Chapter (non-refereed)

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Predicting the effect of habitat change on waterfowl communities: a novel empirical approach

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SUMMARY
Natural environmental changes, such as coastal erosion, and human developments, ranging from roads and marinas to global climate change, are leading to much habitat change in wetlands. It would be valuable to conservationists, governments and developers to be able to predict the likely impact of such evolution on the internationally important waterbird populations in European wetlands. We present a method, based on relatively easily and cheaply determined environmental variables, which allows the effect of habitat change on estuary waterfowl communities to be predicted.

The factors that best describe waterfowl communities are estuary length, channel and shore widths, exposure to swell, sediment type, longitude and latitude. The implications for waterfowl of any habitat change that affects these variables are discussed. It is suggested that when human developments are being designed they should take these factors into account in an attempt to minimise their impact on waterfowl.

IS WETLAND HABITAT LOSS A PROBLEM?

In international terms, the United Kingdom is ornithologically important because of large coastal seabird colonies and the vast numbers of waders and wildfowl that winter on its estuaries (Cayford & Waters 1996; Kirby 1995). These wetland habitats are facing increasing pressure. One third of the UK's human population lives near estuaries, and proposals for housing schemes, marinas, recreational and tidal power barrages comprise more than half of the present land claim proposals in Britain. In total, 88% of British estuaries have been affected by land claim (Davidson & Evans 1986; Davidson *et al.* 1991). The cost to wildlife has been made worse by the increased disturbance associated with the developments which have made human access to the shore easier (Davidson & Rothwell 1993). Future sea level rises due to global warming could make the situation more serious (United Kingdom Climate Change Impacts Review Group 1996).

Developments tend to alter the physical structure of estuaries; for example, marinas and tidal power barrages affect the area, shape, length and tidal range of an estuary. Sea level rises or natural coastal erosion cycles, as witnessed at Spurn Point in the UK, also change the morphology of estuaries. Thus, if robust models describing estuary waterfowl populations could be developed from sedimentological, morphological and geographical variables, the effect of habitat loss and change on waterbirds could be predicted. This prediction would be of obvious conservation importance but also of great practical and economic value as the UK's internationally important populations of waterfowl are a major consideration in estuarine environmental impact assessments. Effective models would allow a balanced case to be made for or against developments and allow the effects of natural changes to be estimated. Such predictions would make adherence to the requirements of both national and European law considerably easier.

ENVIRONMENTAL VARIABLES AS INDICATORS OF HABITAT QUALITY

Habitat is a good indicator of the conditions that lead to reliable feeding opportunities, and thus strongly influences bird populations (Fretwell & Lucas 1970; Goss-Custard 1977; Goss-Custard *et al.* 1995a, b; Watkinson & Sutherland 1995). Differences in food availability account for a large proportion of the variation in feeding bird densities (Prater 1981; Goss-Custard *et al.* 1991; Yates *et al.* 1993), waterfowl tending to concentrate where prey density and availability are relatively high and the energy expenditure required to feed is relatively low (Goss-Custard, Jones & Newberry 1977; Cresswell 1994). Substrate differences influence both plant and invertebrate abundance and their availability to foraging shorebirds (Myers, Williams & Pitelka 1980; Quammen 1982); inter-related variables such as sediment particle size, degree of organic content and salinity, for example, influence invertebrate and, therefore, shorebird distributions (Yates *et al.* 1993; Rehfisch 1994). In combination, these factors can lead to waterfowl food stocks which vary by orders of magnitude between years. As the long-term presence of the plants and invertebrates is related to the environmental variables, the environmental variables are more likely to be effective descriptors of waterfowl densities than are the markedly fluctuating food stocks.

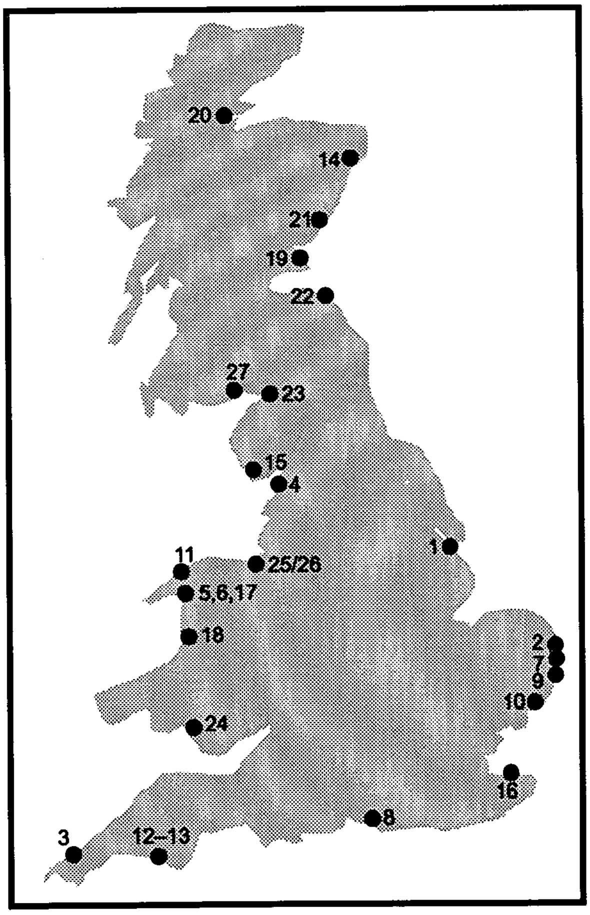

Figure 1. The 27 sites surveyed at low tide during the 1993–94 and 1994–95 winters. 1 Humber, 2 Breydon Water, 3 Hayle, 4 Eden, 5 Glaslyn/Dwyryd, 6 Artro, 7 Blyth, 8 Pagham, 9 Alde, 10 Deben, 11 Foryd Bay, 12/13 Plym/Tamar, 14 Ythan, 15 Duddon, 16 Swale, 17 Mawddach, 18 Dyfi, 19 Eden, 20 Cromarty Firth, 21 Montrose Basin, 22 Tyninghame, 23 Solway, 24 Swansea Bay, 25 Dee, 26 North Wirral and 27 Auchencairn Bay

Having demonstrated the link between habitat variables and waterfowl populations at the local scale (McCulloch & Clark 1991; Yates *et al.* 1993), it became logical to develop nationwide models. Twenty-seven estuaries holding about 10% of the UK's waterfowl were selected for a study which had three aims:

- to predict sediments from estuary morphology and geography (Yates *et al.* 1996);
- to assess whether waterfowl communities were determined by estuary sediments, morphology and geography (Holloway *et al.* 1996); and
- to predict waterfowl densities (and thus numbers) from estuary sediments, morphology and geography (Austin *et al.* 1996).

The study aims were successfully met and we report on how easily quantifiable environmental variables (sedimentological, morphological and geographical) can help determine the waterfowl communities found in UK estuaries. From these models and relationships, it becomes possible to highlight the likely effect of a development or natural change on waterfowl communities as long as the post-event morphology of the estuary can be determined. This enables designers to take into account the abiotic factors that most affect waterfowl communities and allows them to produce developments which minimise detrimental change. This in turn enables conservationists and government agencies to predict the effect of natural environmental change on waterfowl populations and plan ahead.

BIRD COUNTS AND ENVIRONMENTAL VARIABLE MEASUREMENT

During the winters of 1993–94 and 1994–95, feeding waterfowl were counted and mapped up to 14 times between November and

Table 1. Definitions of the whole-estuary environmental and sediment cover variables

Variable name	Units	Definition
EAREA	ha	Total area of estuary from mouth to defined upper limit, including channel
ELENGTH	km	Distance up mid-channel from mouth to upper limit
EWMAX	km	Mean and maximum of the total width of the estuary measured at ten or more representative transects across the estuary
EWMEAN	km	
ESHAPE = ELENGTH / EWMEAN		Estuary shape variable where high values denote relatively long and narrow estuaries
ETRANGE	m	Mean spring tidal range (MSHW–MSLW) (Admiralty Tide Tables Volume 1: Table V, pxxxviii or Part II, pp302–360)
EWSHORE	km	Mean shore (intertidal) width averaged over ten equally spaced transects on each side of the estuary, measured from low water to upper limit of saltmarsh or sea wall
EWCHANN	km	Mean low-water channel width from ten transects
EWMOUTH	km	Estuary mouth width
ESWELL = EWMOUTH / EWMAX		Estuary exposure to swell from the sea
EDEPTHI = EWCHANN / EWMEAN		Estuary depth index; estuaries with relatively wide channels will tend to be deeper.
EFETCH2	km	Estuary fetch: median of the maximum fetch values recorded from all count sections in an estuary (see Yates *et al.* 1996)
EFETCH10	km	Estuary fetch: as above but restricted to a maximum value of 10 km (see Yates *et al.* 1996)
ELAT	°	Latitude
ELONG	°	Longitude
EPMUD	%	Percentage of total sediment area in an estuary which is mud
EPMUDSAND	%	Percentage of total sediment area in an estuary which is muddy sand
EPSAND	%	Percentage of total sediment area in an estuary which is sand
EPOTHER	%	Percentage of total area in an estuary which is not mud, muddy sand or sand

February on 1050 count sections on 27 estuaries around the coasts of England, Scotland and Wales (Figure 1). The complete sampling methods can be found in Holloway *et al.* (1996). Only count sections with sufficient and representative data were included in the analyses in order to reduce noise within the dataset. Finally, as rare species, effectively outliers, increase the likelihood of anomalous results (Hill 1979a; Jongman, ter Braak & van Tongeren 1995), only the 17 most widespread and common waterfowl species known to feed on intertidal mudflats were included in the ordination. The mean density of each species of waterfowl feeding on an estuary of n count sections is:

$$\sum_{i=1}^{n} b_i \Big/ \sum_{i=1}^{n} a_i$$

where b_i is the mean count of the species on count section i of area a_i.

The environmental variables were collected from a variety of different sources but the majority were measured directly from the remotely sensed images (Table 1) and are described in greater depth in Yates *et al.* (1996).

A COMMUNITY APPROACH TO DATA ANALYSES

Multivariate statistics made it possible to determine which species tended to be found together on the same sites and also which sites tended to hold the same species. The sites and species were simultaneously ordered along the ordination axes using detrended correspondence analysis (DECORANA) with no downweighting of rarer species (Hill 1979a; Jongman *et al.* 1995). Sites placed close together have similar bird communities and species placed close together tend to occur on similar sites; sites at the two extremes of the axes tend to have the most dissimilar bird communities.

The analysis was based on a 17 species × 27 sites data matrix of the overall feeding densities of the most widespread and abundant species. To aid interpretation of the axes, site scores for each of the first four ordination axes were plotted against, and correlated with, the individual physical and environmental variables. Stepwise multiple regression was then used to select the combinations of variables which jointly gave the best predictions of the ordination axes (SAS Institute Inc 1989). The residuals were examined to confirm visually that each environmental and sediment cover variable contributed usefully to the model.

In a separate analysis, the communities of feeding waterfowl were classified using two-way indicator species analysis (TWINSPAN) (Hill 1979b; Jongman *et al.* 1995). TWINSPAN, a form of hierarchical divisive classification, was used to examine whether the sites could be classified into a number of groups on the basis of their waterfowl communities. Of particular interest was the effect of geographical location on site classification. The measured environmental variables on each site were used as descriptive variables in a stepwise linear discriminant analysis (James 1985; SAS Institute 1989) in an attempt to identify the factors determining differences between the site groups identified by TWINSPAN. The effectiveness of different models in describing the data were compared using SAS PROC DISCRIM. The North Wirral and Cromarty sites which had missing environmental variable data were excluded from the discriminant analyses.

CONTRIBUTION OF SPECIES AND SITES TO COMMUNITY COMPOSITION

The species and site scores for the DECORANA axes 1 (DCA1) and 2 (DCA2) are represented in Figure 2. DCA1 explained 62.4%, DCA2 24.7% and DCA3 and DCA4 the remaining 12.9% of the variation in the four axes extracted.

Shelduck (*Tadorna tadorna*), dunlin (*Calidris alpina*), redshank (*Tringa totanus*), curlew (*Numenius arquata*) and grey plover (*Pluvialis squatarola*), the most widespread species in UK estuaries, were found in the centre of the species ordination. Three species of dabbling duck, teal (*Anas crecca*), mallard (*A. platyrhynchos*) and wigeon (*A. penelope*), had low DCA1 scores and high DCA2 scores. The close proximity of these species in the ordination space indicated that they tended to be found in association. Pintails (*A. acuta*), which unlike the other

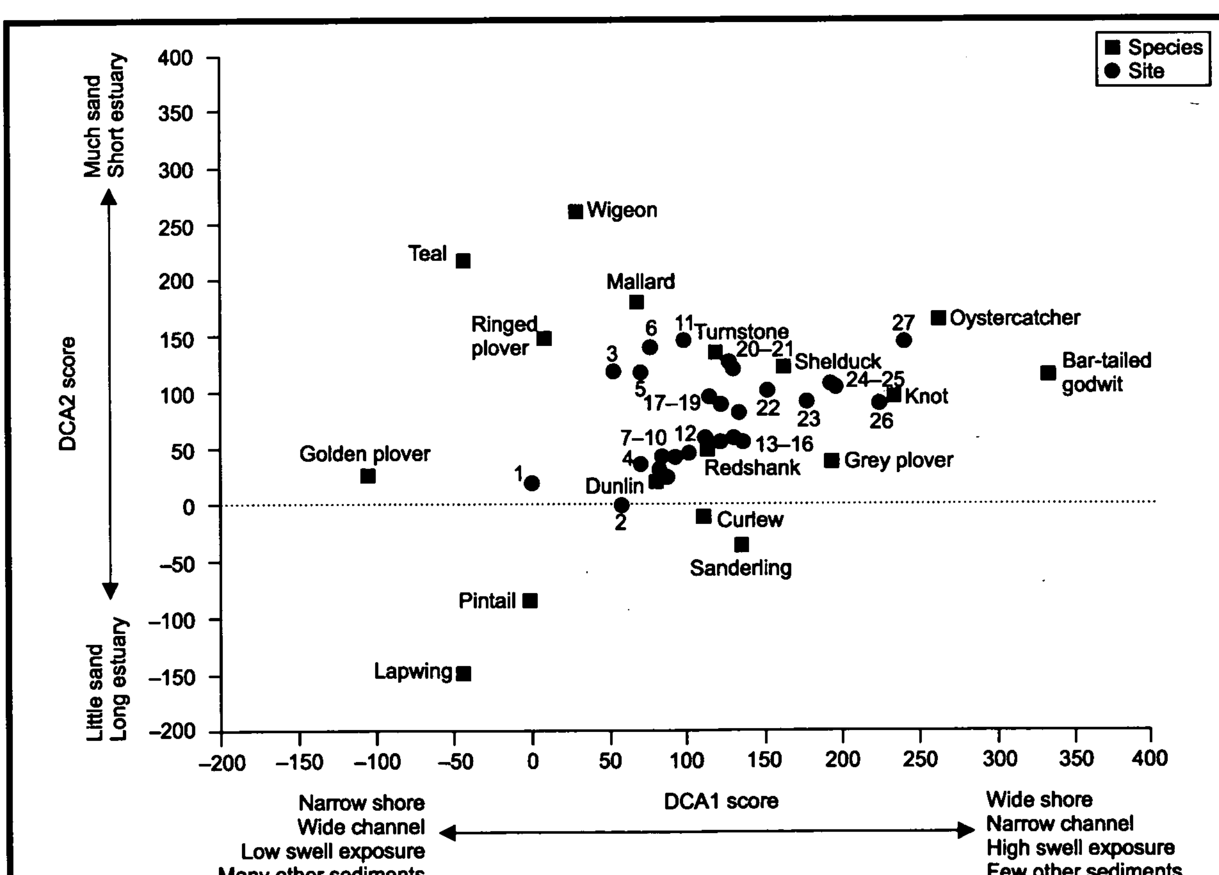

Figure 2. DCA ordination of the waterfowl data from the 27 sites, numbered as in Figure 1. The variables by the axes help explain the site waterfowl communities

ducks have a diet that can be dominated by molluscs, had a much lower DCA2 score and were not necessarily associated with the other ducks. Widely separated positions in the ordination space may have reflected the different habitat requirements of species. Communities that included bar-tailed godwits (*Limosa lapponica*) and oystercatchers (*Haematopus ostralegus*), at one end of the ordination space, tended to have fewer of the lapwings (*Vanellus vanellus*) and pintails found at the opposite end of the ordination space. Lapwings and golden plovers (*P. apricaria*), which occupied similar positions in the ordination space, can be found in very large densities on estuaries where they roost after having fed on inland fields (Prater 1981).

Sites aggregated in the ordination space according to their geographical location. Many of the sites in Wales (Artro, Foryd, Glaslyn, Mawddach, Dyfi), in eastern Scotland (Cromarty, Montrose, Tyninghame, Eden, Ythan), in south-eastern (Breydon Water, Blyth, Alde, Deben) and southern England (Plym, Tamar, Pagham) and in the north-west (Auchencairn, North Wirral, Dee, Solway) therefore had similar waterfowl communities. Even Montrose (41% mud and 39% sand cover) and Tyninghame (no mud and 85% sand cover), adjacent estuaries with very dissimilar sediments and morphology, had similar waterfowl communities. A few sites behaved atypically in this geographical context: the Humber, Hayle, Lune and Swansea Bay. The Humber is very polluted, the Lune is effectively a muddy branch of Morecambe Bay. The Hayle and Swansea Bay are heavily urbanised, and the latter is very disturbed.

ORDINATION AXIS INTERPRETATION ACCORDING TO ENVIRONMENTAL VARIABLES

The DCA1 scores increased with mean estuary width ($r=0.42$, $n=25$, $P<0.05$), mean shore width ($r=0.62$, $n=25$, $P<0.001$), mouth width ($r=0.44$, $n=25$, $P<0.05$), tidal range ($r=0.44$, $n=25$, $P<0.05$), exposure to swell ($r=0.55$, $n=25$, $P<0.01$), exposure to fetch ($r=0.65$, $n=27$, $P<0.001$) and proportion of intertidal area covered by sand ($r=0.57$, $n=27$, $P<0.01$); the scores decreased with the proportion of mud ($r=-0.48$, $n=27$, $P<0.05$), the proportion of cover that is neither mud nor sand ($r=-0.45$, $n=27$, $P<0.05$) and the estuary shape ($r=-0.48$, $n=25$, $P<0.05$).

The DCA2 scores increased with shore width ($r=0.43$, $n=25$, $P<0.05$) and the proportion of sand ($r=0.72$, $n=27$, $P<0.0001$), and decreased with estuary length ($r=-0.51$, $n=25$, $P<0.01$),

Table 2. The intercept, partial regression coefficients and coefficients of determination (r^2) of a multiple regression equation relating the DCA1–DCA4 to the environmental variables. The stepwise technique in the SAS STEPWISE procedure (SAS Institute Inc. 1989) selected models based on independent variables with a $P\geq0.05$ entry and elimination significance level

	Intercept ±SE	Partial regression coefficients±SE									n and overall model sig	Model coeff of determ adjusted for df r^2
		$\log_{10}$ (ELENGTH) (km)	EWCHANN² (km²)	ESHAPE²	EWSHORE (km)	$\log_{10}$ (ESWELL)	ESWELL²	ELONG (°)	EPSAND (%)	EPOTHER² (%)		
DCA1	74.10 ±13.70 ****		−11.60 ±2.94 ***		77.3 ±19.1 ***	180.0 ±58.10 *				−0.02 ±0.01 *	25 ****	0.71
DCA2	76.60 ±20.70 **	−39.80 ±16.10 *							0.93 ±0.20 ****		25 ****	0.59
DCA3	85.40 ±11.90 **			0.05 ±0.02 **				−12.60 ±3.24 ***			25 **	0.40
DCA4	80.70 ±11.60 ****						51.80 ±15.80 **			−0.03 ±0.01 **	25 **	0.40

* P<0.05; ** P<0.01; *** P<0.001; **** P<0.0001

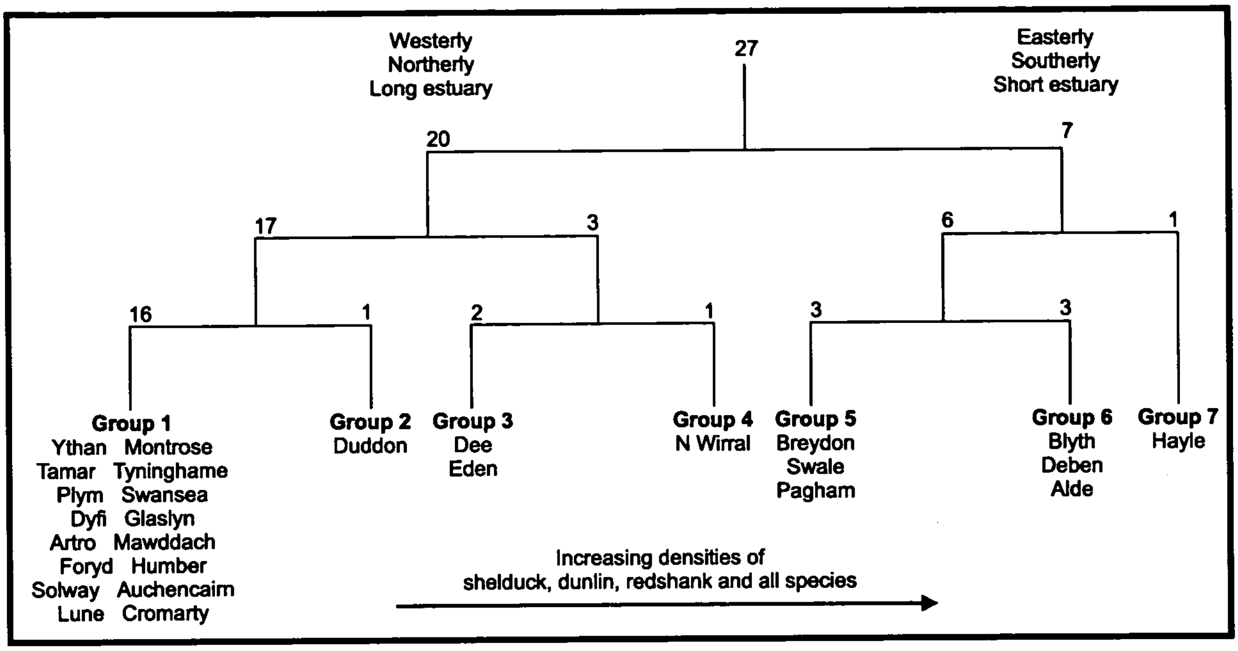

Figure 3. TWINSPAN dendrogram showing the site hierarchical classification on the basis of their wader communities. The variables at the top of the Figure help explain the first division. The arrow at the base of the dendrogram indicates the direction of the species' gradients across the final seven groups

estuary shape ($r=-0.71$, $n=25$, $P<0.0001$), longitude ($r=-0.69$, $n=27$, $P<0.0001$) and the proportion of mud ($r=-0.69$, $n=27$, $P<0.0001$) on each site. The DCA3 scores decreased with longitude ($r=-0.39$, $n=27$, $P<0.05$). The DCA4 scores increased with mouth width ($r=0.40$, $n=25$, $P<0.05$) and exposure to swell ($r=0.49$, $n=25$, $P<0.05$).

Many of these variables were strongly intercorrelated. Based on a stepwise multiple regression analysis, channel width, shore width, exposure to swell and the proportion of total area that was neither mud nor sand jointly explained 70.9% of the variation in the first ordination axis scores (Table 2). Estuary length and the proportion of sand explained 59% of the variation in the second ordination axis scores.

Estuary shape was significantly correlated with the densities of four species of waterfowl, exposure to swell with five species, longitude with five species and total waterfowl, tidal range and the proportion of sand with seven species and total waterfowl, and the proportion of mud with eight species and total waterfowl. Shelduck, pintail, oystercatcher, ringed plover (*Charadrius hiaticula*), golden plover, sanderling (*Calidris alba*), dunlin, curlew and redshank were significantly correlated with five or more of the variables. Shelduck, oystercatcher, dunlin, curlew and redshank are amongst the most common species of waterfowl in the UK; they are species which are near the centre of their wintering ranges and may be present in densities approaching their maximum. Such species were likely to be occupying most of the available suitable habitat and were consequently more likely to be distributed according to variables that may have defined their limiting conditions. There may remain much unoccupied yet suitable habitat for the less common species, and their distribution was more likely to be determined by such non-physical constraints as disturbance.

Multiple regression selected the environmental and sediment cover variables which were significant in determining the densities of individual species of waterfowl on the estuaries. Longitude affected the densities of five species of waterfowl and estuary length, estuary shape and tidal range each affected the densities of four species, as did the pooled sand, mud-sand and sand variables. When stepwise regression was used to select models from all variables, with the exception of longitude and latitude, to separate the effect of the latter from sediment cover, the new models had decreased coefficients of determination ($R^2=0.271$–0.768 *cf* 0.54–0.933). Models restricted to the sediment cover variables were even less effective at predicting waterfowl densities ($R^2=0.238$–0.504).

Table 3. Mean densities of waterfowl (±SD), mean values of the environmental variables (±SD) and mean values of the arcsine transformed sediment cover variables (±SD) of the two groups of estuaries resulting from the first TWINSPAN division

	Groups 1, 2, 3 and 4	Groups 5, 6 and 7
Number of sites	20	7
Shelduck	0.172±0.264	0.613±0.275
Wigeon	0.285±0.464	1.255±2.472
Teal	0.036±0.068	0.073±0.087
Mallard	0.048±0.061	0.061±0.050
Pintail	0.006±0.014	0.053±0.052
Oystercatcher	0.876±0.870	0.354±0.263
Ringed plover	0.027±0.026	0.112±0.064
Golden plover	0.179±0.708	0.123±0.198
Grey plover	0.054±0.128	0.328±0.374
Lapwing	0.116±0.256	0.991±1.215
Knot	0.315±0.468	0.437±0.887
Sanderling	0.006±0.013	0.003±0.006
Dunlin	0.973±0.952	7.530±2.496
Bar-tailed godwit	0.240±0.889	0.033±0.060
Curlew	0.193±0.143	0.419±0.452
Redshank	0.402±0.406	1.472±1.018
Turnstone	0.030±0.045	0.038±0.055
All species	3.960±3.514	13.896±2.525
EAREA ha	6001.40±11778.70	1265.43±1308.04
ELENGTH km	13.182±15.948	10.891±7.209
EWMAX km	3.961±4.080	1.696±1.587
EWMEAN km	1.936±1.831	0.722±0.411
ESHAPE	9.633±9.898	17.009±11.787
ETRANGE m	5.711±1.793	3.686±1.626
EWSHORE km	0.569±0.367	0.248±0.110
EWCHANN km	0.423±0.829	0.136±0.092
EWMOUTH km	2.818±3.614	0.875±1.909
ESWELL	0.584±0.364	0.289±0.340
EFETCH2 km	39.038±68.011	1.591±1.602
EFETCH10 km	5.881±3.920	1.591±1.602
EDEPTHI	0.182±0.188	0.204±0.118
ELAT °	54.036±2.148	51.634±0.894
ELONG °	−3.332±1.016	−0.356±2.569
EPMUD %	25.153±27.796	69.324±25.574
EPMUDSAND %	15.870±12.069	9.070±15.614
EPSAND %	54.206±24.128	16.113±18.471
EPOTHER %	27.283±12.462	28.422±7.455

HIERARCHICAL CLASSIFICATION OF ESTUARIES ACCORDING TO THEIR WATERFOWL COMMUNITIES

The TWINSPAN hierarchical classification divided the sites into seven groups (Figure 3). The largest group included the Plym, Tamar, Lune, Humber and all of the estuaries in Wales and Scotland, with the exception of the Eden. Sites in groups 1–4 had lower shelduck, pintail, ringed plover, dunlin and overall waterfowl densities, more sand, less mud, more fetch, were further to the north-west and larger than sites in groups 5–7 (Table 3). Dunlin, redshank, shelduck and total waterfowl densities tended to increase from groups 1 to 7, but no environmental gradient was detected (Table 4).

The results of the stepwise discriminant analysis indicated that only three of the environmental and sediment cover variables were significant discriminators between groups 1–4 and groups 5–7 identified from the TWINSPAN analysis: longitude (F=17.16, P<0.001), latitude (F=14.34, P<0.001) and estuary length (F=6.169, P<0.05). These variables correctly assigned 23 out of 25 sites, 100% of the sites in groups 1–3 and 71% of the sites in groups 5–7.

FACTORS THAT DETERMINE WATERFOWL COMMUNITIES

The explanatory variable that recurred most frequently in the species and community analyses was longitude. Geographical location is known to affect numbers in wintering species (Newton & Dale 1996), though, unfortunately, few collated data relate the precise wintering grounds of UK waterfowl to their breeding grounds. It is possible that, by opting to spend the winter where they can compete effectively for resources but also remain near their breeding grounds, waterfowl may increase their probability of survival by minimising the energy spent migrating. The restricted mobility of waterfowl on their breeding (Thompson & Hale 1993) and wintering grounds (Rehfisch *et al.* 1996) may help confirm that energy budgets can be difficult to balance (Piersma 1994) and that waterfowl waste as little energy as possible in inessential movements. Under such circumstances, wigeon, and in particular oystercatcher, both of which are unusual in having large breeding populations in Iceland, would tend to winter on the west coast, whereas the other species, which mostly breed to the east of the UK in Fennoscandinavia or the former USSR, would favour the east coast. In our study, wigeon, oystercatcher and bar-tailed godwit were indeed the only species found at greater densities to the west. This hypothesis was further supported by the site ordination which demonstrated that sites that were geographically adjacent, but with very different environmental and sediment cover variables, tended to have similar waterfowl communities (Figure 2), as did the decrease in the explanatory power of the models that excluded the geographical variables. However, an element of doubt must remain in view of the uncertainty about the breeding grounds and relative population sizes on these breeding grounds of many species.

Apart from geographical location, the community composition on a site was also determined by estuary length, channel width, shore width, exposure to swell, and the proportion of sand and sediments other than mud and sand (Table 2). Golden plover and sanderling densities increased with estuary length. Golden plover densities were also positively correlated with estuary width; these waders which use estuaries as day-time roosts may be attracted to large estuaries where they are less likely to be disturbed. Channel width was related to the flushing of a site. A site with little water left in the channel at low water had its fine sediments washed out and therefore tended to be sandier, whereas a site with a wide channel at low tide tended to be muddier. Wider channels led to greater teal and golden plover densities (Figure 2). Wide shores tend to be sandy whereas narrow shores tend to be muddy (Goss-Custard & Yates 1992), which explains why the highest dunlin densities occurred on narrow shores (see McCulloch & Clark 1991) and the highest oystercatcher densities occurred on wide shores (Figure 2). Exposure to swell increased with the relative mouth width of a site. Swell, energy coming in from the sea in the form of waves, led to finer particles being resuspended at high tide and so the greater the swell, the sandier were the sediments. Pintail, ringed plover and redshank densities, species which favour mud, decreased as the

Table 4. Mean densities of waterfowl (±SD), mean values of the environmental variables (±SD) and mean values of the arcsine transformed sediment cover variables (±SD) of the seven groups resulting from the seven final TWINSPAN groups of estuaries

	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7
Number of sites	16	1	2	1	3	3	1
Shelduck	0.134±0.197	0.212	0.542±0.644	0.005	0.638±0.185	0.740±0.247	0.152
Wigeon	0.311±0.492	0.003	0.366±0.518	0.000	0.353±0.304	0.295±0.197	6.840
Teal	0.037±0.072	0.000	0.068±0.081	0.000	0.072±0.104	0.035±0.052	0.190
Mallard	0.055±0.066	0.033	0.025±0.028	0.000	0.087±0.051	0.054±0.045	0.000
Pintail	0.005±0.013	0.037	0.001±0.001	0.000	0.087±0.066	0.038±0.018	0.000
Oystercatcher	0.585±0.603	0.775	2.417±0.074	2.552	0.462±0.408	0.305±0.058	0.174
Ringed plover	0.029±0.029	0.018	0.026±0.007	0.006	0.146±0.084	0.082±0.045	0.101
Golden plover	0.204±0.792	0.000	0.159±0.226	0.000	0.276±0.237	0.012±0.014	0.000
Grey plover	0.012±0.032	0.041	0.194±0.238	0.000	0.584±0.482	0.138±0.121	0.131
Lapwing	0.107±0.254	0.009	0.307±0.422	0.469	1.410±1.939	0.567±0.363	1.008
Knot	0.175±0.304	0.238	0.768±0.222	0.000	1.000±1.235	0.019±0.026	0.000
Sanderling	0.005±0.013	0.015	0.0 01±0.001	1.726	0.008±0.008	0±0	0.000
Dunlin	0.640±0.601	2.128	2.018±1.453	0.023	5.937±0.661	9.346±3.046	6.864
Bar-tailed godwit	0.030±0.060	0.006	0.155±0.218	3.073	0.060±0.093	0.012±0.019	0.017
Curlew	0.190±0.156	0.233	0.238±0.100	4.002	0.665±0.646	0.250±0.186	0.190
Redshank	0.342±0.419	0.339	0.654±0.225	0.107	0.938±0.600	2.437±0.301	0.179
Turnstone	0.029±0.048	0.005	0.030±0.035	0.914	0.082±0.062	0.004±0.006	0.008
All species	2.889±2.364	4.092	7.968±4.422	0.066	12.803±2.808	14.335±2.692	15.855
EAREA ha	5652.73±12621.18	6092.000	8571.00±10649.03	12.944	1874.00±1803.20	1046.33±755.77	97.00
ELENGTH km	13.115±17.316	14.750	12.900±11.101	-	10.643±8.107	14.018±6.172	2.250
EWMAX km	3.657±4.258	5.875	5.288±4.543	-	2.658±2.204	1.133±0.345	0.500
EWMEAN km	1.789±1.857	2.205	2.901±2.538	-	1.059±0.440	0.523±0.030	0.313
ESHAPE	10.514±10.660	6.690	4.495±0.106	-	10.847±8.092	26.443±10.612	7.190
ETRANGE m	5.533±1.797	7.600	6.100±2.263	-	4.000±1.825	2.667±0.814	5.800
EWSHORE km	0.513±0.345	0.739	0.903±0.572	-	0.347±0.091	0.190±0.031	0.126
EWCHANN km	0.432±0.901	0.182	0.477±0.520	-	0.150±0.123	0.148±0.078	0.055
EWMOUTH km	2.348±3.564	5.875	4.813±4.861	-	1.792±2.952	0.183±0.115	0.200
ESWELL	0.526±0.366	1.000	0.817±0.218	-	0.375±0.541	0.167±0.118	0.400
EFETCH^{2} km	12.727±17.782	215.000	91.063±125.777	180	2.596±2.221	0.912±0.291	0.613
EFETCH^{10} km	5.352±3.851	10.000	6.063±5.568	10	2.596±2.221	0.912±0.291	0.613
EDEPTHI	0.194±0.204	0.083	0.140±0.057	-	0.137±0.073	0.280±0.144	0.176
ELAT °	53.979±2.324	54.180	54.806±2.193	53.255	51.571±0.942	52.178±0.136	50.190
ELONG °	-3.397±1.131	-3.240	-2.975±0.189	-3.108	-0.524±1.291	1.504±0.148	-5.431
EPMUD %	27.598±30.227	0.000	24.826±8.288	11.838	55.559±31.943	88.152±3.212	54.135
EPMUDSAND %	14.643±12.451	13.697	27.205±12.479	15.009	19.487±20.906	0±0	5.025
EPSAND %	52.197±25.718	76.309	50.973±17.124	70.715	23.939±20.743	1.855±3.213	35.408
EPOTHER %	28.611±13.239	30.780	18.411±8.648	20.278	32.781±4.231	25.995±9.732	22.629

exposure to swell increased, while oystercatcher densities increased. Swell may also have improved the feeding conditions for filter-feeding mussels, a major constituent of the oystercatcher diet, which in turn may have increased oystercatcher numbers.

Sand is associated with lower invertebrate biomasses and this may have been reflected by the lower densities of shelduck, pintail, ringed plover, lapwing, dunlin, curlew, redshank and all species confounded found on sandy sites. As the proportion of cover of sediments other than mud and sand increased, oystercatcher densities decreased significantly and eleven other species showed a similar trend.

Seven types of waterfowl communities were identified from our sample sites. The only previous large-scale study of wader communities in Britain and possibly the world defined the bird densities from high-tide roost counts (Hill *et al.* 1993). Hill's hierarchical classification of 109 estuaries separated them into groups discriminated by differences in latitude, tidal range and total estuary area, whereas in the present study latitude, longitude and estuary length discriminated between site groupings (Figure 3). These studies confirm the effect of the geographical position of an estuary on its wader community and the importance of site size.

IMPLICATIONS FOR HABITAT CHANGE

These results can help us predict the kinds of habitat change, whether from estuarine developments or from natural causes, which are likely to affect waterfowl communities. Seven environmental variables help describe waterfowl communities on a site: estuary length, channel and shore widths, exposure to swell, sediment type, longitude and latitude. Natural or man-made changes to estuaries will have no impact on the longitude and latitude of a site (unless these variables substitute for some other unmeasured environmental variable), but man-made changes will affect some of the other environmental variables. The estuary length, channel width and shore width will all change if a barrage is built, for example. The intertidal channel width upstream of a barrage will increase and the shore width decrease, leading to muddier conditions, which in turn will lead to lower oystercatcher densities but higher dunlin, and probably total waterfowl, densities. The shortening of the estuary due to the barrage may lead to decreases in golden plover densities. It is important to point out that, post-development, the total intertidal area may be smaller and that increases in species' densities may therefore not be sufficient to maintain the present-day total number of a species. Marinas, ports and land reclamation are also likely to affect these variables. Developments, such as road bridges, that are built either at the widest point or at the mouth of an estuary will change its exposure to swell. Similarly, the breaching of Spurn Point and the continuing erosion of the sand spit is increasing the exposure to swell of the Humber by widening its mouth. This may lead to parts of the Humber becoming sandier, with an attendant change in the waterfowl community.

From these results and the models developed to predict densities of individual species from environmental variables (Austin *et al.* 1996), the changes to waterfowl communities that are likely to result from major estuarine developments, such as global climate change, may now be predicted with a fair degree of confidence. Specific developments and natural changes will have to be assessed in an *ad hoc* manner and the value of the predictions will depend partly on the quality of the post-development environmental variable data and the species affected.

Further work, including analyses at the within-estuary scale, would enhance our understanding of the environmental variables and, possibly, of the processes which are critical in determining within-estuary community structure. It is also of great importance that these models are tested on ongoing developments or on historical data to confirm their value. Once the models have been field-tested, their predictions should allow developments to be designed which minimise the impact on the United Kingdom's internationally important waterfowl populations.

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