-1} (estuary scale). In the case of patch and mudflat scales, the relationships between predicted and observed densities were significantly different from unity (table 3).

Figure 3. Observed and predicted number of black-tailed godwit-days ha^{-1} on (a) small patches of mudflat ($y = 0.82x − 0.34, r^2 = 0.75, p < 0.0001$, 95% CI of the fitted parameters: regression coefficient $= 0.58 − 1.05$, intercept $= −1.87 − + 2.55$), (b) whole mudflats ($y = 0.96x − 0.47, r^2 = 0.72, p < 0.0001$, 95% CI of the fitted parameters: coefficient $= 0.68 − 1.23$, intercept $= −2.01 − + 2.94$) and (c) whole estuaries ($y = 0.64x + 2.33, r^2 = 0.79, p < 0.02$, 95% CI of the fitted parameters: coefficient $= 0.19 − 1.10$, intercept $= −2.15 − + 6.80$). All axes were normalized by square-root transformation. The dashed lines show the lines of unity.

4. DISCUSSION

To use depletion models to predict the impact of habitat change on species, we need to be able to assess the

Table 2. *The effect of varying the number of hours per day spent feeding by black-tailed godwits on the regression coefficient* (*b*, ±*95% confidence intervals) of the relationships between observed and predicted densities of godwits at three different scales*

(All relationships were normalized by square-root transformation. All intercepts were patch: 0.34 (95% CI $-1.87-+2.55$); mudflat: 0.47 ($-2.01-+2.94$); estuary: 2.33 ($-2.15-+6.8$).)

hours feeding	patch		mudflat		estuary	
	b	95% CI	*b*	95% CI	*b*	95% CIs
8	0.73	0.52 − 0.94	0.85	0.61 − 1.10	0.58	0.17 − 0.99
9	0.77	0.55 − 1.00	0.91	0.64 − 1.17	0.61	0.18 − 1.05
10	0.82	0.58 − 1.05	0.96	0.68 − 1.23	0.65	0.19 − 1.10
11	0.85	0.61 − 1.10	1.00	0.71 − 1.29	0.68	0.20 − 1.16
12	0.89	0.63 − 1.15	1.05	0.74 − 1.35	0.71	0.21 − 1.21
13	0.93	0.66 − 1.20	1.09	0.77 − 1.41	0.74	0.21 − 1.26
14	0.96	0.68 − 1.24	1.13	0.80 − 1.46	0.76	0.22 − 1.31

resources that are being used by the species within that habitat and the manner in which those resources are exploited. Functional responses provide a means of quantifying resource exploitation patterns and depletion models provide a means of predicting the number of animals that a given resource density can support. In this study, we used the functional response of black-tailed godwits measured within mudflats to predict abundance within mudflats, within estuaries and between estuaries. The close correlation of these predictions with observed counts means that it is possible predict the impact of habitat change on population size at larger spatial scales than those over which the functional response can be quantified.

The effect of the loss or degradation of the habitat can be incorporated into the model as changes in the area of available prey, f_j. Figure 4a describes a theoretical distribution of prey densities. The loss of habitat will result in a reduction in the area of given prey densities, such as is shown in figure 4b. Habitat degradation, on the other hand, will reduce the density of prey within sites and hence will skew the distribution of prey densities as shown in figure 4c, such that the area of low prey densities is increased and the area of high prey densities decreased. Thus the magnitude of the effect on godwits of any process altering prey density (such as pollution or sediment changes) can be explored by incorporating the potential change in prey density in the model and calculating the resulting change in godwit density.

The patch-scale functional response (figure 3) refers only to godwits consuming bivalves. The success of this response in predicting densities of godwits at both mudflat and estuary scales (where any prey types could have been consumed) indicates that bivalves constitute the vast majority of black-tailed godwit prey on these sites. If other prey types, such as polychaetes, were important in the diet of godwits at these sites, the godwit densities predicted from bivalve abundance would tend to be lower than the actual densities. The predicted values actually tend to slightly overestimate godwit densities. This overestimation could be caused by predators other than godwits consuming the bivalves. While there are other predator species present on these sites, the close correlation between predicted and observed godwit densities suggests that locally, godwits appear to be the most
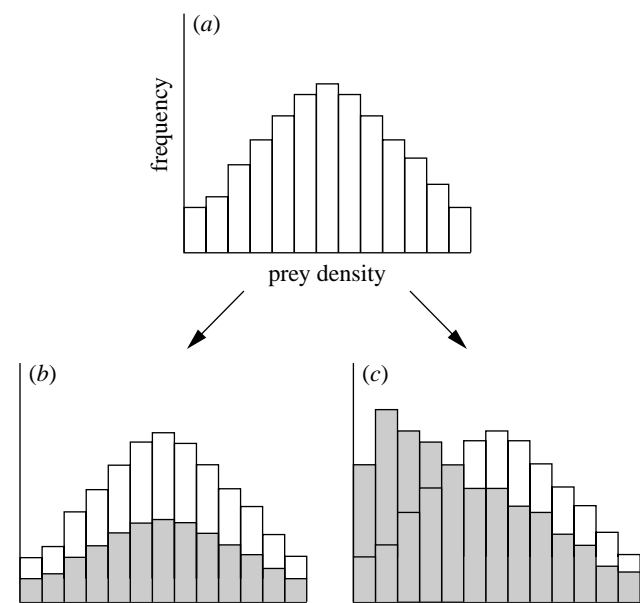

Figure 4. The effect of (b) habitat loss and (c) habitat deterioration on a theoretical distribution of prey densities (a). In (b) the shaded area shows the distribution of prey densities resulting from a 50% loss of habitat across all sites. In (c) the shaded area shows the skewed distribution of prey densities resulting from habitat deterioration reducing the area of high prey density and increasing the area of low prey density.

important predators of these bivalves. This is quite likely to be the case given the strong prey selectivity and flocking behaviour of black-tailed godwits in winter. This approach is likely to be less successful for species that consume a greater range of prey items and compete with other species for those prey.

The 95% confidence intervals of the regression coefficients of the patch- and mudflat-scale relationships (figure 3a,b) are ±30%, whereas those of the estuary-scale relationship (figure 3c) are ±70%. This difference in accuracy may simply be due to the relatively small number of estuaries involved or it may be that larger-scale predictions will be inherently less accurate, as a greater number of other factors may be important in determining distribution between estuaries. The estuaries examined in this study are all close to one another

Table 3. *The effect of varying the searching efficiency* (a') *and handling time* (T_h) *parameters by 5%, 10% and the standard error of the mean, the lowest spring bivalve density* (d_c) *by 10% and removing the avoidance of bivalves of* $< 4.0\,mm$, *on the regression coefficient* (b, $\pm 95\%$ *confidence intervals*) *of the relationships between observed and predicted densities of godwits, at three different scales*

(All relationships were normalized by square-root transformation. At the patch scale, the actual spring bivalve densities were known and were therefore not varied.)

	amount varied	patch		mudflat		estuary	
		b	95% CI	b	95% CI	b	95% CI
a'	+ 5%	0.83	0.59 − 1.08	0.98	0.69 − 1.26	0.63	0.15 − 1.12
	− 5%	0.79	0.56 − 1.02	0.93	0.66 − 1.20	0.60	0.14 − 1.06
	+ 10%	0.85	0.61 − 1.10	1.00	0.71 − 1.29	0.65	0.15 − 1.14
	− 10%	0.77	0.55 − 1.00	0.91	0.64 − 1.17	0.58	0.14 − 1.03
	+ s.e.	0.90	0.64 − 1.16	1.05	0.75 − 1.36	0.62	0.13 − 1.10
	− s.e.	0.72	0.51 − 0.93	0.85	0.60 − 1.09	0.50	0.11 − 0.89
T_h	+ 5%	0.80	0.57 − 1.04	0.95	0.67 − 1.22	0.61	0.14 − 1.07
	− 5%	0.82	0.58 − 1.06	0.97	0.68 − 1.25	0.62	0.14 − 1.11
	+ 10%	0.80	0.57 − 1.02	0.94	0.67 − 1.20	0.60	0.14 − 1.06
	− 10%	0.83	0.59 − 1.08	0.98	0.69 − 1.26	0.63	0.14 − 1.12
	+ s.e.	0.76	0.55 − 0.97	0.89	0.64 − 1.14	0.52	0.12 − 0.91
	− s.e.	0.88	0.61 − 1.16	1.03	0.72 − 1.35	0.62	0.11 − 1.12
d_c	+ 10%	not applicable		0.98	0.71 − 1.24	0.64	0.18 − 1.09
	− 10%	not applicable		0.93	0.65 − 1.22	0.65	0.19 − 1.11
no size selection		0.41	0.12 − 0.69	0.58	0.32 − 0.84	0.62	0.19 − 1.05

geographically and are therefore similar in factors such as latitude, climate and tidal regime. It will clearly be important to assess whether this technique is also accurate in predicting bird densities at even greater spatial scales. This will only be possible if the prey selection behaviour of the birds is constant across those scales.

It seems inevitable that at increasing spatial scales there will be other factors that affect distribution, such as sampling constraints in relation to fluctuating prey densities, weather, roost site availability, predation risk and location with respect to migration route. Although the depletion model provided good predictions of godwit distribution over a wide range of spatial scales, at some scale, the predictive ability of these models is likely to decline.

Predictions of the number of bird-days supported on different sites and at different scales can thus be derived from functional responses based on measures of prey selection behaviour and the availability of different prey types. In this study, scaling up from patches to mudflats worked well and scaling up again to entire estuaries produced encouragingly good correlations. Identifying whether the inclusion of other factors at larger scales improves the fit further will clearly be an important next step. Functional responses are relatively easy to measure and have been described in a wide variety of organisms (Bradbury *et al.* 1996; Norris & Johnstone 1998; O'Donoghue *et al.* 1998). If functional responses can be used to predict accurately abundance at large spatial scales, then there is real potential for assessing the likely impact on species of any process that alters resource abundance, by incorporating these changes in abundance into the model. Resource depletion models can therefore be powerful tools for predicting patterns of abundance and the impact of environmental change at a range of spatial scales.

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