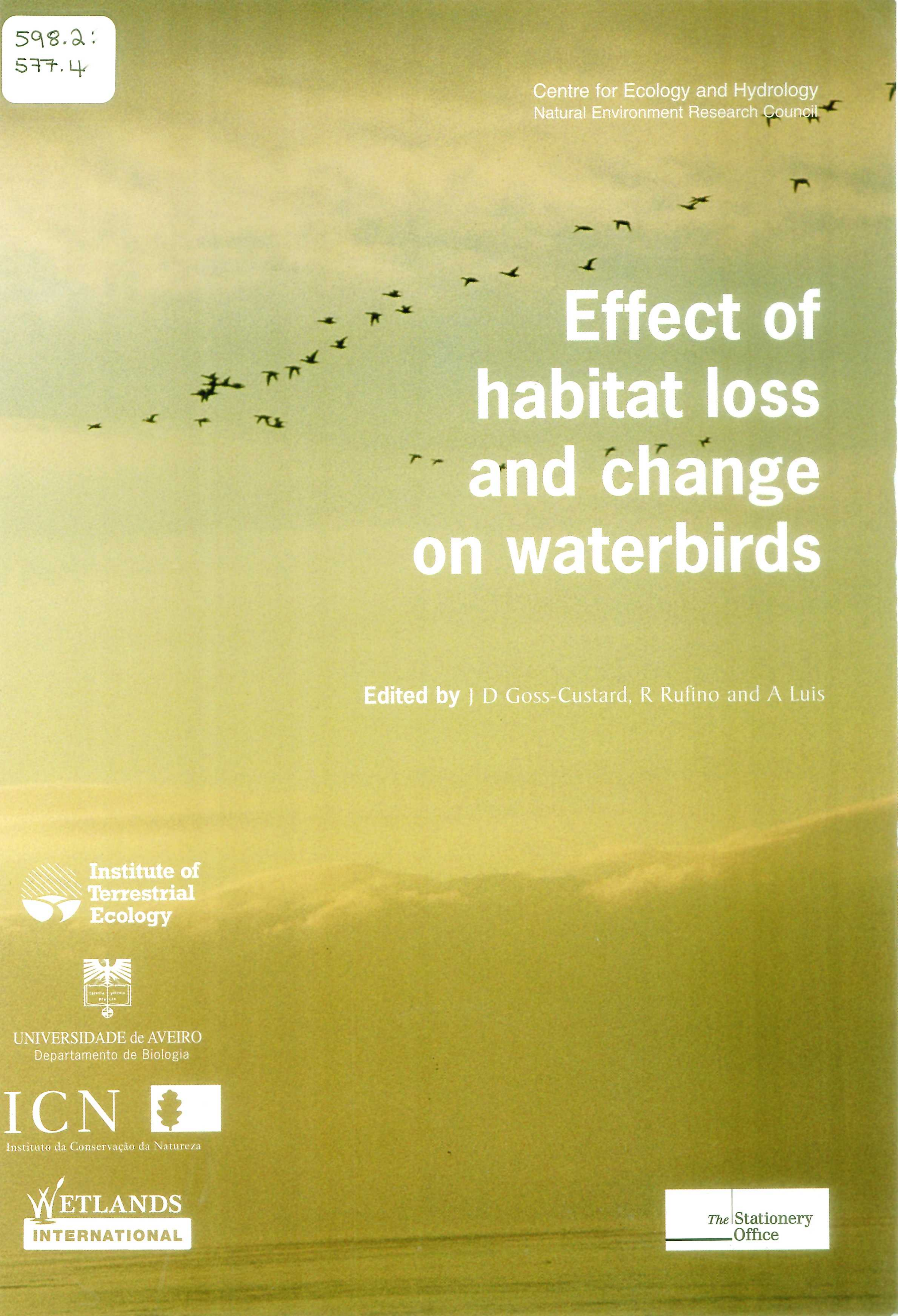

Centre for Ecology and Hydrology
Natural Environment Research Council

Effect of habitat loss and change on waterbirds

Edited by J D Goss-Custard, R Rufino and A Luis

Institute of Terrestrial Ecology

UNIVERSIDADE de AVEIRO
Departamento de Biologia

ICN
Instituto da Conservação da Natureza

WETLANDS
INTERNATIONAL

The Stationery Office

ICN
Instituto da Conservação da Natureza

Institute of
Terrestrial
Ecology

WETLANDS
INTERNATIONAL

UNIVERSIDADE de AVEIRO
Departamento de Biologia

EFFECT OF HABITAT LOSS AND CHANGE ON WATERBIRDS

ITE Symposium no. 30
Wetlands International publication no. 42

Proceedings of
10th International Waterfowl Ecology Symposium
held at the University of Aveiro, Portugal
18–21 September 1995

Edited by
J D Goss-Custard, R Rufino and A Luis

Centre for Ecology and Hydrology

Natural Environment Research Council

London: The Stationery Office

ISBN 0 11 702171 7

Contents

Acknowledgements

Acknowledgements

This Symposium was jointly organised by the *Universidade de Aveiro* (UA) and the *Instituto da Conservação da Natureza* (ICN) for the Waterfowl Ecology Specialist Group of the International Waterfowl and Wetlands Research Bureau (now Wetlands International).

We would like to thank all those at ICN/Habitats and Ecosystems Division and at the UA/ Department of Biology who helped setting up this organisation, as well as Dr John Goss-Custard and Dr Janine van Vessem who provided the organising team with extremely valuable advice.

The *Fundação João Jacinto Magalhães* took care of the accounting as well as many other financial and organisational matters in a very smooth and efficient way, and we wish to thank all the staff members of the Foundation who were actually involved with this Symposium, and especially Dra Maria de Jesus Galaricha.

We wish to thank the *Junta Nacional de Investigação Científica e Tecnológica* (JNICT), which funded the organisation of this Symposium as well as the *Câmara Municipal de Aveiro*, the *Comissão Vitivinícola da Bairrada* and Mr Luis Pato for the wonderful wine reception at the Council Museum. We also thank the Institute of Terrestrial Ecology, Wetlands International and the Universidade de Aveiro for their financial contributions to these Proceedings.

Finally, we are extremely grateful for the tremendous amount of help and effort which Penny Ward and Karen Goodsir of the Institute of Terrestrial Ecology at Merlewood have put into producing this volume.

Introduction

J D Goss-Custard[1], R Rufino[2] & A Luis[3]

[1]Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset BH20 5AS, UK
[2]Instituto da Conservação da Natureza/CEMPA, Rua Filipe Folque 46 5°, 1050 Lisbon, Portugal
[3]Departamento de Biologia, Universidade de Aveiro, 3810 Aveiro, Portugal

The tenth International Waterfowl Ecology Symposium was held at the University of Aveiro, Portugal, on 18–21 September 1995. Arranging this triannual Symposium is the responsibility of the Waterfowl Ecology Specialist Group of Wetlands International (previously known as the International Waterfowl and Wetlands Research Bureau, IWRB). The Symposium was attended by almost 200 people from all parts of the world. Its success in attracting contributions meant that, for the first time in its history, the Symposium had to be subdivided for part of each day into parallel sessions. There was also a very large number of posters, with a prize being awarded to the one that, on the basis of delegate votes, was the most original, innovative and informative.

The Symposium covered many aspects of the ecology of waterbirds, but the majority at least touched upon the plenary theme. This theme was 'approaches to predicting the effects of habitat loss and change on populations of waterbirds and to detecting when populations have been affected'. This Proceedings volume contains many of the papers that, in a variety of ways, addressed this theme directly. In an attempt to benefit from the world-wide experience represented at the Symposium, we were particularly keen to include papers reporting attempts to make predictions before a loss of habitat or a habitat change had taken place. In these cases, authors were asked: 'With the benefit of hindsight, what research should we have done before the habitat was changed to have predicted what actually happened afterwards'. Several authors were able to answer this question, and their valuable experiences are reported here. However, many authors have not yet been able to test whether their expectations as to the effects of habitat loss and change have been realised. Their contributions describe a variety of studies designed to enable us to make better predictions in the future. The result is a series of papers which cover a wide range of issues relating to habitat loss and change across a variety of wetland habitats and species. As so many of the individual papers deal with several of the issues relating to the Symposium theme, we felt it was not helpful to force the papers into arbitrary groupings within these Proceedings. For this reason, papers are presented in alphabetical order of their senior author.

Restoration of wetland habitat in a Dutch dune reserve

G Baeyens, B W J Oosterbaan & L van Breukelen
Amsterdam Water Supply, Department of Research and Development, Vogelenzangseweg 21, 2114 BA Vogelenzang, The Netherlands

SUMMARY
The Dutch dune reserves of north and south Holland are artificially recharged with pretreated river water for drinking water production. In the Amsterdam Waterworks Dunes, the infiltration beds, seepage ponds and extraction canals originally attracted a large number of breeding ducks because:

- the food abundance was high due to the eutrophic character of the water;
- the food was accessible because ponds and banks were only sparsely covered with pioneer vegetation;
- predation pressure was relatively low.

From 1980 onwards, foxes colonised the area and caused a dramatic decrease in the waterfowl population. Slightly earlier, foraging opportunities had started to decline due to the encroachment of reed on ponds and banks. Especially filter-feeding species – shelduck, shoveler and teal – suffered from predation and also from a diminished food accessibility. Because the river water had been dephosphated from 1975 onwards, the biomass of macro-invertebrates in the recharge area dropped well below the level that is still present in the canals. This explains why the main species – mallard, tufted duck, pochard and gadwall – shifted their relative nesting preference from infiltration beds to canals. Moreover, foxes can more easily prey upon incubating females and their nests in infiltration beds, where water levels fluctuate strongly, than in canals, where water levels are maintained constant.

Without further measures, the Amsterdam Waterworks Dunes do not provide a rich wetland for breeding waterfowl. In the recharge area the feeding opportunities are rather low because of the mesotrophic water conditions, the reduced accessibility of food, and the food competition with fish. Due to the frequent water fluctuations, the foxes get excellent predation opportunities. In the area where only groundwater is extracted, the ecosystem is too desiccated for any waterfowl species to find suitable breeding sites. Therefore, the water catchment in one of the southern canals has been ended so that a restoration of moist and wet dune slacks can spontaneously follow the rising water table. In the recharge area, some of the banks of infiltration beds and seepage ponds are being rearranged and regularly stripped so as to encourage the re-establishment of pioneer vegetation. The hydrological regime will be adjusted as closely as possible to the natural seasonal water fluctuations. The fox population is deliberately not regulated.

INTRODUCTION

The Amsterdam Waterwork Dunes constitute a 3400 ha coastal dune reserve where drinking water production as well as nature conservation are the prime functions. Both tasks are accomplished by the Municipality of Amsterdam as the drinking water produced serves the Dutch capital. Nature management and ecological research are defrayed by the income from the drinking water which therefore provides a solid economic basis to nature preservation. However, the technical limitations imposed by the hydrological regime partly restrain the ecosystem from full natural development. Nevertheless, the unnatural surface of open water attracts a rich aquatic flora and fauna, including waterfowl. Gradually, the Amsterdam Water Board has grown aware of the nature value that can be promoted by water production.

From 1988 onwards, the Amsterdam Water Supply Company has conducted an eco-hydrological study into the interaction between drinking water catchment and nature conservation. Part of the study focuses on consoliding the wetland function of this dune reserve by the reallocation and rearrangement of water bodies. Waterfowl numbers – in this case the seven most common breeding duck species – are used as one yardstick of nature quality. The lessons

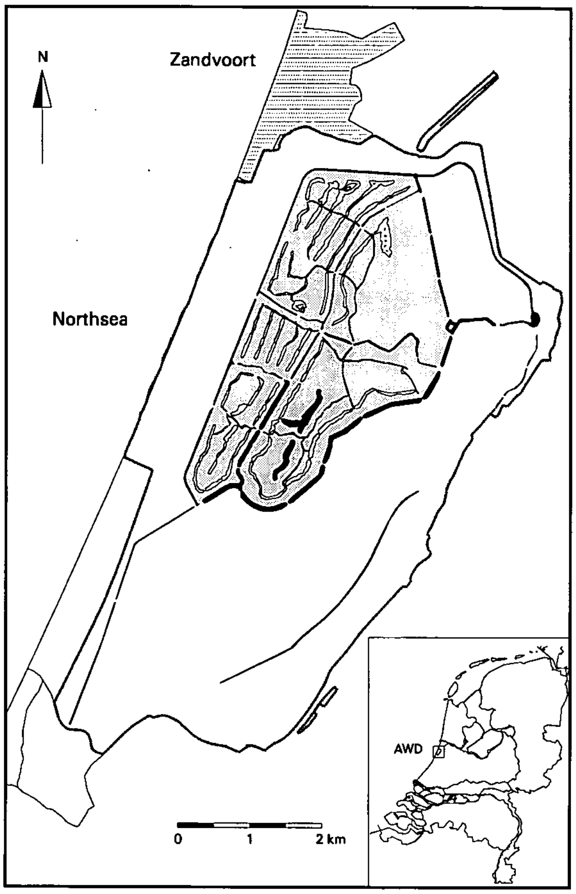

Figure 1. Map of the study area and location of the Amsterdam Waterwork Dunes in The Netherlands. The recharge area is shaded, canals are shown in black and infiltration beds in white

that have been learned enable us to formulate the predictions and goals for future management that are summarised in this paper.

SITE DESCRIPTION AND METHODS

The drinking water reservoir is fed by rainfall and by artificial recharge. For the latter, pretreated water from the River Rhine is stored in shallow infiltration beds. The percolating water is extracted by deep canals. The total surface of open water is 180 ha including up to 24 km of infiltration beds and 49 km of canals (Figure 1). Infiltration beds are 20–45 m wide and 1–3 m deep and their banks are smooth. Canals are 8–50 m wide and 1–8 m deep and their banks are either steep or smooth. Scattered throughout the recharge area are up to 50 seepage ponds, varying from 5 m^2 to 50 m^2 in surface and from 0.30 m to 1 m in depth. Water levels in the recharge area fluctuate weekly over a 5–90 cm range so that large parts of ponds and banks are intermittently flooded.

Each year on 15 May, all open water bodies are censused for waterfowl by volunteer bird-watchers. Vegetation succession is monitored by aerial false colour photography. Foxes (*Vulpes vulpes*) are monitored by mapping burrows and counting offspring. Fox pellets were analysed in 1984 and 1993 to define the dry weight of non-digestible food remains. Aquatic macro-invertebrates were sampled in 1990 by sweep net and a corer and were identified to species level; emerging water insects were caught in cylindrical tangle traps.

RESULTS

The numbers of individuals of seven duck species are given in Figure 2 for the breeding seasons from 1970 to 1993. The species are: mallard (*Anas platyrhynchos*), shelduck (*Tadorna tadorna*), shoveler (*Anas clypeata*), teal (*Anas crecca*), gadwall (*Anas strepera*), tufted duck (*Aythya fuligula*) and pochard (*Aythya ferina*). The populations seemed to be stable up to 1981 but, over the following five years, numbers dropped drastically. A new, much lower equilibrium seems to have developed since 1986. This local trend does not quite correspond with the national trend in The Netherlands between 1975 and 1990 (Meininger, Schekkerman & Van Roomen 1995), when the populations of all species, expect the pochard, either increased or stabilised.

The sudden decrease undoubtedly reflects a catastrophe which, in this case, was probably the expansion of the fox into the Dutch coastal dunes since 1980 and the consequent losses amongst ground-nesting bird species (Baeyens 1989). The proportion of the non-

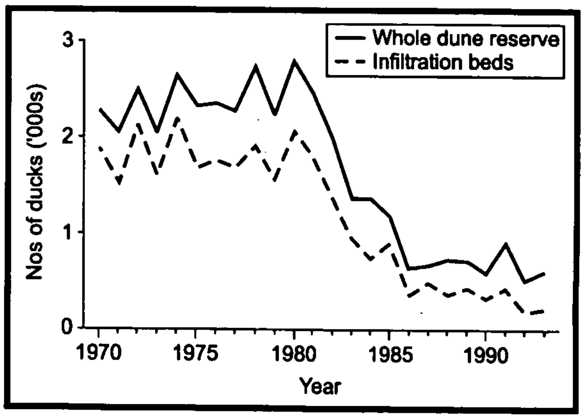

Figure 2. Numbers of seven duck species (see text) counted annually on 15 May on all open water surfaces in the Amsterdam Waterwork Dunes. The continuous line indicates the numbers added up for the whole dune reserve; the dotted line shows the numbers of individuals present in the infiltration beds

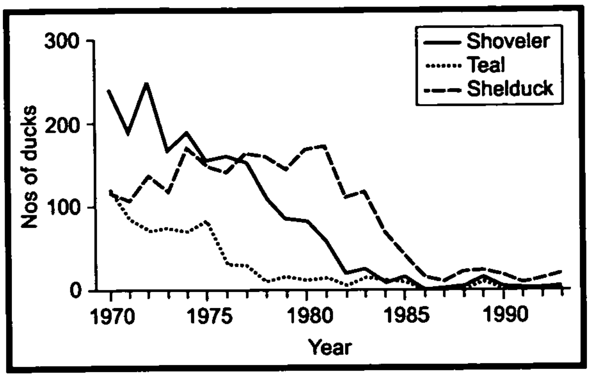

Figure 3. Numbers of shelduck, teal and shoveler counted annually on 15 May on all open water surfaces in the Amsterdam Waterworks Dunes

digestible dry weight remains that consisted of adult ducks was 5.4% in 1984 (Van der Vliet & Baeyens 1995) and increased to 6.4% in 1993, even though the number of ducks had fallen by 45%. The shelduck, which nests in rabbit burrows, is particularly vulnerable to fox predation and its numbers have so far not recovered (Figure 3). However, the numbers of teal had decreased five years before foxes colonised the dune reserve due to a botulism epidemic (Vader & Koning 1981).

Habitat changes also contributed to the reduction in duck numbers. Teal and shoveler disappeared gradually from the seepage ponds, their favourite habitat. Between 1963 and 1968, when the recharge area was designed, approximately 20.4 ha of seepage ponds had been created in the bare sand. Over the course of time, these became overgrown by reed (*Phragmites australis*), cattail (*Typha latifolia*) and sedges (*Carex* sp.). The result was that, by 1995, less than 5% of the original pond shoreline remained; this bordered a few large seepage ponds which constituted 23% of the original surface. Nowadays most of the ponds are fully covered reed beds, suitable for warblers but inaccessible to teal, shelduck and shoveler. Therefore, it seems that at least two factors have been responsible for the decrease in duck numbers: fox predation and a loss of foraging habitat.

There is also some evidence that, apart from the reduction in the accessibility of food caused by the spread in vegetation, the abundance of food in the accessible areas that remained may also have gradually decreased. At the beginning of the recharge process, river water was let in with its original load of phosphates (±0.70 mg PO_4 l^{-1}). Since 1975 the water has been dephosphatised, current levels being reduced by more than 90% (van Dijk 1984). In the years prior to dephosphating, the biomass of macro-invertebrates must have been many times greater than it is at present. Birdwatchers mentioned that, apart from the massive bloom of algae, the underwater bottoms were reddish coloured by thousands of chironomid larvae. Nowadays, chironomid larvae can hardly be found (de Bokx 1991). The total biomass of macro-invertebrates in canals far exceeds the biomass in the infiltration beds (Figure 4), probably because the phosphate loads are higher in the canals (0.08–0.16 mg P l^{-1} compared with 0.03 mg P l^{-1}). The densities of emerging insects were also higher in the canals (120.25 individuals per sample) than in the infiltration beds (83.50) and seepage ponds (29.55). In particular, the percentage of Chironomidae that emerged was higher (83%) from canals than from infiltration beds (39%) and seepage ponds (43%) (Huitema 1991).

The changed amounts of animal food partly explain the changes in the pattern of fledgling movement that has taken place from the infiltration beds to the canals. Between 1980 and 1990, breeding success in the recharge area was virtually zero but, since 1990, the most abundant species – mallard, gadwall and tufted duck – have been able to fledge young again (van der Valk 1994). Apparently, the breeding pairs learned to hide their nests from foxes by taking advantage of the large reed beds which colonised the shorelines. As soon as the eggs hatch, many broods now leave the recharge

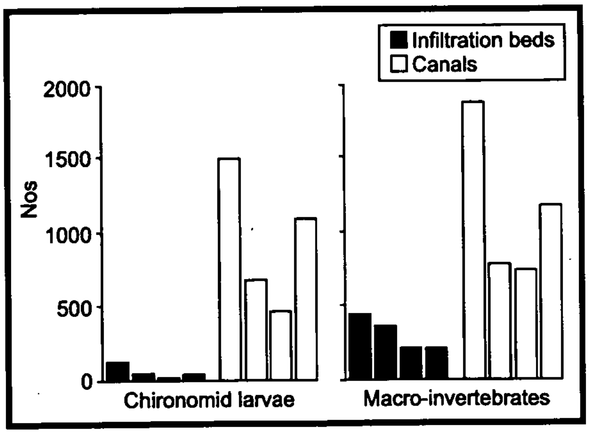

Figure 4. Numbers of chironomid larvae (left) and of all macro-invertebrates, including chironomids, (right) in samples from infiltration beds and canals in 1990

Table 1. Influence of some environmental factors on duck populations in time and space

	1970–79		1980–89		1990–now	
	Recharge area	Canals	Recharge area	Canals	Recharge area	canals
Nesting opportunity	↑	↑	↑↑	↑↑	↑↑	↑↑
Foraging opportunity	↑↑	↑	↓	↑	↓	↑
Food abundance	↑↑	↑	↓	↑	↓	↑
Predation pressure	–	–	↓↓	↓↓	↓↓	↓

– = absent; ↓=disadvantageous; ↓↓=detrimental; ↑=supportive; ↑↑=beneficial

area in search of the nearest canals where the young can forage until they are fully grown. Furthermore, it can be deduced from Figure 2 that the proportion of ducks breeding in the infiltration beds has gradually decreased. Between 1970 and 1975 this proportion sometimes exceeded 80%, whereas, in the latest counts, it has dropped well below 50%. The changing preference from infiltration beds to canals may correlate with the change in relative food abundance.

CONCLUSIONS

In summing up, we consider the recharge area (+ infiltration beds + seepage ponds) and the extraction canals separately and refer the readers to Table 1 which summarises the recent ecological history of the site. Initially (1970–79) nesting opportunities were present everywhere in the grass- or shrub-covered banks. Because of an undisturbed vegetation succession, large reed beds developed and provided even more nesting space close to the water. However, vegetation succession also entailed a decrease in foraging opportunities in the shallow areas. By reducing the water phosphate load, food abundance decreased in the recharge area while remaining constant in the canals. Prior to this, the phosphate load, and hence the trophic level in the recharge area, had been unnaturally high. Before dephosphating took place, duck numbers had artificially exceeded the levels that are typical for a natural dune ecosystem (Baeyens & Vader 1990). Moreover, predation pressure was exceptionally low because the formerly indigenous fox had been heavily hunted (Mulder 1990). After having been made temporarily extinct, the fox population peaked in the 1980s and stabilised later. In the recharge area, however, fox predation pressure remains high as a result of the unnatural hydrological regime. When the water level is at a high or an intermediate level, foxes can hardly penetrate the vegetation on the banks. When the water level drops, the exposed sand bank provides an easy pathway for foxes. Footprints then reveal how foxes systematically explore the shoreline, and the observations are consistent with the still relatively high numbers of duck remains in fox pellets.

The infiltration beds and seepage ponds in the recharge area have become less and less favourable in comparison with the extraction canals. Those canals which are used for water storage (the wider canals in Figure 1) in particular provide a relatively good breeding habitat for the main species – mallard, tufted duck, gadwall and pochard. There are ample nesting opportunities, the water level is constant, so decreasing the risk of predation, and the food is abundant and accessible. The banks are, however, too steep for shoveler, teal and shelduck. For these three species, the wetland function of the dune reserve has become a disadvantage.

DISCUSSION

The impact of the food supply, foxes and landscape succession on breeding waterfowl numbers has been similar in all coastal dunes where artificial recharge was set up for drinking water production (Baeyens & Vader 1990). Trends differ only slightly, and in accordance with the particular environmental factors. Thus, shelduck numbers did not decrease in a recharge area where foxes were still shot. In all five recharge areas in north and south Holland, the high breeding densities in the 1960s and early 1970s can be explained by the high trophic levels that preceded the purification of the river water (van Tol 1979; Schekkerman 1991). Eutrophication, and hence high densities of macro-invertebrates (Chironomidae), are known to increase waterfowl breeding densities (Joyner 1980; Kaminski & Prince 1981a; Håland 1983; Siira & Eskelinen 1983; Fox 1986; Murkin & Kadlec 1986). In the recharge areas, an additional benefit resulted from the maintenance of the infiltration beds where every four or five years the bottoms were scraped to improve permeability. This technical measure decreased food abundance only temporarily but, for many years, prevented fish populations from becoming established; fish preying on macro-invertebrates can be severe food competitors for ducks (Kaminski & Prince 1981b; Eriksson 1983; Pehrsson 1984; Wright & Street 1985). This competition between ducks and fish was suppressed until dephosphatisation in 1975, after which the bottom-scraping became unnecessary. Since 1977, the infiltration ponds have also been used by great crested grebes (*Podiceps cristatus*), which indicates the continuous presence of fish. Canals, by contrast, were colonised by grebes earlier, from 1973 onwards.

The carrying capacity of the dune area for waterfowl could be assessed by measuring waterfowl productivity because breeding success is influenced directly by macro-invertebrate, especially chironomid, biomass (Bengtson 1971; Street 1977; Danell & Sjöberg 1982; Talent, Krapu & Jarvis 1982; Hill & Ellis 1984) and indirectly by fish (Pehrsson 1979; Phillips & Wright 1993). Unfortunately, no data on fledgling production are available from the period before 1975, although Schekkerman (1991) reported from one other recharge area that fledglings were numbered in thousands before the dephosphatisation whereas nowadays they are numbered in tens. A diminishing food supply as well as an increasing predation pressure together account for the lower breeding success.

Studies of the selection of vegetation types by nesting waterfowl revealed that most species prefer a dense cover of tall grasses and herbs, bordering or interspersed with shallow open water (Haapaanen & Nilsson 1979; Kaminski & Prince 1981a, b; Nummi & Pöysä 1995). Danell and Sjöberg (1982) followed successional patterns of vegetation along with those of ducks and found that teal, especially, react positively to the pioneer plant stages but disappear as vegetation cover reaches a maximum. It could thus be predicted that the filter-feeding duck species would abandon the Dutch dune reserves as long as the encroachment by reed into ponds and banks proceeds.

In the Amsterdam Waterwork Dunes mammalian predators seem to limit duck breeding density more than avian predators. As predation is likely to be density-dependent (Hill 1984; Sargeant, Allen & Eberhardt 1984), one would expect that the percentage of duck remains in fox pellets would have been lower in 1993 than in 1984. As expected (Hill & Ellis 1984), predation during egg-laying and incubation, from late April to mid-May, was lower in 1993 than in 1984 when breeding density had been decreased. However, when fox predation is considered over the whole research period, from February until the end of August, predation was actually higher in 1993 for reasons that are not fully understood.

IMPLICATIONS FOR MANAGEMENT

The simple identification of causal mechanisms has not yet provided a clear-cut tool for dune management. The conclusions from considering landscape succession, fox density and waterfowl numbers help to pinpoint the unnatural impact of drinking water production in a dune reserve but do not dictate natural goal values. Certainly, it is not the manager's purpose only to maximise the abundance of one single species or one group of species. Dune-managing water companies aim to achieve a complete, well-balanced and sustainable coastal ecosystem in which water production and other public functions are only encouraged when they are compatible with nature preservation. This involves a compromise in which nature development is not impeded but reinforced by the other functions. In this study, only the production of drinking water is considered as coastal defence and tourism either do not or hardly affect the wet parts of the dune.

By comparing breeding habitats over time (1970–90) and space (recharge area – canals), some guidelines for optimising the wetland function of the Waterwork Dunes can be formulated.

- Trophic levels of the water bodies should be maintained as low as possible because dune lakes are naturally oligotrophic or mesotrophic.

- Competition with fish should be regarded as a natural phenomenon. A well-structured mosaic of submerged vegetation interspersed with stands of emergent hydrophytes provides sufficient food and foraging opportunities for adult waterfowl as well as ducklings, and thereby offsets the worst effects of food competition.

- Bearing in mind the role of fish, the recent establishment (1994) of a cormorant colony (*Phalacrocorax carbo*) will be monitored for its effect on other fish-eating birds and on macro-invertebrate densities.

- Canal banks will be or are already made smooth to facilitate nesting and to connect nesting habitat with feeding habitat.

- The banks of infiltration beds and seepage ponds will be, or are already, partly rearranged to stimulate pioneer vegetation so as to enlarge floral and animal richness. The pioneer stages of bank vegetation are, or will be, stripped regularly, thereby encouraging the filter-feeding duck species to recolonise the area. Waders have already responded positively to these measures.

- The hydrology of the recharge area is now subject to a micro-scale study to adjust the demands of water production to nature requirements. The approximation of the natural fluctuation patterns will not only benefit plants and waterfowl but also the entire community of aquatic insects. This in turn enables the development of bat populations (Huitema 1991).

- A more natural hydrological regime will stabilise the predation pressure of foxes. The fox population is deliberately not regulated by man.

- The extraction of groundwater will be partly diminished and the water table will locally rise to its former level. The canal in the bottom left of Figure 1 (south-west of the dune reserve) has been filled up with the original sand, thus restoring the natural geomorphology. According to the hydrological predictions, restoration of moist and wet dune slacks is quite possible (Geelen, Cousin & Schoon 1995). Ending drinking water production in some parts of the dune reserve is compensated by storage and catchment elsewhere in the aquifers. Fifty per cent of the funds for such an elaborate project were provided by government subsidies and incentives. Reducing the desiccating effects of dune water catchment is a major concern in Dutch environmental policies, and waterfowl can only benefit from that.

REFERENCES

Baeyens, G. 1989. Wildlife management in Dutch coastal dunes. In: *Perspectives in coastal dune management*, edited by F. van der Meulen, P.D. Jungerius & J.H. Visser, 111–119. The Hague: SPB Academic Publishing bv.

Baeyens, G. & Vader, H. 1990. Aantalsontwikkelingen van eenden in drie duinwaterwingebieden. In: *Natuurwaarden en waterwinning in de duinen; mogelijkheden voor behoud, herstel en ontwikkeling van natuurwaarden*, edited by W. Koerselman *et al. KIWA-mededeling*, **114**, 103–118.

Bengtson, S.A. 1971. Variations in clutch size in ducks in relation to the food supply. *Ibis*, **113**, 523–526.

Bokx, E.M. de. 1991. *Macrofauna en kuifeenden in de Amsterdamse Waterleidingduinen*. Amsterdam: Amsterdam Water Supply.

Danell, K. & Sjöberg, K. 1982. Successional patterns of plants, invertebrates and ducks in a man-made lake. *Journal Applied Ecology*, **19**, 395–409.

Dijk, H.W.J. van. 1984. *Invloeden van Oppervlakte-Infiltratie ten behoeve van Duinwaterwinning op Kruidachtige Oevervegetaties*. PhD thesis, Agricultural University of Wageningen.

Ehrenburg, A. 1990. *Stofbalansen van de Amsterdamse Waterleidingduinen*. Amsterdam: Amsterdam Water Supply.

Eriksson, M.O.G. 1983. The role of fish in the selection of lakes by non-piscivorous ducks: mallard, teal and goldeneye. *Wildfowl*, **34**, 27–32.

Fox, D.M. 1986. The breeding teal (*Anas crecca*) of a coastal raised mire in central west Wales. *Bird Study*, **33**, 18–23.

Geelen, L.H.W., Cousin, E.F.H. & Schoon, C.F. 1995. Regeneration of dune slacks in the Amsterdam Waterwork Dunes. In: *Directions in European coastal management*, edited by M.G. Healy & J.P. Doody, 525–532. Cardigan: Samara Publishing Limited.

Haapaanen, A. & Nilsson, L. 1979. Breeding waterfowl populations in nothern Fennoscandia. *Ornis Scandinavica*, **10**, 145–219.

Håland, A. 1983. Home range use and spacing in mallard *Anas platyrhynchos* broods. *Ornis Scandinavica*, **14**, 24–35.

Hill, D.A. 1984. Clutch predation in relation to nest density in mallard and tufted duck. *Wildfowl,* **35,** 151–156.

Hill, D.A. & Ellis, N. 1984. Survival and age related changes in the foraging behaviour and time budget of tufted ducklings *Aythia fuligula. Ibis,* **126,** 544–550.

Huitema, H. 1991. *Watervleermuizen* (Myotis daubentonii) *in de Amsterdamse Waterleidingduinen; jachtbiotoopkeuze in relatie tot insektenaanbod.* Amsterdam: Amsterdam Water Supply; Groningen: State University of Groningen.

Joyner, D.E. 1980. Influence of invertebrates on pond selection by ducks in Ontario. *Journal of Wildlife Management,* **44,** 700–705.

Kaminski, R.M. & Prince, H.H. 1981a. Dabbling duck activity and foraging responses to aquatic macroinvertebrates. *Auk,* **98,** 115–126.

Kaminski, R.M. & Prince, H.H. 1981b. Dabbling duck and aquatic macroinvertebrates responses to manipulated wetland habitat. *Journal of Wildlife Management,* **45,** 1–15.

Meininger, P.L., Schekkerman, H. & Van Roomen, M.W.J. 1995. Population estimates and 1%-levels for waterbird species occurring in The Netherlands: suggestions for standardisation. (Dutch with English summary.) *Limosa,* **68,** 41–48.

Mulder, J.L. 1990. The stoat *Mustela erminea* in the Dutch region, its local extinction, and a possible cause: the arrival of the fox *Vulpes vulpes. Lutra,* **33,** 1–21.

Murkin, H.R. & Kadlec, J.A. 1986. Relationships between waterfowl and macroinvertebrate densities in a northern prairie marsh. *Journal of Wildlife Management,* **50,** 212–217.

Nummi, P. & Pöysä, H. 1995. Breeding success of ducks in relation to different habitat factors. *Ibis,* **137,** 145–150.

Pehrsson, O. 1979. Feeding behaviour, feeding habitat utilization and feeding efficiency of mallard ducklings (*Anas platyrhynchos* L.) as guided by a domestic duck. *Vittrevy,* **10,** 193–218.

Pehrsson, O. 1984. Relationship of food to spatial and temporal breeding strategies of mallards in Sweden. *Journal of Wildlife Management,* **48,** 322–339.

Phillips, V.E. & Wright, R.M. 1993. The differences in behaviour and feeding success of tame mallard ducklings *Anas platyrhynchos* in the presence of high and low fish populations at a gravel pit site, with reference to wild brood distribution. *Wildfowl,* **44,** 69–74.

Sargeant, A.B., Allen, S.H. & Eberhardt, R.T. 1984. Red fox predation on breeding ducks in midcontinent North America. *Wildlife Monographs,* **89,** 1–41.

Schekkerman, H. 1991. De broedvogels van het infiltratiegebied Castricum (1): aantalsontwikkelingen van het waterwild in 1961–1990. *Winterkoning,* **26,** 3–23.

Siira, J. & Eskelinen, O. 1983. Changes in the abundance of breeding waterfowl in the Liminka Bay in 1954 – 1981. *Finnish Game Research,* **40,** 105–121.

Street, M. 1977. The food of mallard ducklings in a wet gravel quarry, and its relation to duckling survival. *Wildfowl,* **28,** 113–125.

Talent, L.G., Krapu, G.L. & Jarvis, R.L. 1982. Habitat use by mallard broods in south central North Dakota. *Journal of Wildlife Management,* **46,** 629–635.

Tol, J. van. 1979. Een onderzoek naar de populatie-oecologie van de kuifeend in het bijzonder in het gebied van de DWL's-Gravenhage. *Meijendel Mededeling,* **7,** 18–24.

Vader, H. & Koning, F.J. 1981. Kunstmatige duinmeren als broedgebieden voor watervogels. *Watervogels,* **6,** 148–159.

Valk, R. van der. 1994. *Verslag onderzoek broedvogelstand in het eerste infiltratiegebied van de Amsterdamse Waterleidingduinen in 1993 en 1994.* Personal report.

Van der Vliet, F. & Baeyens, G. 1995. *Voedsel van vossen in de duinen: variatie in ruimte en tijd.* Amsterdam: Amsterdam Water Supply; Utrecht: Association for Zoology and Mammal protection VZZ (mededeling 29).

Wright, R. & Street, M. 1985. The influence of fish on the survival of wildfowl broods. *Game Conservation Annual Review,* **1016,** 77–80.

Predicting the effects of habitat loss and change on estuarine birds: are we asking the right questions?

L Batty

Department of Countryside Management, Bishop Burton College, Beverley, East Riding of Yorkshire HU17 8QG, UK
Present address: 28 Laughton Rd, Beverley, East Riding of Yorkshire HU17 9JR, UK

SUMMARY
There is a tendency to view all habitat change, whether resulting from natural or anthropogenic sources, as having a negative impact on bird populations. Using the Humber estuary as an example, this paper argues that disturbance and change are natural features which are important for the maintenance of estuaries and their bird populations. Human activities have restricted the ability of estuaries to respond to environmental changes such as sea level rise, but managed retreat offers the opportunity for returning estuaries to their natural dynamics. Environmental impact predictions need to discriminate between the results of natural and anthropogenic change and to consider the positive impacts of environmental change on estuarine birds.

WHAT DO WE MEAN BY HABITAT LOSS AND CHANGE?

It is in the interests of bird conservation to be able to predict the consequences of habitat loss and change arising from development proposals. This information is needed for environmental impact assessments, public inquiries and conservation planning. In relation to wetland sites of international importance, the Ramsar Convention requires contracting parties to monitor changes in the 'ecological character' of sites which result from anthropogenic sources. However, Dugan and Jones (1993) point out that 'there has been no clear definition of what is meant by change in ecological character'. Accordingly they have defined ecological change as 'alteration of the biological and/or physical components of the ecosystem, and/or the interaction between them, in a manner which results in a reduction in the quality of those functions, products and attributes which give the wetland value to society'.

Two points should be noted in relation to this definition.

i. Dugan and Jones (1993) have defined ecological change only in terms of perceived adverse or negative impacts. Elsewhere in their paper they also recognise that ecological change could enhance ecological value, but they do not include this in their definition. Anon (1993), writing in the same volume, recommends the use of other words (eg restoration) for positive impacts.

ii. Change also takes place in wetlands as a result of natural processes. In estuaries there are habitat changes resulting from geomorphological processes; saltmarsh growth and decay; sand dune dynamics; the mobility of intertidal flats; and plant succession on shingle banks. Dugan and Jones (1993) recognise that the alterations included in their definition could be a result of both human action and natural processes.

A key requirement for impact assessment studies is that of describing the baseline conditions. Such baseline information should include information on natural changes that are likely to occur without the proposed development (eg Royal Society for the Protection of Birds 1995). However, there is a tendency amongst conservationists to view even natural change with alarm. Prater (1981), for example, in considering threats to estuary birds, includes 'many natural changes taking place, some for the benefit of birds while others can be detrimental'. There is an assumption that some ideal natural feature or wildlife community is to be achieved and preserved indefinitely and that we should manage ecosystems to prevent change. Indeed, English Nature (1993) has stated that its overall objective for the coast is 'the maintenance of coastal habitats and natural features at a level equivalent to their 1992 distribution and in a sustainable condition'. However, although some ecosystems may be relatively changeless, estuaries are not, and efforts to preserve the *status quo* can only lead to frustration. Warren (1993) has classified estuarine habitats as 'r-landscapes' or 'landscapes that favour r-selected species' and described them as depending on disturbance for their existence. Describing the Virginia Coast Reserve, USA, Hayden *et al.* (1991) refer to both succession and disturbance as being fundamental, essential processes which are necessary for the maintenance of coastal ecosystems.

The aim of this paper is to show, with particular reference to the Humber estuary, that:

- change is a natural feature of estuaries;
- estuarine birds are adapted to a changing environment;
- it is therefore necessary, though often difficult, to separate natural from anthropogenic change when making predictions;
- we should pay more attention to predicting the positive effects of habitat change.

A CASE STUDY – HABITAT LOSS AND CHANGE IN THE HUMBER ESTUARY

Introduction

The Humber (Figure 1) is situated on the east coast of England and is one of the largest estuaries in Britain, draining one fifth of the land area of England. It is more than 50 km in length and has one of the largest tidal ranges in the world (over 7 m). The tidal area is more than 30 000 ha, including 11 900 ha of tidal flats and 1420 ha of saltmarsh (8.6% of the intertidal area). The saltmarshes were previously much more extensive and merged into freshwater wetlands and coastal grasslands.

The estuary is listed as a Wetland of International Importance under the Ramsar Convention and has been designated as a Special Protection Area under the terms of the European Community Directive 79/409/EC on the Conservation of Wild Birds. It is the fourth most important estuary for wintering waterfowl in the United Kingdom, and is home to several important breeding species.

A general history of the estuary

The original estuary is represented by the inner Humber which entered a large marine bay at the position of the Humber Bridge, 100 000 years ago, and was about 40 km shorter than at present (Institute of Estuarine and Coastal Studies (IECS) 1994a). As the Devensian ice sheet advanced southwards across the region, about 50 000 years ago, it filled the bay with boulder clay deposits and dammed the estuary mouth. As the ice retreated at the end of the glaciation, from

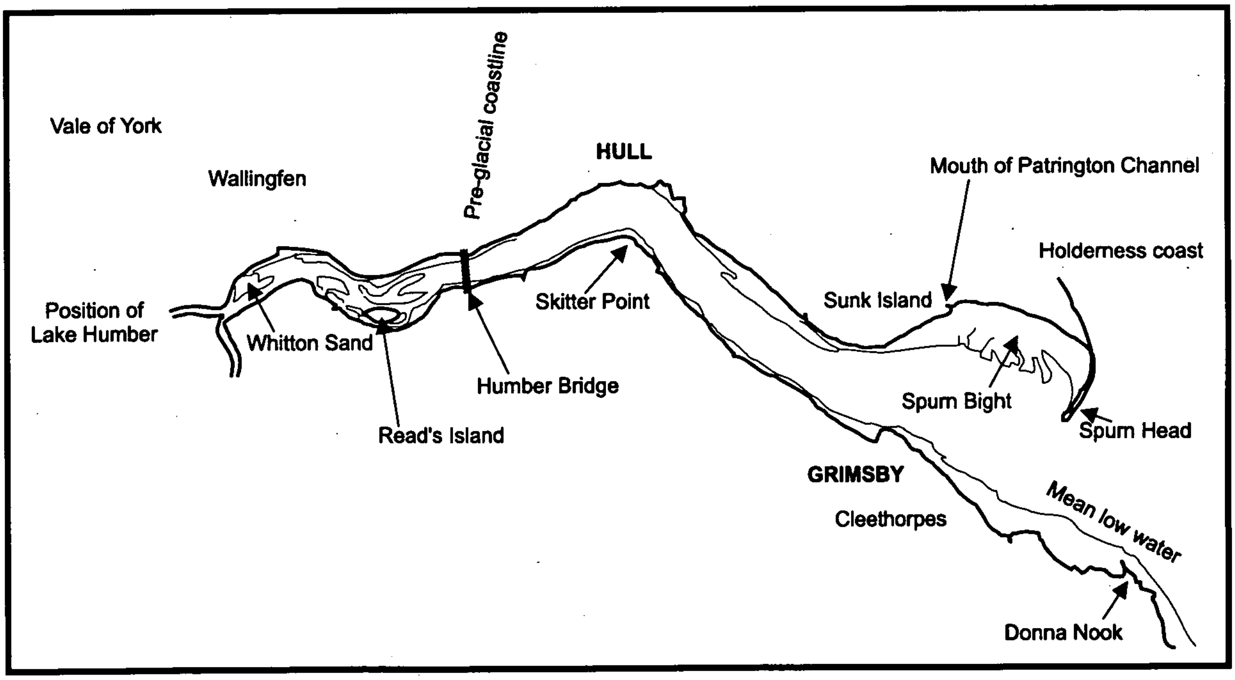

Figure 1. *The Humber estuary*

about 14 000 years BP, the waters that had been dammed up in the Vale of York poured across the boulder clay deposits as a non-tidal river cutting itself a deep valley through these deposits. As sea level rose, following the melting of the ice sheets, sea water began to enter the river, beginning around 9000 years BP and finally flooding the river valley to reform an estuary in the period 7000–6000 years BP (IECS 1994a). The outer part of the present estuary, from the Humber Bridge to Spurn, is therefore only about 6000 years old. However, the sea level in about 6000 BP was still approximately 5 m below present levels and the upper estuary was not directly tidal. Modern sea levels were only reached about 3000 years BP. Since then there have been fluctuations (transgressions) of up to 1–2 m above the present level caused both by land sinking and sea rising, resulting in considerable alterations in the extent of intertidal habitats (IECS 1994a).

Originally the Humber was a complex estuary, but infilling of sand and mud plus the reclamation of saltmarshes during the last 2000 years has produced the classic trumpet shape of the estuary as a response to tidal hydraulics (IECS 1994a; Pethick 1984). Since the 17th century 33% (6400 ha) of the estuary's saltmarsh has been reclaimed behind sea walls. Before then there was a limited amount of reclamation, but areas of the Wallingfen, adjacent to the upper estuary, are known to have been drying out naturally during the 13–15th centuries (Sheppard 1958).

Changes in the inner estuary

Because of its age, the morphology of the inner estuary appears to have had a sufficiently long period of adjustment to assume its stability, and there is net sediment deposition. Nevertheless, it is characterised by extremely rapid channel movements, and during the period 1980–91 the main channel swung across the entire width of the estuary. There has been a dramatic loss of saltmarsh along the eastern section of the north bank during the past 20 years, but this has been balanced by the development of new saltmarsh on a large mud bank – Whitton Sand. Read's Island, on the south side of the estuary, was a small mud bank in the mid-19th century, when it was 'reclaimed'. It suffered erosion between 1950 and 1992 when the main channel flowed around it, but is now accreting as the main channel has moved northwards (IECS 1994a).

Changes in the outer estuary

Although the morphology of the outer estuary has quickly adapted to tidal conditions, there has not been sufficient time for it to reach a hydrodynamically stable form (IECS 1994b). Sedimentation resulted in an overall reduction of 14% in the width of the outer estuary during the period 1851–1966, compared with a greater reduction in the inner estuary (Pethick 1990). Pethick (1990) argues that the present mouth of the estuary is several kilometres wider than the equilibrium width, suggesting that Spurn Bight is a permanent feature which should continue to accrete. However, there are two areas where the estuary is narrower than equilibrium width – at Sunk Island and at Skitter Point. Reclamation of 10 km^2 of Sunk Island between 1675 and 1970 (IECS 1987) and the resulting narrowing of the channel have produced higher velocities and erosion of the banks and bed as the estuary 'attempts' to regain its wider cross-section (IECS 1994a). This erosion is especially serious along the south bank.

The area between Cleethorpes and Donna Nook in the mouth of the estuary is protected by an offshore boulder clay ridge which formed an island chain before the 13th century. Since the Iron Age (*ca* 2000 years BP) the coast has advanced up to 10 km as a result of a combination of dyking, reclamation and natural accretion (IECS 1994a).

Guarding the northern entrance to the Humber is the Spurn peninsular. The northern end of this peninsular was once composed of shingle, and storm washovers moved the shingle bank inwards, enabling Spurn to keep up with the line of the eroding Holderness coast. In the 18th and 19th centuries shingle was removed by the bargeload to be sold as ballast for whalers sailing out of the ports of Hull and Grimsby, and this led to the breaching of the peninsular between 1849 and 1851 (IECS 1994a). It was repaired with groins, rock infill and other coastal engineering techniques which encouraged sand dune development and lasted for about 100 years. However, the protection of Spurn has resulted in its protruding beyond the natural line of the Holderness coast. The defences now need repairing and serious erosion is taking place, but the management policy is to allow the peninsular to return to being controlled by natural processes, moving west with the coastline as a result of erosion of the sea coast and accretion of the estuarine side.

Sea level changes

In historical times sea level reached its lowest level around 1200 AD, rising rapidly again towards the beginning of the 14th century (de Boer 1970) but, for the last 100 years, sea levels have been rising at an increasing rate owing to both isostatic and eustatic changes, including the effects of global warming. In the Humber there has been a relative sea level rise of 3.5 mm yr^{-1} over the last 50 years, as a combined result of isostatic lowering of the land and eustatic increase in sea level, which, if it continued at that rate, would result in a rise of 19.2 cm by the year 2050 (IECS 1994a), the isostatic component being around 2 mm yr^{-1}. However, if we take into account the effects of global warming, we have a predicted relative sea level rise of 6–15 mm yr^{-1} by the year 2030, resulting in a level 0.5 m higher than at present by 2050 (IECS 1994a, b).

Rising sea levels increase wave and tidal energy in the estuary so that landward movement of the intertidal zone should take place as a result of the erosion of intertidal flats and saltmarsh and the inundation of supratidal habitats. Unfortunately, the shoreline of most of the Humber estuary is almost entirely protected by a flood embankment, which restricts the landward movement, so that the intertidal zones become 'squeezed' between rising sea level and the flood embankments, resulting in loss of intertidal area.

Theoretically, sediment deposition should keep up with rising sea level, as has happened in other east coast estuaries. However, evidence suggests that this is not the case in the Humber (IECS 1994a), or, for example, along the southern North Sea coast (Siefert 1990). As a result of analysing charts of the Humber, IECS (1994a) has shown that the estuary 'entered a phase of environmental deterioration' about 40 year ago, with a change from accretion to long-term erosion of the intertidal zone. Sea level rise in the Humber is one of the most rapid in the country, and consequently there are increased risks of flooding over large areas of land and large centres of human population.

If sediment deposition is not able to keep up with rising sea level, the likely reason is that there is a shortfall in the supply of sediment. This 'sediment starvation' could be a result of (IECS 1994a, b):

- reduced erosion of the Holderness coast because of sea defences;
- the dredging which takes place in the outer estuary, and which may intercept sediment entering the estuary;
- a possible reduction in the suspended sediment in the North Sea for reasons unknown; and/or
- the delayed effect of the reclamation of Sunk Island.

Conclusion

We have seen that there have been changes in the 'ecological character' of the estuary so that the Humber as we know it today is the result of changes arising as a result of both natural processes and human agency. Current human pressures on the estuary include wharf development and port expansion, but the problem of sea level rise is the result of natural processes responding to a mixture of natural and human-induced changes.

We have seen that change is necessary for the maintenance of Spurn peninsular; interference with the natural processes of change has produced problems for the peninsular and its management. In the face of sea level rise, the estuary may be able to maintain its habitats if it were allowed to change its form, but this is currently prevented by flood defences.

We have also seen that the effects on the estuarine system of land claim may not be evident for many years. We may then be faced with the problem of deciding whether the cause of observed changes is natural long-term geomorphological adjustment or delayed adjustment to anthropogenic change, or both. In the case of effects resulting from sea level rise, how much of the rise is due to man-induced global warming and how much to natural eustatic and isostatic changes?

HOW DO ESTUARINE BIRD POPULATIONS RESPOND TO HABITAT LOSS AND CHANGE?

Estuarine birds have a long history of change and they respond by changing population sizes and changing sites.

Hale (1984) suggests that, at the height of the Devensian glaciation (about 50 000 years ago), breeding populations of knot (*Calidris canutus*), sanderling (*Calidris alba*), dunlin (*Calidris alpina*), turnstone (*Arenaria interpres*) and bar-tailed godwit (*Limosa lapponica*) were larger than at any other period, because their tundra habitat (in central Europe, Russia and eastern Siberia) covered a larger area than at any other time. The Humber was not active as an estuary during this period, and the only estuaries available for non-breeding waders were in southern Europe and north Africa. These therefore had to accommodate winter populations higher than on the more extensive system now in existence. Consequently, present winter populations are probably well below the carrying capacity of the total estuary stock available (Hale 1984).

Immediately following the end of the glaciation, as sea level began to rise, the Humber and other new estuaries would have lacked the extensive mudflats of mature estuaries (Hale 1984). As an estuary matures, it develops sand banks and mudflats so the pattern of use by wading birds changes. In time the intertidal flats may grow higher and drier at low tide and become less suitable for several species which then have to move elsewhere. This development is shown dramatically by the situation on the Ribble estuary, where saltmarsh extended over 800 m in ten years at the end of the last century (Hale 1984). However, in the long term, sea level changes may be causing the development of new mudflats in other estuaries. At the same time as estuaries in eastern England are losing intertidal habitats as a result of sea level changes, a number of estuaries in Wales and NW England are gaining ground through a combination of accretion and isostatic uplift (Davidson *et al.* 1991).

We have already seen how Warren (1993) has classified estuarine habitats as 'r-landscapes' or landscapes that favour 'r-selected species', and Hayden *et al.* (1991) have described how ecosystem disturbance in the Virginia Coast Reserve is necessary for maintaining breeding habitat for those bird species that need areas of open, active sand. The little tern (*Sterna albifrons*) is an interesting example on the Humber of one of these species. Its breeding habitat normally consists of bare shingle or sand, very close to normal tide or flood limits. It sometimes nests amongst sand dunes, or on dry mud, but normally in areas clear of vegetation. Disturbance on open beach habitats has forced little terns at Spurn to nest in an open area amongst sand dunes. An intensive protection scheme has been very successful in building up the size of the colony and allowing birds to nest. However, predation by foxes (*Vulpes vulpes*), carrion crow (*Corvus corone*) and merlin (*Falco columbarius*) has still been a serious problem, leading to total or substantial failure in most years. Sears and Avery (1993) point out that little terns may be adapted to move site when faced with problems of predation or flooding, so their breeding strategy and success depend at least partly on the provision of unvegetated, ephemeral habitats. It seems that, whilst our present management strategy for little tern is maintaining breeding colonies in an artificially stable situation within nature reserves, the species requires a number of alternative nesting sites to which the colony can move or amongst which it can disperse, forming a number of smaller colonies that ensures that some colonies will be successful. The supply of such a stock of open unvegetated areas away from predators depends on coastal geomorphological change.

WHAT QUESTIONS SHOULD WE BE ASKING?

So, if estuaries are dynamic systems and estuarine birds depend on disturbance to maintain their habitats, what should we be researching and predicting?

To begin with, we have seen that estuaries are being limited in the extent to which they can respond to disturbance. Changes are taking place in estuaries as a result of reclamation and sea level rise which are disturbing their equilibrium and leading to erosion of intertidal flats, saltmarshes and sea walls. A study by Burd (1992) showed that the estuaries of Suffolk, Essex and north Kent lost 10–44% of their saltmarsh between 1973 and 1988–91, more of this being due to erosion than reclamation.

Reclamation of shallow intertidal areas effectively increases the mean depth of the estuary but reduces its width. The result is an increase in tidal propagation and range, as well as increasing wave action on the estuary shore (including the flood embankments). A new equilibrium can only be reached by sediment deposition which will decrease the depth of the estuary. This sediment demand can only be satisfied by erosion of the banks or import from beyond the estuary. In the Humber this sediment demand cannot currently be satisfied and the situation may deteriorate further as sea level continues to rise (Humber Estuary Management Strategy 1996).

Management options for the Humber have been suggested by IECS (1994b).

- Dredged spoil taken from the mouth of the estuary should be reintroduced into the estuary.
- Coastal defence strategies on the Holderness coast should be reviewed.
- Managed retreat should be used to restore the natural hydrodynamics of the estuary, lower tidal levels and reduce flood risk. By doing this new areas of intertidal habitat will be created, giving a positive impact. This involves some degree of abandonment of the current sea defences and the establishment of a new inner line of defence, the intervening land replacing lost intertidal habitat and functioning to reduce wave power.

Predicting the effects of habitat loss on populations of estuarine birds is beset with difficulties, not the least of which is knowing whether current populations can be accommodated in a smaller area. We do, however, have a better idea of what size an estuary should be and how to achieve it. We know, for example, that the Humber does not have enough saltmarsh, and computer simulation also predicts that reinstatement of Patrington Channel, finally reclaimed at the beginning of the 18th century, may cause a drop in high-tide levels at Hull of up to 0.5 m (IECS 1994b). If an estuary is restored to its correct dimensions, it follows that it will accommodate the 'correct' bird populations. In the UK, Pye and French (1992) have estimated that there is a need for the recreation of 2750 ha of saltmarsh in the next 20 years, mainly in the south-east of England; 500 ha of land in Essex have already been restored to the estuaries as a result of sea wall failure. Restoration of the Patrington Channel on the Humber estuary would involve the recreation of hundreds of hectares of intertidal habitat and greatly exceed recent losses due to development. We should support the initiatives taken by the geomorphologists and coastal planners to return estuaries to their natural morphology and dynamics. There are strong arguments in favour of managed retreat from the point of view of security against flooding, but more research into the responses of estuarine birds to change, and predictions of the effects of habitat gain or restoration on their populations, would support this effort.

REFERENCES

Anon. 1993. Conclusions from workshop B: measuring ecological change in wetlands. In: *Waterfowl and wetland conservation in the 1990s – a global perspective*, edited by M. Moser, R.C. Prentice & J. Van Vessem, 83–84. (IWRB Special Publication no. 26.) Slimbridge: International Waterfowl Research Bureau.

Boer, G. de. 1970. Accretion and reclamation in the River Humber. *East Yorkshire Field Studies*, **3**, 15–29.

Burd, F. 1992. *Erosion and vegetation change on the saltmarshes of Essex and north Kent between 1973 and 1988.* (Research and survey in nature conservation report no. 42.) Peterborough: Nature Conservancy Council.

Davidson, N.C., Loffoley, D.d'A., Doody, J.P., War, L.S., Gordon, J., Key, R., Drake, C.M., Pienkowski, M.W., Mitchell, R. & Duff, K.L. 1991. *Nature conservation and estuaries in Great Britain.* Peterborough: Nature Conservancy Council.

Dugan, P.J. & Jones, T. 1993. Ecological change in wetlands: a global overview. In: *Waterfowl and wetland conservation in the 1990s – a global perspective*, edited by M. Moser, R.C. Prentice & J. Van Vessem, 34–38. (IWRB Special Publication no. 26.) Slimbridge: International Waterfowl Research Bureau.

English Nature. 1993. *Coastal zone conservation. English Nature's rationale, objectives and practical recommendations.* Peterborough: English Nature.

Hale, W.G. 1984. The changing face of European wintering areas. In: *Coastal waders and wildfowl in winter*, edited by P.R. Evans, J.D. Goss-Custard & W.G.

Hale, 311–323. Cambridge: Cambridge University Press.

Hayden, B.P., Dueser, R.D., Callahan, J.T. & Shugart, H.H. 1991. Long-term research at the Virginia Coast Reserve. *BioScience*, **41,** 310–318.

Humber Estuary Management Strategy. 1996. Consultation draft.

Institute of Estuarine and Coastal Studies. 1987. *The Humber estuary – environmental background.* The University of Hull Institute of Estuarine and Coastal Studies & Shell UK.

Institute of Estuarine and Coastal Studies. 1994a. *Humber estuary and coast.* The University of Hull Institute of Estuarine and Coastal Studies & Humberside County Council.

Institute of Estuarine and Coastal Studies. 1994b. *Humber estuary and coast: management issues.* The University of Hull Institute of Estuarine and Coastal Studies & Humberside County Council.

Pethick, J. 1984. *An introduction to coastal geomorphology.* London: Arnold.

Pethick, J. 1990. The Humber estuary. In: *Humber perspectives: a region through the ages*, edited by S. Ellis & D.R. Crowther, 54–67. Hull: Hull University Press.

Prater, A.J. 1981. *Estuary birds of Britain and Ireland.* Calton: Poyser.

Pye, K. & French, P.W. 1992. *Targets for coastal habitat creation.* (Report no.35.) Peterborough: English Nature.

Royal Society for the Protection of Birds. 1995. *Wildlife impact – the treatment of nature conservation in environmental assessment.* Sandy: RSPB.

Sears, J. & Avery, M.I. 1993. Population and productivity trends of little terns *Sterna albifrons* in Britain, 1969–89. *Seabird,* **15,** 3–16.

Sheppard, J.A. 1958. *The draining of the Hull valley.* York: East Yorkshire Local History Society.

Siefert, W. 1990. Sea-level changes and tidal flat characteristics. In: *Expected effects of climatic change on marine coastal ecosystems*, edited by J.J. Beukema, 105–112. Amsterdam: Kluwer.

Warren, A. 1993. Naturalness: a geomorphological approach. In: *Conservation in progress*, edited by F.B. Goldsmith & A. Warren, 15–24. Chichester: Wiley.

Estuarine wader impact assessments: possibilities and pitfalls

N A Clark
British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

SUMMARY
There are currently no generally accepted methodologies for undertaking impact assessments in the estuarine environment in Britain. This paper outlines a range of methods that have been used for different types of impact assessment and evaluates their applicability with respect to the spatial-scale habitat type. In particular, differences in approaches are advocated when whole-estuarine systems are likely to be affected as opposed to a small proportion of the estuarine system. In some circumstances, there is a requirement for night-time observations as well as for studies throughout the day because day-time disturbance may affect bird distribution in some circumstances. The relative merits of empirical and predictive studies are considered, together with the advantages of using a combination of both approaches.

WHY DO WE NEED IMPACT ASSESSMENTS?

The estuarine environment is a very limited resource which is used by man in a number of ways, most notably for industrial and harbour development, land claim for agricultural use and the exploitation of its fisheries. Land claim in Britain has been going on since at least Roman times and many estuaries have lost very substantial proportions of their intertidal habitat. For instance, it has been estimated that some 47 000 ha of intertidal habitat on the Wash has been claimed since Roman times (Davidson *et al.* 1991). In past centuries, land claim occurred without any controls. However, throughout this century there has been an increasing understanding of the need to plan the way we use our environment. Studies of the importance of the estuarine ecosystem to waders began in earnest in the 1970s with a plethora of construction proposals. These included:

- storage schemes, for example at the Wash (Goss-Custard 1977; Goss-Custard *et al.* 1977; Goss-Custard, Jones & Newberry 1977), Morecambe Bay (Prater 1972), and the Dee (Buxton, Gillham & Pugh-Thomas 1977);
- tidal power barrages such as that at the Severn (Shaw 1975; Mudge 1979);
- airports such as Foulness (Boorman & Ranwell 1977; Goss-Custard, Kay & Blindell 1977).

Impact assessments are now required under the EC Directive *The assessment of the effects of certain public and private projects on the environment* (1988) and in Britain this acts through the Town and Country Planning (Assessment of Environmental Effects) Regulations of 1988. The term 'environmental assessment' has been defined as 'a technique and a process by which information about the environmental effect of a project is collected' (Department of the Environment/Welsh Office 1989). In terms of waders, the aim of an environmental assessment should be to assess whether the development will affect bird populations on the estuary, whether such an effect is positive or negative, and, if so, whether the effect is significant at the local, national or whole-population (international) scale. In addition, it is important to assess whether these effects are likely to have a short-term or permanent impact.

PROBLEMS OF ENVIRONMENTAL ASSESSMENTS

Ornithological environmental assessments have often been criticised for not answering clearly the question of whether there will be a significant impact. This is partly because all biological systems are subject to a high degree of stochastic variation induced by weather and other environmental factors. Impacts on birds and other organisms form only part of an environmental assessment and it is rare for sufficient time to be allowed to gather the data required to reach definitive conclusions. Developers often assume that by paying a small amount for a few bird counts they will have done enough for an environmental assessment. There are few standard practices for undertaking environmental assessments on birds; this results in the current marketplace economy of individuals or organisations offering to undertake environmental assessments which, when peer reviewed, are shown to be too limited in scope ever to assess whether there will be significant impacts or not.

TYPES OF ENVIRONMENTAL ASSESSMENT

Environmental assessments of bird populations can be broadly placed in one of three categories.

- **Predictive assessments**
  Future bird populations are predicted from a knowledge of the habitat requirements of the species and the changes to its habitat that are expected to occur.
- **Analogous assessments**
  Predictions are made of the bird populations on the future available habitat from the bird populations on similar habitats on matching estuaries.
- **Empirical assessments**
  Numbers of birds that currently use areas that will be lost in a development are assessed, on the assumption that it is this number of birds that will be lost from the population.

Table 1. The advantages (+) and disadvantages (–) of the three categories of impact assessment

Predictive	
+	Should ultimately produce the best estimates
+	Ultimately should make predictions easier
–	Difficult and expensive to undertake
–	Difficult to convince a non-scientific audience
–	Opportunity for positive or negative assessments depending on standpoint
Analogous	
+	Comparatively simple to undertake
+	Possible to undertake with present knowledge
–	Often difficult to convince a non-scientific audience
–	Requires several years of data
–	Difficult to find analogous sites
Empirical	
+	Easy to undertake
+	Easy to convince a non-scientific audience
–	Needs several years of data
–	Opportunity for positive or negative assessments, depending on standpoint

Each of these methods has advantages and disadvantages and these are summarised in Table 1. Inevitably the scale of the development being assessed will in part determine the amount of finance available for impact assessment studies. Under ideal circumstances, full predictive assessments should be made for every study. However, with our current knowledge of estuarine wader biology, we would be unable to answer definitively, for any site, the question 'what impact will this development have?' The exception is a small isolated site which has only local importance and which will be lost completely by a development. Here, there will be a high, locally significant impact on the fauna of the area as all the estuarine waders would be lost. However, there would be no significant regional or international impact of the development.

Until common practices are agreed for the most suitable methodology to be used for undertaking impact assessments, there is likely to be a wide range of approaches to impact assessments for similar types of development. Different developments, however, require different types of assessment. There follow three case studies which outline the approaches to assessing the impact of three different developments which have been investigated by the British Trust for Ornithology (BTO).

CASE STUDY 1: LOSS OF A WHOLE ESTUARINE UNIT – THE CARDIFF BAY BARRAGE

In the late 18th century, the estuaries of the Taff and Ely were an integral part of the north-western side of the Severn estuary. The Cardiff dock complex was built by reclaiming intertidal land on the Severn and creating what is now called Cardiff Bay. An amenity barrage is being built which will result in all the intertidal flats of Cardiff Bay being inundated by a freshwater lake. Wetland Bird Survey (WeBS) counts, which monitor Britain's estuarine bird population annually (Cranswick *et al.* 1995), are used as the standard method of assessing the importance of individual estuaries in Britain. The five-year average peak winter count that was

Table 2. The numbers and national importance of wader populations wintering in Cardiff Bay. Figures are based on the five-year average peak winter count. The numbers in brackets give the percentage of the national population

Species	Impact assessment[1]	Maximum	Minimum
Dunlin (*Calidris alpina*)	3973 (0.9)	6316 (1.2)	3793 (0.7)
Redshank (*Tringa totanus*)	549 (0.7)	1076 (1.1)	460 (0.4)
Knot (*Calidris canutus*)	341 (0.2)	2133 (0.8)	0 (0.0)
Ringed plover (*Charadrius hiaticula*)	53 (0.2)	75 (0.6)	21 (0.1)

[1] 1983/84–1987/88

used in the impact assessment is given in Table 2 (Environmental Advisory Unit 1991). Wader populations are not static and since regular counting was started in 1969 the British wintering populations have changed by factors of between 1.4 and 4.3 (Clark 1989).

Impact assessments typically use the five-year peak winter average for the last five years. Table 2 shows that for the impact assessment no species reached the 1% level for national importance. However, if a different set of years had been used, then both dunlin (*Calidris alpina*) and redshank (*Tringa totanus*) might have been shown to be of national importance. It is unlikely that there has been a substantial change in the attractiveness of Cardiff Bay to waders during this period, but as population changes on each estuary do not precisely mirror national population changes (Moser 1988) such changes should be expected. Given the high level of importance attached to the 1% criterion, perhaps the use of the most recent five-year peak winter count information for a site needs to be reviewed. Otherwise, the importance of some sites is likely to be downgraded after periods of decline in wader populations. For instance, sites which were important for knot (*Calidris canutus*) in the early 1970s were no less so after the population crash that occurred as a result of a series of very bad summers in the high Arctic (Davidson & Wilson 1992).

Although Cardiff Bay now forms a clear discrete unit, it is not totally isolated from the rest of the Severn estuary. Counts throughout the tidal cycle in Cardiff Bay show that dunlin are present only on the rising and falling tides and almost completely leave the bay at low tide (Figure 1i). In contrast, redshank remain in the bay throughout the tidal cycle (Figure 1ii). Their apparent decline near high tide results from birds that roost in the saltmarshes often being out of view.

The closest area of mudflats to Cardiff Bay is the Rhymney estuary and this has exceptionally high densities of dunlin together with a substantial population of redshank. Cardiff Bay is largely used by some of the dunlin that feed on the Rhymney mudflats near low tide, which move to Cardiff Bay as the lower flats on the Rhymney are covered. Colour-marking studies have shown, however, that populations of redshank wintering at the Rhymney show little interchange with those wintering in Cardiff Bay. It is currently unclear whether the dunlin that move in to the Cardiff Bay flats on the rising tide would be able to remain at the Rhymney estuary throughout the tidal cycle, or whether redshank currently wintering on Cardiff Bay will be displaced to the Rhymney mudflats (and other parts of the Severn estuary) after barrage closure. The results of these studies will have particular relevance to future impact assessments.

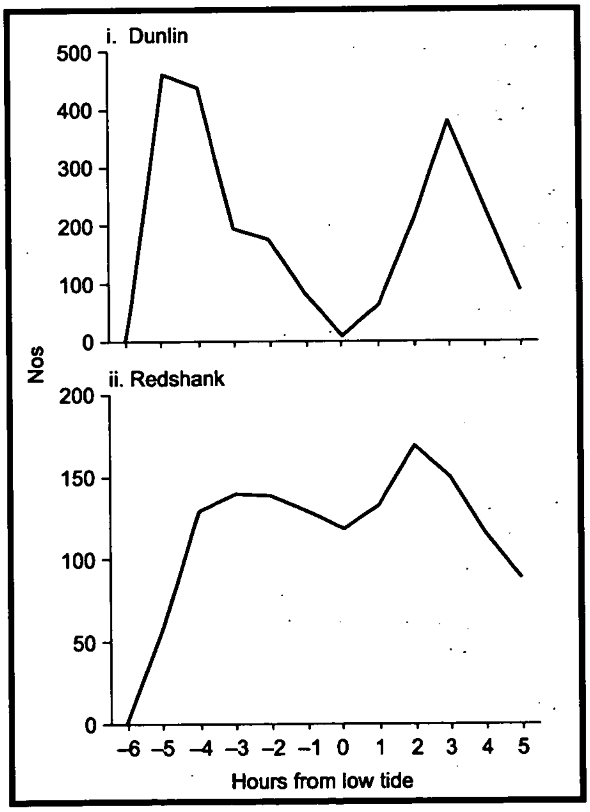

Figure 1. The numbers of dunlin and redshank present in Cardiff Bay at different stages of the tidal cycle between November 1995 and March 1996

Table 3. The proportion of the wintering population of waders that currently feed at low tide in areas that would be inundated after barrage construction

Species	Percentage (%)
Redshank (*Tringa totanus*)	80[1]
Dunlin (*Calidris alpina*)	50
Grey plover (*Pluvialis squatarola*)	45
Curlew (*Numenius arquata*)	41
Ringed plover (*Charadrius hiaticula*)	23

[1] May be an overestimate as based on a small sample of the wintering population

CASE STUDY 2: MODIFICATION OF A WHOLE ESTUARY – THE SEVERN TIDAL POWER BARRAGE

The Severn is a large funnel-shaped estuary with the second highest tidal range in the world (after the Bay of Fundy). Its large tidal range has meant that it has been seriously considered as a potential site for building a tidal power barrage. If a barrage was built across the Severn, it would reduce the tidal range by approximately half, permanently inundating a substantial portion of its intertidal flats (Mettam 1982). Sediments in the Severn are currently extremely well sorted as a result of the very high tidal currents set up on spring tides. The currents in turn lead to high levels of turbidity within the estuary. These high levels of turbidity have been thought to be the major reason for the lack of filter-feeding bivalves within the Severn. As a result, the bird community is dominated by those species that feed on small invertebrates, notably dunlin.

Initial studies undertaken by the BTO mapped the low-tide distribution of waders on the Severn estuary in winter. These studies showed clearly that waders were not evenly distributed around the Severn. Just 12% of the total intertidal area held half the birds whilst half of the intertidal area held 90%. A sample of the low-tide counting units was split so that the proportion of birds that fed below mid-tide could be assessed. Mid-tide is the approximate limit of the low-tide mark after barrage closure, and birds that presently feed in the area below mid-tide and inside the line of the barrage would be displaced from their present low-tide feeding grounds (Table 3). This method was thought likely to give a pessimistic view, as any birds that feed at low tide on the lower tidal flats spend a substantial portion of their feeding time on upper flats. In order to correct for this bias through the tidal cycle, a count methodology was developed (Clark 1989), which enabled the amount of feeding time to be estimated from hourly counts through the tidal cycle. These through-the-tidal-cycle counts showed that the proportion of the population feeding below mid-tide did not necessarily equate to the total amount of feeding time spent on these lower levels. This was particularly important for dunlin, curlew (*Numenius arquata*) and oystercatcher (*Haematopus ostralegus*) (Figure 2).

By taking the data in Table 3 and analysing the WeBS counts for estuaries in south-west Britain following the methodology of Moser (1988), it was possible to predict whether birds that might be displaced from the Severn estuary could be accommodated on other estuaries in south-west Britain. All species that occur on the Severn in substantial numbers showed evidence of their population reaching ceiling densities on some estuaries within Britain. It was therefore possible to compare the current density of those estuaries considered to be at carrying capacity with the density to which estuaries, currently not considered to be at capacity, would have to rise if all the birds potentially displaced from the Severn were to settle on these estuaries.

Figure 3 shows that, for two species – redshank and curlew, predictions of the density to which their population would have to rise on estuaries currently not at capacity would be well above those levels on estuaries considered to be at capacity in order to accommodate displaced birds. If a barrage was built across the Severn, however, the substantial changes in turbidity

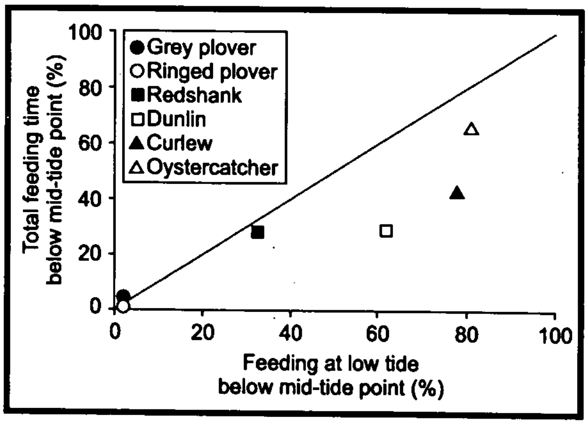

Figure 2. The proportion of birds feeding below mid-tide at low tide compared to the proportion of total feeding time below mid-tide on the Severn estuary

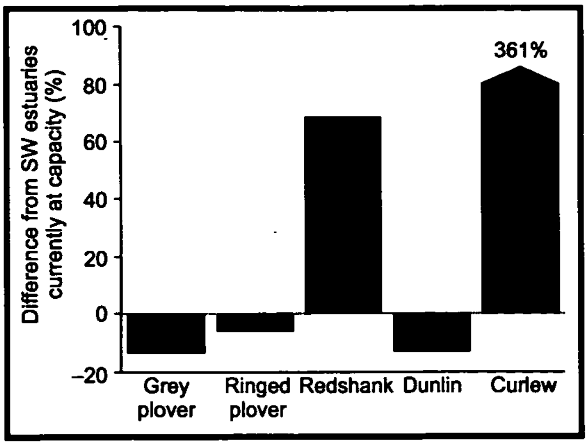

Figure 3. The difference between the predicted post-barrage density of waders on south-west estuaries currently considered not to be at capacity and the present density on south-west estuaries considered to be at capacity

that would occur as a result of the reduced tidal current may lead to changes in sedimentation. McCulloch and Clark (1991) showed that for a sample of estuaries throughout Britain the density of dunlin, the key species on the Severn, was directly related to the proportion of silt in the surface sediments of the estuary (Figure 4). Approximately 50% of the sediments on the Severn are silt. From Figure 4 it would be expected that the density of dunlin on the Severn would be likely to double if there was just a 10% increase in the amount of silt in the surface sediments of the Severn estuary. This finding, together with the application of remote sensing technology, led the BTO and the Institute of Terrestrial Ecology to undertake a project to collect information on bird distribution, sediment distribution and a range of physical variables for 27 estuaries throughout the UK. The aim was to produce predictive models which would enable accurate predictions to be made of post-barrage densities (Austin *et al.* 1996; Holloway *et al.* 1996; Rehfisch *et al.*, this volume, pp116–126; Yates *et al.* 1996; Yates & Goss-Custard, this volume, pp138–144).

The results of this series of projects leading towards an environmental assessment of the impacts of the Severn barrage have greatly increased our understanding of estuarine bird distribution. The initial empirical assessments were too pessimistic but the use of a combination of empirical, analogous and predictive studies is leading to a much better understanding of the likely impacts of a Severn tidal power barrage on bird populations.

CASE STUDY 3: SHORT-TERM DISTURBANCE EFFECTS – THE NORTH MORECAMBE GAS PIPELINE

During 1993, a gas pipeline was constructed across three intertidal areas in north Morecambe. As little information was available on the effect of laying pipelines across intertidal flats, the BTO was commissioned to monitor the long-term implications of pipeline construction. Data were collected for two years prior to pipeline construction and, ultimately, will be collected for at least four years post-construction. Construction took place during the summer months and took three months to complete. The 1 m diameter pipe was pulled across the 4 km of intertidal flats between Westfield and Walney Island; this necessitated digging a trench 4 m deep in which to lay the pipe. Through-the-tidal-cycle methodology was used to survey a series of transects parallel to the pipeline to compare the effect of the disturbed pipeline area with any effects of sediment drift to transects next to the pipeline. When the relative changes in distribution were analysed for each species, pre- and post-pipeline construction, it became clear that the pipeline transect had been used less by most species of waders after construction (Figure 5). After nearly two years this anomaly has largely recovered; however, bird population levels have not yet quite done so. In particular, the high-energy rocky shore on the marine side of Walney is showing only limited recovery. This study reveals that the recovery time after such construction projects depends on the environmental influences on the area concerned.

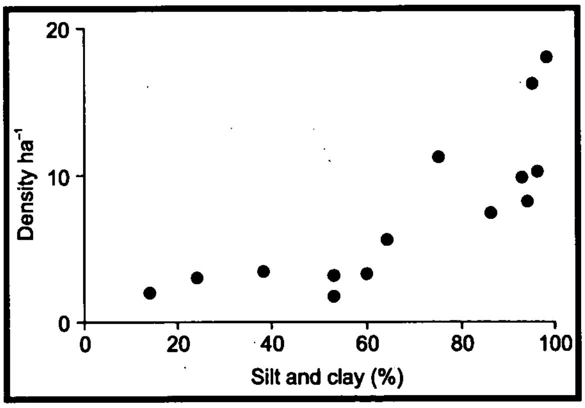

Figure 4. The relationship between dunlin density and the proportion of silt in the surface sediments on a sample of 14 estuaries in Britain

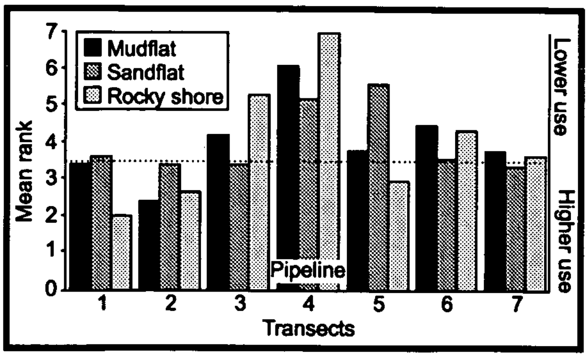

Figure 5. The change in transect rank for seven species of wader in the winter after the laying of a pipeline across Morecambe Bay

OVERALL CONCLUSIONS

The theoretical consequences of habitat loss on shorebird populations have been discussed in a number of recent papers (eg Sutherland & Goss-Custard 1991; Evans *et al.* 1991). There are still comparatively few case studies where predictions have been tested after developments have been completed. Schekkerman, Meininger and Meire (1994) showed that, after the loss of one third of the intertidal area of the Dutch delta region between 1982 and 1987, the intertidal foraging species forced to move from parts of the estuary which became non-tidal were unable to settle on the remaining intertidal areas. Lambeck (1991) showed that this resulted in increased mortality of oystercatchers; birds that originated from the areas where the habitat was lost had a higher level of mortality than those from nearby areas unaffected by reclamation. After the reclamation of the Nordstrander Bucht in the Northern Waddensea, Hötker (1996) showed that previously productive intertidal flats inside the line of the new sea wall, which subsequently had a greatly reduced tidal range, had very substantial declines in the density of feeding birds.

Almost every environmental impact assessment on an estuary has features which make it unique so that comparison between studies is extremely difficult. There is, however, a need for detailed post-development appraisal as part of the planning consent process so that it is possible to learn from past studies. Scientists making predictions as part of impact assessments should endeavour to obtain research grants to test their predictions after developments have occurred. Without testing the accuracy of predictions, it is unlikely that an appropriate methodology for impact assessments will become generally accepted. Only when there are accepted criteria and protocols will it be possible to convince developers of the level of work that is required to assess the impacts of developments on bird populations.

ACKNOWLEDGEMENTS

The case studies reported here were funded by Cardiff Bay Development Corporation, Energy Technology Support Unit on behalf of the Department of Trade and Industry, the Severn Tidal Power Group, and British Gas Exploration and Production Ltd. The work was carried out by staff members in the BTO's Habitats Advisory Unit. The Wetland Bird Survey is a joint scheme of the British Trust for Ornithology, the Wildfowl and Wetlands Trust, Royal Society for the Protection of Birds, and the Joint Nature Conservation Committee (the last on behalf of the Countryside Council for Wales, Department of the Environment Northern Ireland, English Nature, and Scottish Natural Heritage).

REFERENCES

Austin, G., Rehfisch, M.M., Holloway, S.J., Clark, N.A., Balmer, D.E., Yates, M.G., Clarke, R.T., Swetnam, R.D., Eastwood, J.A., Durell, S.E.A. le V. dit, West, J.R. & Goss-Custard, J.D. 1996. *Estuaries, sediments and shorebirds. III. Predicting waterfowl densities on intertidal areas.* (BTO Research Report no. 160.) Thetford: British Trust for Ornithology.

Boorman, L.A. & Ranwell, D.S. 1977. *The ecology of Maplin Sands and the coastal zones of Suffolk, Essex and North Kent.* Cambridge: Institute of Terrestrial Ecology.

Buxton, N.E., Gillham, R.M. & Pugh-Thomas, M. 1977. *The ecology of the Dee estuary.* Report to Central Water Planning, Dee and Clwyd River Division and Welsh National Water Development Authority. Unpublished.

Clark, N.A. 1989. *Wader migration and distribution in south-west estuaries.* (BTO Research Report no. 40.) Tring: British Trust for Ornithology.

Cranswick, P.A., Waters, R.J., Evans, J. & Pollitt, M.S. 1995. *The Wetland Bird Survey 1993–94: wildfowl and wader counts.* Slimbridge: British Trust for Ornithology/Wildfowl and Wetlands Trust/Royal Society for the Protection of Birds/Joint Nature Conservation Committee.

Davidson, N.C. & Wilson, J.R. 1992. The migration system of the European wintering knot *Calidris canutus islandica. Wader Study Group Bulletin,* **14** (suppl.), 39–51.

Davidson, N.C., Laffoley, D. d'A., Doody, J.P., Way, L.S., Key, R., Drake, D.M., Pienkowski, M.V., Mitchell, R. & Duff, K.L. 1991. *Nature conservation and estuaries in Great Britain*. Peterborough: Nature Conservancy Council.

Department of the Environment/Welsh Office. 1989. *Environmental assessment. A guide to procedures*. London: HMSO.

Environmental Advisory Unit. 1991. *Cardiff Bay barrage environmental statement*. Cardiff Bay Barrage Bill, October 1991.

Evans, P.R., Davidson, N.C., Piersma, T. & Pienkowski, M.W. 1991. Implications of habitat loss at migration staging posts for shorebird populations. *Acta XX Congressus Internationalis Ornithologici*, 2199–2207.

Goss-Custard, J.D. 1977. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology*, **14**, 721–739.

Goss-Custard, J.D., Jones, R.E. & Newberry, P.E. 1977. The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology*, **14**, 681–700.

Goss-Custard, J.D., Kay, D.G. & Blindell, R.M. 1977. The density of migratory and overwintering redshank, *Tringa totanus* (L.) and curlew, *Numenius arquata* (L.), in relation to the density of their prey in south-east England. *Estuarine and Coastal Marine Science*, **5**, 497–510.

Goss-Custard, J.D., Jenyon, R.A., Jones, R.E., Newberry, P.E. & Williams, R. le B. 1977. The ecology of the Wash. II. Seasonal variation in the feeding conditions of wading birds (Charadrii). *Journal of Applied Ecology*, **14**, 701–719.

Holloway, S.J., Rehfisch, M.M., Clark, N.A., Balmer, D.E., Austin, G., Yates, M.G., Swetnam, R.D., Eastwood, J.A., Clarke, R.T., Durell, S.E.A. le V. dit, Goss-Custard, J.D. & West, J.R. 1996. *Estuaries, sediments and shorebirds. II. Shorebird usage of intertidal areas*. (BTO Research Report no. 156.) Thetford: British Trust for Ornithology.

Hötker, H. 1996. Habitat loss in the Waddensea – consequences for waders and waterfowl of the land claim in the Nordstrander Bucht, Germany. *Wader Study Group Bulletin*, **74**, 48.

Lambeck, R.H.D. 1991. Changes in abundance, distribution and mortality of wintering oystercatchers after habitat loss in the Delta area, SW Netherlands. *Acta XX Congressus Internationalis Ornithologici*, 2208–2218.

McCulloch, M.N. & Clark, N.A. 1991. *Habitat utilisation by dunlin on British estuaries*. (BTO Research Report no. 86.) Thetford: British Trust for Ornithology.

Mettam, D.J. 1982. Tidal power from the Severn estuary: an essay review. *Nature in Wales*, **1**, 50–61.

Moser, M. 1988. Limits to the numbers of grey plovers *Pluvialis squatarola* wintering on British estuaries: an analysis of long-term population trends. *Journal of Applied Ecology*, **25**, 473–486.

Mudge, G. 1979. *The feeding distribution of wintering wading birds (Charadriiformes) in the Severn estuary in relation to barrage proposals*. Nature Conservancy Council. Cyclostyled report.

Prater, A. J. 1972. The ecology of Morecambe Bay. III. The food and feeding habits of knot in Morecambe Bay. *Journal of Applied Ecology*, **9**, 179–194.

Rehfisch, M.M., Holloway, S.J., Yates, M.G., Clarke, R.T., Austin, G., Clark, N.A., Durell, S.E.A. de V. dit, Eastwood, J.A., Goss-Custard, J.D., Swetnam, R. & West, J.R. 1997. Predicting the effect of habitat change on waterfowl communities: a novel empirical approach. In: *Effect of habitat loss and change on waterbirds*, edited by J.D. Goss-Custard, R. Rufino & A. Luis, 116–126. (ITE symposium no. 30.) London: The Stationery Office.

Shaw, T.L., ed. 1975. *An environmental appraisal of the Severn barrage*. University of Bristol. Cyclostyled report.

Schekkerman, H., Meininger, P.L. & Meire, P.M. 1994. Changes in waterbird populations of the Oosterschelde (SW Netherlands) as a result of large-scale coastal engineering works. *Hydrobiologia*, **282/283**, 509–524.

Sutherland, W.J. & Goss-Custard, J.D. 1991. Predicting the consequence of habitat loss on shorebird populations. *Acta XX Congressus Internationalis Ornithologici*, 2199–2207.

Yates, M.G. & Goss-Custard, J.D. 1997. The development of a correlative approach relating bird distribution and remotely sensed sediment distribution to predict the consequences to shorebirds of habitat change and loss. In: *Effect of habitat loss and change on waterbirds*, edited by J.D. Goss-Custard, R. Rufino & A. Luis, 138–144. (ITE symposium no. 30.) London: The Stationery Office.

Yates, M.G., Clarke, R.T., Swetnam, R.D., Eastwood, J.A., Durell, S.E.A. le V. dit, West, J.R., Goss-Custard, J.D., Clark, N.A. & Rehfisch, M.M. 1996. *Estuaries, sediments and shorebirds. I. Determinants of the intertidal sediments of estuaries*. (Natural Environment Research Council contract report.) Huntingdon: Institute of Terrestrial Ecology.

Habitat preferences of wintering wildfowl in Portugal

L T Costa
ICN/CEMPA, Rua Filipe Folque 46-3º, 1050 Lisboa, Portugal

SUMMARY
National or regional wildfowl census is widely used as a tool for estimating population numbers and monitoring trends. In addition to the censuses carried out in Portugal, a simple method involving habitat description and the use of an index evaluates the habitat preference of wintering wildfowl. Population trends were found to be related to the habitat preferences of the species. An increasing population is usually related to the increasing use of expanding man-made habitats or a less selective behaviour in some species. In contrast, species using more threatened habitats are declining in numbers. The method is proposed as a first-step process to predicting population trends from habitat change, using data from existing wildfowl censuses.

INTRODUCTION

Wildfowl censuses are widely carried out throughout the world as a tool for evaluating the size of bird populations and for monitoring population trends. These censuses are currently carried out at national (eg Costa & Guedes 1994; Martí & Ruiz 1994; Cranswick *et al.* 1995; Delany 1996) and international levels (eg Perennou & Mundkur 1994; Rose 1995). The gathering of data on the numbers of swans, geese and ducks throughout their range usually allows us to estimate population size and trends (Rose & Scott 1994; Rose 1995).

The large number of volunteers available combined with the rather simple technique that is used for counting wildfowl, along with the suitable nature of the habitat, allow these censuses to be undertaken over vast territories. However, the resulting data are usually restricted to the numbers of birds of each species counted at a single point in time. This makes it quite difficult to assess how to interpret changes in counts that might be due to factors such as the weather, pollution and habitat change or loss.

Most frequently, studies of the effect of habitat change and loss on the numbers and distribution of anatids are only made *a posteriori*. However, habitat selection and preference studies should make it possible to predict whether a species is going to be affected by some change in the habitat. By simply investing a little extra work when organising a national or international census, it should be possible to answer broadly questions relating to habitat selection and preferences, namely:

- what habitats are preferred by wildfowl in winter?
- is habitat change and loss affecting population trends?

In this paper, some suggestions are made as to how we might profit from extracting additional data from wildfowl counts. This can be done by properly describing the wetland areas that are counted and by using a simple habitat preference index to relate wildfowl species to their habitats and to their population estimates.

HABITAT DESCRIPTION

A major step when undertaking studies on habitat selection or preference is to choose or define a habitat classification system. Many such systems are available, ranging from the simplest to the more complex. Some are very broad systems adapted for every ecosystem on earth (European Commission 1991), while others are specific to wetland habitats (eg Cowardin *et al.* 1979; Ramsar Convention Bureau 1990; Dignard *et al.* 1991; Farinha *et al.* 1996).

For the purpose of this study, certain conditions must be met by the classification

Table 1. MedWet Habitat Description System structure (adopted from Farinha *et al.* 1996)

Level	Categories				
System	Marine	Estuarine	Riverine	Lacustrine	Palustrine
Subsystem	–	–	Tidal	Limnetic Lower perennial Upper perennial Intermittent	– Littoral
Class	Water surface Non-vegetated Aquatic bed Reef	Water surface Non-vegetated Aquatic bed Reef	Water surface Non-vegetated Aquatic bed Emergent Emergent Scrub-shrub Forested	Water surface Non-vegetated Aquatic bed Emergent	Water surface Non-vegetated Aquatic bed Moss-lichen Emergent Scrub-shrub Forested
Subclass	As an example: the class non-vegetated has subclasses rock, cobbles/gravel, sand, mud, organic, salt crust and vegetated pioneer				

system chosen.

- Habitats should be defined on the basis of their ecological character.
- It should apply specifically to wetland habitats, as these are the only habitats considered when counting wildfowl.
- It should be easily translated on to maps so that surface areas can be estimated and census information can be recorded on the map.

Given these considerations, the MedWet Habitat Description System (Farinha *et al.* 1996) was adopted. This is a hierarchical classification system based on the USA wetland and deepwater habitat classification (Cowardin *et al.* 1979), but adapted specifically for mediterranean conditions. The system is organised into several levels, from systems to subsystems, classes and subclasses (see Table 1); it also includes some extra descriptors concerning water regime, salinity and artificiality.

INDEX OF PREFERENCE

A simple index was used to measure habitat preference in the wildfowl species we censused in Portugal. This index of preference (IP) relates the proportion of the area of the habitat to the proportion of birds using it, following the formula below:

$$IP=\log\left(\frac{U_i}{A_i}+1\right)$$ (Duncan 1983)

Thus, the index is larger than 0, with values above 0.3 indicating a marked preference for the biotope, as the proportion of birds using the habitat exceeds the proportion of the area of the habitat. However, an index less than 0.3 does not prove that a species avoids the habitat, as birds do occur there. Avoidance is indicated by an index of preference of zero.

Although not providing very accurate and statistically based values for studies of habitat selection, the index broadly indicates the habitats used by a species. It is easy to use and has been employed in several studies of habitat preference in birds (eg Bignal, Curtis & Matthews 1988; Farinha 1991; Almeida & Pinto 1992).

RESULTS: A CASE STUDY IN PORTUGAL

Study areas

In addition to the International Waterfowl Census (IWC) carried out each January in Portugal, monthly counts of wintering wildfowl species have been made from October to March each year since 1992 (Costa 1994; Costa & Guedes 1994, 1997). Of the average of 60 sites covered by these counts, five have been counted regularly by the author and the birds there allocated to habitats. The five sites are the Muge marshes (39°06'N 8°42'W), Cascavel pond (38°58'N 8°38'W), the Tagus (38°50'N 8°57'W) and Sado (38°27'N 8°43'W) estuaries and the Santo André lagoon (38°01'N 8°49'W). In order to simplify the results, only the two levels (systems and classes) of the hierarchical habitat system were used. Six habitat classes were identified and mapped

Table 2. Habitat composition (in ha) of the five study sites (EW=Estuarine, Water surface; EE=Estuarine, Emergent vegetation; PW=Palustrine, Water surface; PE=Palustrine, Emergent vegetation; PN=Palustrine, Non-vegetated; LW=Lacustrine, Water surface)

	Muge Freshwater marsh and pond for irrigation	Cascavel Small pond for irrigation	Tagus Estuary and salt marshes	Sado Estuary, salt marshes and small freshwater ponds	S. André Coastal lagoon
EW	0	0	10 898	2 527	158
EE	0	0	2 679	388	7
PW	0	9	0	9	158
PE	4	2	0	0	44
PN	4	0	0	0	0
LW	43	0	0	0	0
Total area (ha)	51	11	13 577	2 924	367

within each of the five sites. The main characteristics of these sites are described in Table 2. In addition to these four levels of the classification system, some further information was also recorded on water regime and salinity (see Farinha *et al.* 1996). The habitats were mapped following basic photo-interpretation of aerial infra-red photographs (scale 1:15 000) and their surface area was measured in hectares.

Species counts and habitat preferences

Eight species of anatids were considered, as the remaining ones occurred in such low numbers that they did not provide sufficient data for interpretation. The species were wigeon (*Anas penelope*), gadwall (*A. strepera*), teal (*A. crecca*), mallard (*A. platyrhynchos*), pintail (*A. acuta*), shoveler (*A. clypeata*), red-crested pochard (*Netta rufina*) and pochard (*Aythya ferina*).

Some species, such as gadwall, shoveler, red-crested pochard and pochard, preferred markedly freshwater habitats. When analysing the more detailed levels of the habitat classification, it was noted that gadwall, shoveler and pochard seem to avoid vegetated habitats, preferring open-water surfaces. The red-crested pochard showed a preference mainly for palustrine open-water surfaces of low surface area.

The wigeon was the only species to show a marked preference for brackish habitats and was found primarily on estuarine waters with muddy bottoms. The rest of the species studied proved to be much less selective. The mallard, teal and pintail were present in fresh- and brackish water habitats, both palustrine and estuarine. However, mallard seemed to avoid open-water surfaces in the estuarine habitats, whereas pintail was regularly found in tidal estuarine habitats and teal occurred mainly in vegetated plots.

DISCUSSION

Population trends

When comparing the habitat preferences to the population trends of the species studied (available from Rose & Scott 1994), some relations could be noted. Mostly, the anatid species wintering in Portugal are part of the mediterranean/Black Sea population (Atkinson-Willes 1976; Monval & Pirot 1989; Rose & Scott 1994). The exception is the red-crested pochard, a species whose population trends and movements are still not well understood, because it is partially migratory and has a very patchy distribution. At present, this species in Portugal is usually considered to belong to the central European/west mediterranean population (Rose & Scott 1994).

The mediterranean and Black Sea populations of most species of anatids occurring in Portugal are increasing; in the present study, this includes gadwall, teal, mallard and shoveler. These are, in fact, the

Table 3. Index of preference, as measured by Duncan's (1983) equation, of each species for each habitat (habitat codes as in Table 2)

Species	EW	EE	PW	PE	PN	LW
Wigeon	0.39	0.00	0.20	0.00	0.00	0.00
Gadwall	0.38	0.00	1.20	0.00	0.00	0.66
Teal	0.13	0.54	0.73	0.40	1.69	0.00
Mallard	0.22	0.34	1.72	0.79	1.50	0.41
Pintail	0.38	0.00	0.93	0.14	0.00	0.28
Shoveler	0.38	0.00	0.58	0.29	0.00	0.83
Red-crested pochard	0.12	0.00	2.52	0.00	0.00	0.70
Pochard	0.38	0.00	0.79	0.00	0.00	0.91

species that prefer a broad range of habitats. In addition, both gadwall and shoveler can often be found in artificial wetlands (namely reservoirs and especially small irrigation ponds). These artificial wetlands are increasing – mainly in south Portugal – whereas many small natural wetlands have been drained during the last few decades.

Other species within the mediterranean/ Black Sea range show a decline in numbers, particularly wigeon and pochard. A slight decline has been recorded for pintail (Rose & Scott 1994). Both wigeon and pintail markedly prefer the most threatened habitats in Portugal. In fact, their estuarine and palustrine habitats face some major threats in Portugal, such as drainage, change in agricultural practices, industrial and urban pollution and road development (Farinha & Trindade 1994).

Only in the pochard does there seem to be no clear link between habitat preference and population trend. Finally, it is impossible to make such comparisons for the red-crested pochard, as no population trend is yet available from the irregular counts made over the last years.

Use of the method

In general, some relationship was found between population trends in the eight duck species and changes in the extent of their preferred habitats. At first glance, species preferring some of the threatened habitats are declining while those that prefer increasingly common habitats are increasing in numbers, as are the numbers of the less selective species. I conclude that the use of a habitat description and an index of preference can indicate the effects of habitat loss and change on wildfowl abundance.

However, many limitations must be recognised. First, the index is not a detailed and accurate measure of habitat use by the birds. It must be seen only as giving an indication of preference, taken from discrete counts of birds. Second, habitat preference was evaluated only in the birds' winter quarters, and obviously many other factors influence the population fluctuations of each species, including climate, breeding success, predation, and human disturbance. Nonetheless, the method provides a good starting point method for predicting the effects of habitat changes on wildfowl populations. The small amount of extra work involved when organising wildfowl census can thus provide a basis for further detailed studies that are designed to understand fully population fluctuations and their causes.

REFERENCES

Almeida, J. & Pinto, M. 1992. Selecção dos biótopos de alimentação pelo Grou-comum *Grus grus*: o caso de Moura (Alentejo). *Airo*, **3**, 1–8.

Atkinson-Willes, G.L. 1976. The numerical distribution of ducks, swans and coots as a guide in assessing the importance of wetlands in midwinter. In: *The conservation of wetlands and waterfowl*, edited by M. Smart, 199–255. Slimbridge: International Waterfowl Research Bureau.

Bignal, E.M., Curtis, D.J. & Matthews, J.L. 1988. *Islay: landtypes, bird habitat and nature conservation. Part 1: land use and birds on Islay.* (CST Report no. 809.) Peterborough: Nature Conservancy Council.

Costa, L.T. 1994. Censos de anatídeos em Portugal. In: *Métodos de censos e atlas de aves*, edited by J. Almeida & R. Rufino, 33–35. Lisboa: Sociedade Portuguesa para o Estudo das Aves.

Costa, L.T. & Guedes, R.S. 1994. *Contagens de Anatídeos Invernantes em Portugal – 1992/93.* (Estudos de Biologia e Conservação da Natureza 14.) Lisboa: Instituto da Conservação da Natureza.

Costa, L.T. & Guedes, R.S. 1997. *Contagens de Anatídeos Invernantes em Portugal Continental – Invernos de 1993/96.* (Estudos de Biologia e Conservação da Natureza 19.) Lisboa: Instituto da Conservação da Natureza. In press.

Cowardin, L.M., Carter, V., Golet, F.C. & Laroe, E.T. 1979. *Classification of wetlands and deepwater habitats of the United States.* Washington DC: US Fish and Wildlife Service.

Cranswick, P.A., Waters, R.J., Evans, J. & Pollitt, M.S. 1995. *The Wetland Bird Survey 1993–94: wildfowl and wader counts.* Slimbridge: British Trust for Ornithology/Wildfowl and Wetlands Trust/Royal Society for the Protection of Birds/Joint Nature Conservation Committee.

Delany, S. 1996. *Irish Wetland Bird Survey 1994–1995.* Dublin: IWC Birdwatch Ireland.

Dignard, N., Lalumière, R., Reed, A. & Julien, M. 1991. *Habitats of the northeast coast of James Bay.* (Occasional Paper no. 70.) Ottawa: Canadian Wildlife Service.

Duncan, P. 1983. Determinants of the use of habitat by horses in a mediterranean wetland. *Journal of Animal Ecology*, **52**, 93–109.

European Commission. 1991. *CORINE biotopes: the design, compilation and use of an inventory of sites of major importance for nature conservation in the European Community*. Luxembourg: Office for Official Publications of the European Communities.

Farinha, J.C. 1991. Garça-boieira *Bubulcus ibis*, na região de Sagres-S. Vicente: biótopos de alimentação e grau de associação com o gado. *Airo*, **2**, 1–9.

Farinha, J.C. & Trindade, A. 1994. *Contribuição para o inventário e caracterização de zonas húmidas em Portugal Continental.* Lisboa: Publication MedWet/ Instituto da Conservação da Natureza.

Farinha, J.C., Costa, L.T., Zalidis, G., Mantzavelas, A., Fitoka, E., Hecker, N. & Tomàs Vives, P. 1996. *MedWet wetland inventory: habitat description system.* Lisboa: MedWet ICN/Wetlands International/EKBY publication.

Martí, R. & Ruiz, A. 1994. *Compilación de los censos de aves acuáticas invernantes y nidificantes en España en los años 1991 y 1992.* Madrid: Sociedad Española de Ornitología.

Monval, J.-Y. & Pirot, J.-Y. 1989. *Results of the IWRB International Waterfowl Census 1967–1986.* (IWRB Publication no. 8.) Slimbridge: International Waterfowl Research Bureau.

Perennou, C. & Mundkur, T. 1994. *Asian waterfowl census 1987–1991 – status and trends of waterfowl populations in Asia.* (IWRB Publication no. 24.) Slimbridge: International Waterfowl Research Bureau.

Ramsar Convention Bureau. 1990. *Proceedings of the fourth meeting of the conference of contracting parties.* Montreux, 27 June to 4 July, Vol. 1.

Rose, P.M. 1995. *Western Palearctic and South-Asia waterfowl census 1994.* (IWRB Publication no. 35.) Slimbridge: International Waterfowl Research Bureau.

Rose, P.M. & Scott, D.A. 1994. *Waterfowl population estimates.* (IWRB Publication no. 29.) Slimbridge: International Waterfowl Research Bureau.

The use of WeBS low-tide counts in predicting the effects of habitat loss

J Evans
British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK
Present address: Royal Society for the Protection of Birds, The Lodge, Sandy, Beds SG19 3HW

SUMMARY
In 1992, a new, long-term, volunteer-based scheme for monitoring estuary birds began in the UK. The WeBS low-tide counts were designed to be complementary to the WeBS core counts, which have been taking place for more than 25 years, by providing information on waterfowl feeding distribution on the main UK estuaries. More informed decisions could then be made during site designation and site protection work. However, because it is a volunteer-based scheme, the methods used and the frequency with which they take place have had to be a compromise between the practical and the ideal. These methods are described and discussed in relation to their role in estuary conservation in the UK and, more specifically, in relation to their potential use in predicting the effects of habitat loss.

WHY ARE WeBS LOW-TIDE COUNTS NECESSARY?

The statutory protection of estuaries in the UK is achieved at an international level through the designation of RAMSAR sites and Special Protection Areas (SPAs) using the 1% criterion, and at a national level through the designation of Sites of Special Scientific Interest using analogous national 1% thresholds. These designations are possible because the size of the wintering population of each species of wader and wildfowl on almost every UK estuary is known. A thousand or so volunteers go out every month and count them as part of the Wetland Bird Survey (WeBS) core counts, a long-term monitoring scheme jointly organised by the British Trust for Ornithology, the Wildfowl and Wetlands Trust, the Royal Society for the Protection of Birds (RSPB) and the Joint Nature Conservation Committee (on behalf of the Countryside Council for Wales, Department of the Environment Northern Ireland, English Nature, and Scottish Natural Heritage).

WeBS core counts are usually made at spring-tide roosts where birds can be counted quickly and accurately. Until recently, the potential effects of a proposed development have been considered using a combination of these counts and an environmental impact assessment (EIA). The latter is usually commissioned after the development has been proposed and is some way through the planning stage. Both sources of information have their drawbacks, particularly where only a small proportion of an estuary is likely to be affected. First, where birds roost within an estuary is often completely unrelated to where they feed. In some cases, it may even be in a different estuary. Second, the amount of time available for an EIA may be limited and therefore the information gathered may be misleading, and, third, by the time an EIA takes place the company proposing the development may already have invested a considerable amount of time and money in the scheme.

The Medway estuary in south-east England was notified as a RAMSAR site in 1993. One relatively small area of intertidal mudflats, known as Lappel Bank, was omitted (Figure 1), despite the fact that available information suggested that it was an important area for waterfowl. There were plans to reclaim the area for development and, it was argued, this would have little or no effect on the important populations of wintering waterfowl on the Medway. At the time, two datasets were available: WeBS core counts, which had been carried out once a month since 1969, and low-tide counts, organised

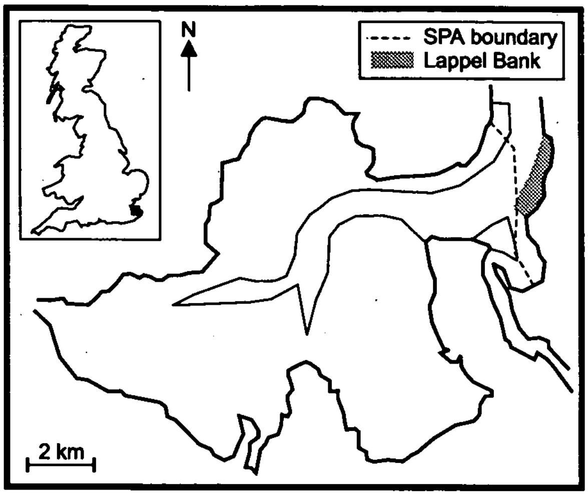

Figure 1. The Medway estuary showing the position of Lappel Bank in relation to the SPA boundary

by the RSPB, which had been carried out once each winter since 1989. Using high-tide counts, the only way to predict the effect on wintering wildfowl of removing this intertidal area was to assume that, if Lappel Bank occupied 1% of the area of the Medway, then 1% of the total WeBS core count of each species present might be lost. However, the low-tide counts suggested a different outcome (Table 1) and demonstrated that it is misleading to use high-tide counts to predict how many birds would be affected by the loss of a low-tide feeding area. In addition, because the low-tide counts had been carried out only once each winter, the low-tide data were themselves open to the suggestion that they were unrepresentative. The development went ahead.

At the time, the Medway was unusual in having had even this limited number of low-tide counts carried out. On the majority of estuaries, WeBS core count data were the only data with which to predict the effects of development on waterfowl. Cases like Lappel Bank highlighted the need for better baseline information on the importance of different feeding areas for birds and a second long-term scheme to monitor estuarine waterfowl was proposed. The WeBS low-tide counts began in 1992 sponsored by the same organisations as the high-tide counts.

Table 1. Bird usage of Lappel Bank

Species	Predicted (WeBS core counts)	Actual (low-tide counts)	Density (birds ha^{-1})
Oystercatcher *(Haematopus ostralegus)*	36	28	1.3
Grey plover *(Pluvialis squatarola)*	46	12	0.5
Redshank *(Tringa totanus)*	31	200	9.1
Dunlin *(Calidris alpina)*	298	520	23.6

COUNTING PROCEDURE

As with any volunteer-based national scheme, the WeBS low-tide counts had to be a compromise between a statistical ideal and what was practical, possible and cost-effective. It was therefore decided:

- to count the main UK estuaries, defined as those regularly holding more than 5000 waders, on a five-year rotating basis, using volunteer labour as far as possible;
- to focus on the winter (November–February) with one simultaneous complete count per estuary being planned for each of the four months;
- to conduct counts between two hours before and two hours after low tide;
- to base data collection for each estuary on pre-established subdivisions of the intertidal area.

The WeBS core count subdivisions are subdivided to give WeBS low-tide count sections which can be covered by a single person. The counter then subdivides his or her section to give much smaller subdivisions which are called mudflats (Figure 2). The boundaries of these subdivisions are defined using topographical features and sight-lines.

ASSUMPTIONS

When the scheme was set up several assumptions were made.

Count accuracy

WeBS core counts take place at high tide because they aim to provide accurate population estimates and this is when it is thought that waterfowl counts are most accurate. The accuracy of low-tide counts is much more variable because of the difficulties of seeing birds at long distances, in bad weather, and when the topographical characteristics of the intertidal area mean that birds may remain

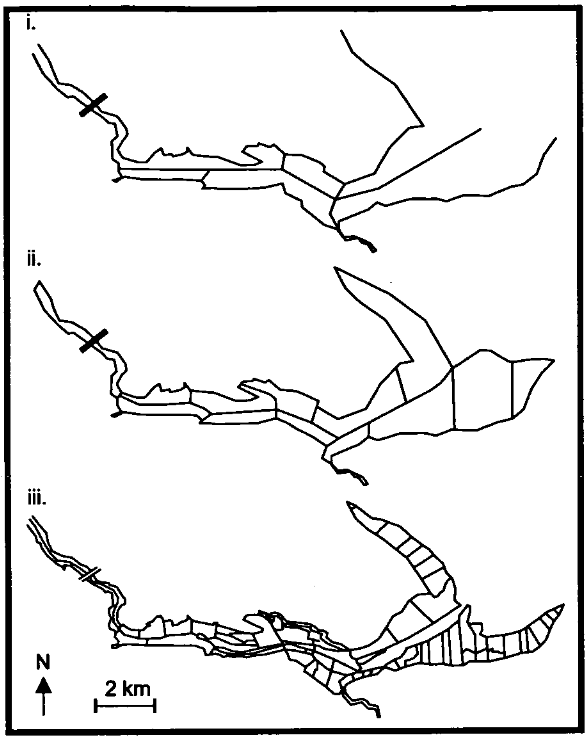

Figure 2. WeBS core count sectors (i) were subdivided to form (ii) WeBS low-tide count sections which were further subdivided to give (iii) WeBS low-tide counts recording units

undetected. However, because the main aim of the low-tide counts is to demonstrate the relative importance of different areas within an estuary, rather than obtain a precise estimate of the numbers supported by each estuary, the counts do not need to achieve the precision of the high-tide counts. Areas with relatively high numbers of birds will always be detected, even if the exact numbers present are not known. Obviously, within these constraints they should be as accurate as possible. An additional problem, which cannot be avoided, is observer variability but this problem is inherent in all large-scale surveys.

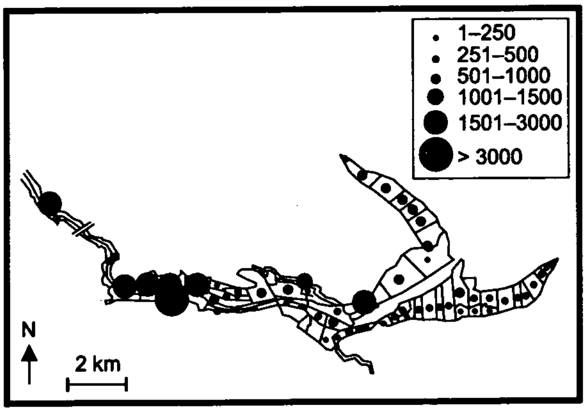

Figure 3. Low-tide distribution of all species combined on the Swale estuary during the 1992–93 winter

Pre-established subdivisions of the intertidal area

This approach has a number of advantages. Used in conjunction with standard forms it makes data collection and processing a relatively simple process. The commonest alternative approach involves the use of large-scale maps to plot the positions of individual birds or flocks. This can be cumbersome and time-consuming as well as introducing variability in interpretation, both in the field assessment of distance and direction and in post-observation transcription to recording forms. Fixed unit boundaries can also reflect broad changes in habitat type, although the mapping technique is more flexible from this point of view. However, fixed unit boundaries have the added advantage that they divide the count section into manageable areas, making the counter's task seem less daunting and enabling any new counter taking over to recognise the same areas, thus ensuring standardisation between years.

Timing and frequency of counts

It was decided that the counts should concentrate on the low-tide period, because this is generally when bird distribution is least variable, that four counts per winter were enough to establish patterns of distribution, and that counting during one winter in five was sufficient to detect changes.

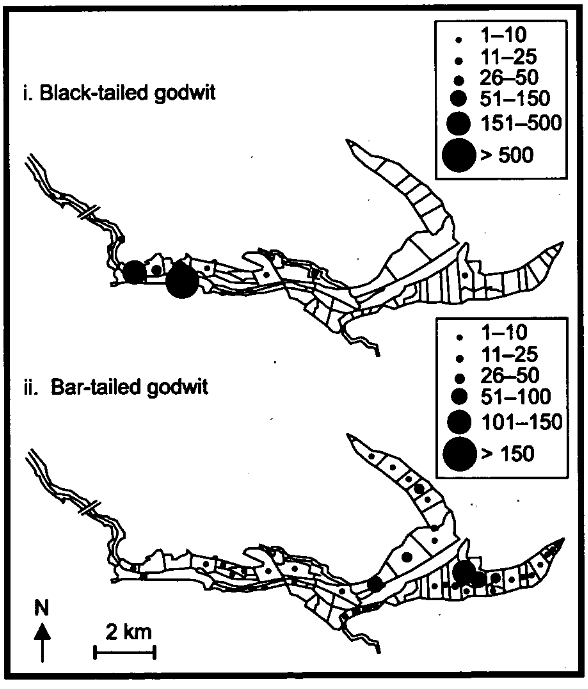

Figure 4. Differences in distribution between (i) black-tailed godwit and (ii) bar-tailed godwit on the Swale estuary during the 1992–93 winter

USES OF WeBS LOW-TIDE COUNT DATA

So far the results have been used in three main ways.

To identify the relatively important low-tide feeding areas on an estuary

This can be carried out at two levels. Distribution maps for all species combined depict the overall usage by waterfowl (Figure 3). Distribution maps for individual species demonstrate that different areas of an estuary are important for different species (Figure 4).

To identify changes in distribution throughout the winter which may be related to food supply

When pale-bellied brent geese (*Branta bernicla hrota*) first arrive on Strangford Lough in Northern Ireland, they concentrate at the northern end of the Lough where there are extensive *Zostera* beds on which they feed. Later in the winter, when these food supplies are depleted, the numbers of geese present on the estuary at low tide decline and they become more widely distributed and occur at lower densities (Figure 5).

To obtain a clearer picture of the use made by waterfowl of the estuarine system throughout the tidal cycle

Used in conjunction with the high-tide counts, low-tide counts can illustrate more clearly what has happened post-development, for example at Portsmouth Harbour on the south coast of England. High-tide counts suggest that grey plover (*Pluvialis squatarola*) numbers crashed after an area of land claim was developed in 1987. However, low-tide counts reveal that substantial numbers still feed within the harbour (Figure 6) and it is their roosting behaviour that has changed. Because this development took place before the WeBS low-tide counts began, there is no information on how many birds fed in the harbour before this development took place. It is possible that more birds fed in the harbour when a roosting area was available that was nearer their feeding areas. WeBS low-tide counts mean that in future the baseline information will be available.

WeBS LOW-TIDE COUNTS AS A PREDICTIVE TOOL

If the overall objective is to be able to predict

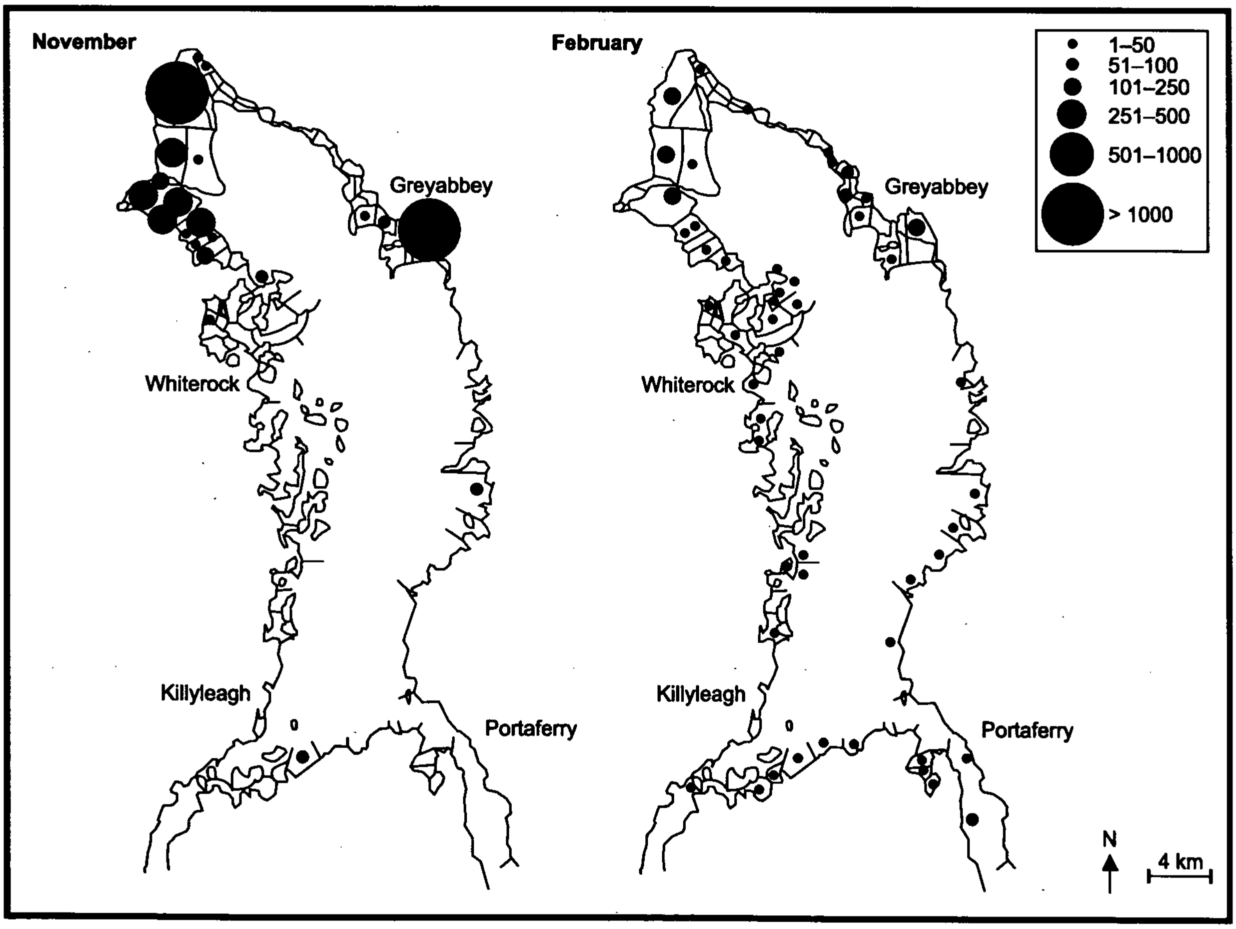

Figure 5. Differences between the low-tide distribution of pale-bellied brent geese in November and that in February during the 1992–93 winter

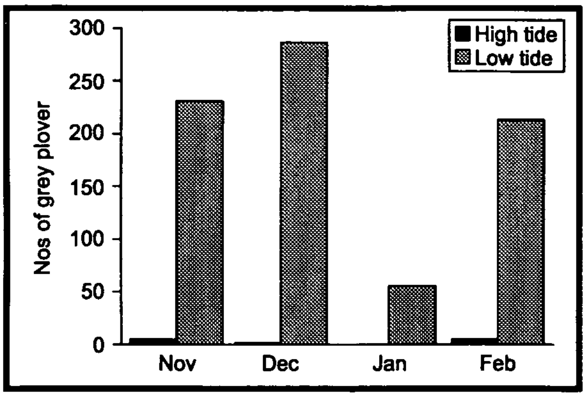

Figure 6. Differences between the high-tide and low-tide counts of grey plover in Portsmouth Harbour during the 1992–93 winter

the numbers of birds whose feeding areas would be affected by a given land claim, then the first step would be to identify the important feeding areas, which is what low-tide counts seem to do (Figures 3 & 4). However, if we are to use these counts predictively, we need to know how consistent they are between months and between years.

Consistency between months

So far, data have been collected from 29 estuaries round the UK and data for 20 of these were used to test for consistency. The data were analysed on a species-by-species basis because, as demonstrated earlier, there is variability between species in the extent to which low-tide distribution and numbers are likely to change within sites.

I made a between-month comparison of the density of each species on each mudflat using Spearman rank correlation. I then calculated the percentage of significant results obtained for each species in order to provide a crude measure of differences in the predictability of different species' distribution within estuaries. Overall there was extremely good consistency (Table 2) and the consistency ranking of each species was compatible with the species' ecology. Oystercatchers (*Haematopus ostralegus*), for example, tend to feed on localised food sources such as mussel (*Mytilus edulis*) or cockle (*Cerastoderma edule*) beds and therefore one would expect their distribution to be consistent between counts. Golden plovers (*Pluvialis apricaria*), on the other hand, roost on the intertidal area but feed on surrounding farmland, and the numbers present tend to vary according to the severity of the weather. It is not surprising, therefore, that this is the species with the least consistent distribution between counts. Interestingly, wader distribution appeared to be no more consistent than wildfowl distribution, despite differences in the species' feeding ecology.

In addition to confirming that waterfowl distribution is consistent between counts, we may also be able to use these measures of predictability as a measure of vulnerability to development. Those species with a less predictable distribution, ie more mobile species, which are less obviously threatened by a localised development may in fact require a larger intertidal area to be safeguarded than those which are less mobile.

Consistency between years

It will not be possible to test whether counting once every five winters is adequate for conservation purposes until the scheme has been running for several more years, and the second round of counts on each estuary has begun. However, on a few estuaries, low-tide counts had already taken place before the WeBS low-tide counts began, using the same methods. I used data

Table 2. Percentage of significant correlations between counts for each of the 19 most frequently recorded species

Species	%	Species	%
Oystercatcher *(Haematopus ostralegus)*	79.5	Lapwing *(Vanellus vanellus)*	63.3
Wigeon *(Anas penelope)*	75.5	Mallard *(Anas platyrhynchos)*	63.2
Pintail *(Anas acuta)*	75.4	Shelduck *(Tadorna tadorna)*	62.7
Redshank *(Tringa totanus)*	72.6	Knot *(Calidris canutus)*	55.7
Teal *(Anas crecca)*	71.8	Ringed plover *(Charadrius hiaticula)*	50.5
Turnstone *(Arenaria interpres)*	71.7	Brent goose *(Branta bernicla)*	49.4
Dunlin *(Calidris alpina)*	71.2	Sanderling *(Calidris alba)*	48.0
Bar-tailed godwit *(Limosa lapponica)*	65.8	Black-tailed godwit *(Limosa limosa)*	44.8
Curlew *(Numenius arquata)*	65.2	Golden plover *(Pluvialis apricaria)*	43.3
Grey plover *(Pluvialis squatarola)*	64.5		

Table 3. Consistency of bird distribution between years on the Duddon estuary (*** P>0.001)

	1992–93	1993–94	1994–95
Shelduck	0.75***	0.78***	0.73***
Oystercatcher	0.78***	0.80***	0.76***
Grey plover	0.84***	0.56***	0.55***
Lapwing	0.16	0.28	0.18
Dunlin	0.82***	0.69***	0.76***

from two estuaries, the Duddon and Southampton Water, to make between-year comparisons of waterfowl distribution.

The Duddon estuary is a large estuary in the north-west of England, of which a large proportion of the intertidal area consists of highly mobile sediments. It might therefore be expected that waterfowl distribution would differ significantly between years. However, a comparison of waterfowl distribution using low-tide counts carried out between 1992 and 1995 suggested that the distribution of all species had changed very little during this period (Table 3).

Southampton Water, on the south coast of England, is a large estuary of which a high proportion of the original intertidal area has suffered land claim and development. The threat of future development means that it is important to know whether low-tide counts can be used to predict the effects of development on waterfowl. A comparison of waterfowl distribution using counts carried out in the winters of 1990–91 and 1994–95 showed that the distribution was very similar between the two years for all species, except teal (*Anas crecca*), dunlin (*Calidris alpina*) and black-tailed godwit (*Limosa limosa*). All three of these species tend to be associated with areas of muddy sediment rather than sand, suggesting that a particular change or combination of changes within the estuary, which took place between 1990–91 and 1994–95, resulted in this apparent change in distribution. The ongoing effects of land claim and dredging, which alter the siltation processes within the estuary, are one possible reason. However, what these changes may have been is largely a matter of guesswork and highlights the need for a multidisciplinary approach to predictive studies. These results suggest that WeBS low-tide counts can be used as one component of these studies.

The WeBS low-tide count scheme is still a relatively young scheme which may require further refinements. It will need to continue for a few more years before its full potential can be realised. In the meantime, however, it remains a further improvement in our ability to predict the effects of habitat loss on waterfowl in the UK.

ACKNOWLEDGEMENTS

I would like to thank all the volunteers who take part in WeBS for the immense amount of hard work that went in to the datasets I have used in this paper, and my colleagues and friends at the BTO for their help and support with the setting up and running of the WeBS low-tide counts.

Improving the accuracy of predicting the local effects of habitat loss on shorebirds: lessons from the Tees and Orwell estuary studies

P R Evans

Department of Biological Sciences, University of Durham, Science Laboratories, South Road, Durham DH1 3LE, UK

SUMMARY

Two case studies are summarised to indicate the limitations of attempts to predict how many shorebirds will use an estuary or intertidal site after the loss of some feeding areas and some feeding time. The importance of including consideration of the method of land claim is stressed, as this may have profound effects on the nature of the sediments, and therefore feeding opportunities for different species, in the habitats that remain.

Losses of intertidal habitats from coasts and in estuaries have occurred in two main ways:

- by enclosure of upper tidal zones, often followed by infilling to raise the level of the land, to prevent further inundation and allow building to take place upon it,
- by excavation of a strip of land covering all tidal levels from high-water mark to low water and below, to allow the creation of port facilities.

In the future, a third situation may arise in many parts of the world in which, through sea level rise, the lower intertidal zones will be lost as they will remain permanently submerged. A similar situation, *viz* raised low-water levels, can occur upriver of some estuarine barrages built to generate tidal power. All three scenarios result in the loss of feeding areas for shorebirds (unless, with sea level rise, land at present above high-water mark is allowed to be inundated by the sea). Removal of only the upper tidal zones will also lead to a reduction in the maximum time for which shorebirds can feed during each tidal cycle.

RESEARCH REQUIRED TO PREDICT LOCAL EFFECTS OF HABITAT LOSS

In attempting to predict the effects of loss of habitat, the question most often posed by planners and developers is whether the existing numbers of birds could be supported by the smaller area that would remain and, if not, how many would be lost. A variety of empirical approaches have been or could be used to address this question:

- calculation of the total biomass of different major invertebrate prey species in the area that would remain and comparison with the estimated food requirements of the different shorebird species that use the total area of habitat at present (Evans *et al.* 1979);
- measurement of the time required during a tidal cycle for each species to obtain its normal requirements;
- measurement of spacing behaviour of different species which might set an upper limit to the density of birds ha^{-1};
- measurement of areas of each substrate type (and present usage) within the total area, and within the area that would remain, together with studies on substrate preference of each bird species.

Such approaches have almost always predicted reductions in the numbers of at least some of the shorebird species present if some habitat was to be lost. However, possible interactions between two or more bird species over feeding space or, in some cases, over a particular prey species have usually been ignored. Studies of interspecific competition in shorebirds are few, so predictions are uncertain.

TESTING THE ACCURACY OF PREDICTIONS

A major problem in moving towards *quantitative* assessment of the accuracy of predictions is to choose the most relevant data for before/after comparisons, particularly when the datasets cover a period of only a few years. For calculation of local (within-estuary) effects of habitat loss on wintering populations of shorebirds, some authors have compared the mean value of *the maximum count in December–February* of each year, before loss of habitat, with the mean value afterwards (eg Schekkerman, Meininger & Meire 1994). This method may be appropriate in areas which lose birds by emigration if severe weather occurs during a winter, but may lead to unreliable conclusions if applied to areas such as eastern England which may receive influxes of certain species during severe weather.

For example, if the winter before habitat loss occurs is mild, but that after habitat loss is severe, more dunlin (*Calidris alpina*) may be present in the second winter, suggesting that the capacity of the reduced area of estuary to hold birds had somehow increased. In reality, in the second (severe) winter, birds had been forced to leave their normal wintering areas (or die) and had then reached the estuary where habitat had been lost. It is very difficult to measure the proportion of such an influx, or of the numbers of pre-existing birds they join, that can be supported over a sustained period. In total, they may exceed the 'carrying capacity' defined by Goss-Custard (1985) as the number above which addition of another bird would lead to the death or emigration of one already present. This capacity varies seasonally, because the density of invertebrate prey of shorebirds declines from autumn to spring and, more importantly, its availability varies with temperature (Evans & Dugan 1984). Most prey species living in, rather than on, soft sediments become least available in the coldest conditions.

It might be argued, therefore, that the best season in which to compare carrying capacities, before and after habitat loss, would be during the winter when they are at their lowest. (Indeed, if predation on shorebirds by raptors does not remove many individuals after mid-winter, then the numbers of birds surviving that cold period of the year should be closely related to the potential breeding populations for the following summer.) At present, no formula has been produced to allow quantitative prediction of the change in instantaneous carrying capacity with differing degrees of severity of weather, independent of habitat area and absolute density of prey. Hence, testing the accuracy of predictions of the local effects of habitat loss on bird populations by comparing numbers in winters of different severity is fraught with difficulty.

I suggest that the most appropriate numbers for before/after comparisons are the *mean numbers* choosing to settle on an estuary *at the end of the normal migration period* in autumn. For most species in Britain, October or November counts provide such figures, but early December counts are more appropriate for grey plover (*Pluvialis squatarola*), at least in north-east England (as may be deduced from Townshend 1985). Ideally, the usual pattern of month-to-month change should be established for each species in the estuary where habitat loss is anticipated, so that the appropriate month can be chosen for the comparison of before/after site use. From amongst those arriving at the site during migration, some individuals of a species may be pre-programmed to go further, others will settle briefly but then move on, others may be driven out, yet others will remain (Townshend 1985; Evans & Townshend 1988). The choice made by individuals will depend upon the area of the site, numbers of conspecifics already there, predation risk, and the density of available food. Provided that the site does not lie at the end of a migration route, and so receive migrants in only those autumns following high production of young, the numbers settling should be limited only by the 'carrying capacity' of the area (*sensu* Goss-Custard 1985). These numbers should be independent of the numbers arriving, though this has not been tested.

TYPES OF RESPONSE TO HABITAT LOSS

Different species of shorebird differ in their degree of faithfulness, between years, to a non-breeding ('wintering') site. If the ability of a site to support a species is reduced considerably, one could envisage several outcomes for a site-faithful species when birds return in the autumn after habitat loss.

- All surviving adults crowd into the smaller area, so that numbers settling decrease from those in the previous year by the

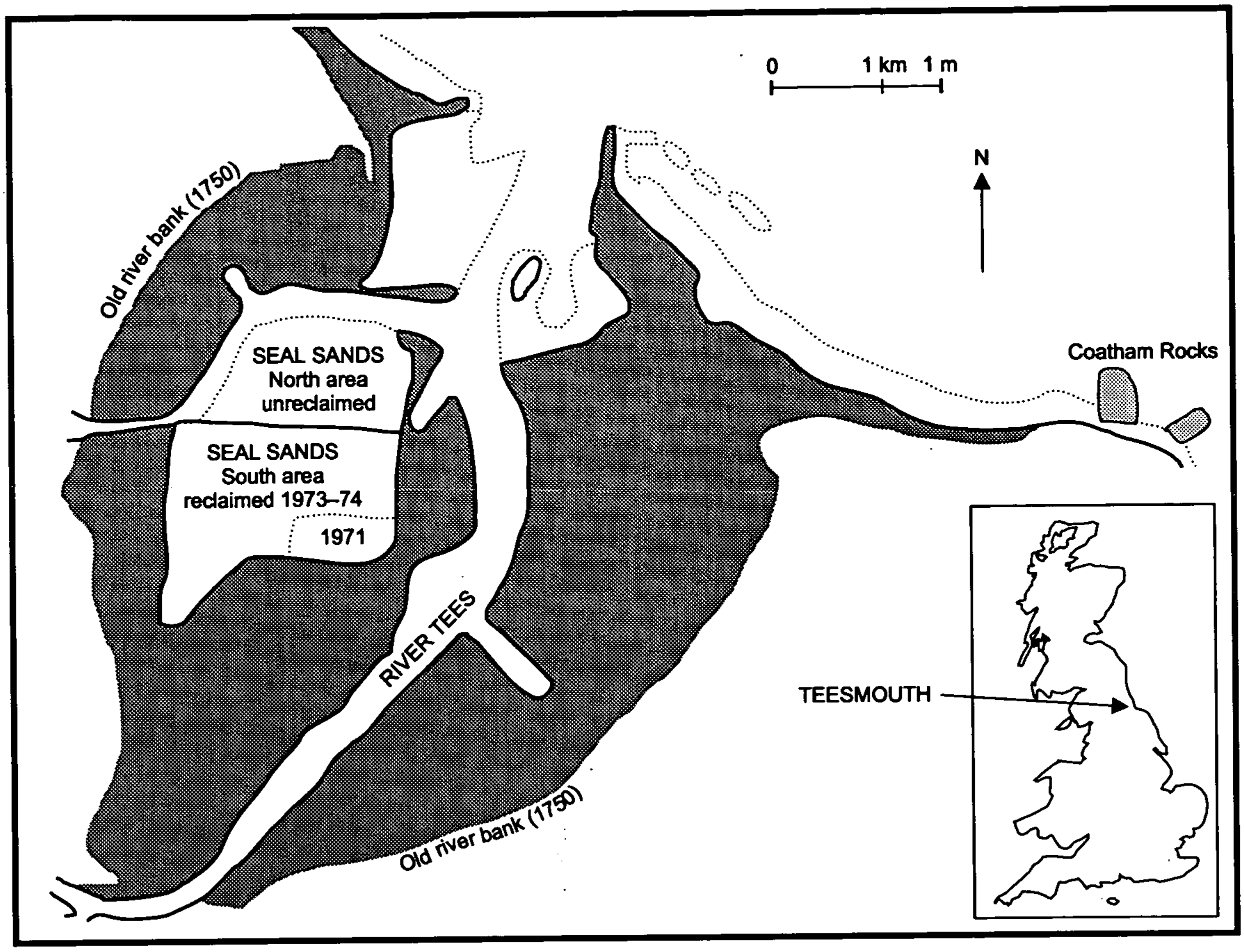

Figure 1. The Tees estuary

annual adult mortality; no juveniles choose/ are allowed to settle.

- Fewer adults than those which survive from the previous year choose to settle; some move elsewhere; no juveniles settle.
- Fewer birds in total settle, but they comprise both adults and juveniles; some adults and juveniles move elsewhere.

The outcome may be influenced by the relative timing of the arrival of adults and juveniles. In Europe, adults of many species moult in early autumn on a few large estuaries; only after their new plumage is complete do they move to their final wintering sites, many on smaller estuaries. The result of their arrival after many juveniles have already settled may be to displace some juveniles (eg grey plover; Townshend 1985). If applied to the situation resulting from habitat loss, one might expect that the birds unable to settle would be those with lower competitive abilities, often juveniles. No details have been published of the proportions of juveniles using a site before and after habitat loss.

THE EFFECTS OF LOSS OF HABITAT ON THE TEES ESTUARY

Background

The Tees estuary (Figure 1) is one of the most heavily industrialised sites in Europe. By 1971, only 15% remained of the 2500 ha of intertidal areas present at the beginning of the 19th century. Also by 1971, 60% of the main feeding area of shorebirds on the estuary, Seal Sands, was enclosed by a porous slag wall, through which the tide ebbed and flowed some two hours behind the tidal cycle in the rest of the estuary. This enclosed area was infilled by stages with dredgings pumped from the river, from summer 1973 to early spring 1974, by which time only 140 ha remained. The method of infilling led to deposition of larger-grained sediments within the enclosures, but silt and water flowed out through the porous wall, carving several channels through the remaining outer mudbanks and depositing liquid muds over the surface for some hundreds of metres from the wall (Figure 1).

The announcement that infilling would proceed in summer 1973 was made at six

Table 1. Numbers of shorebirds settling in autumn on Seal Sands, Teesmouth, during and after loss of habitat and feeding time

Year	1972	1973	1974	1975	1976	1977	1990–94
Intertidal area (ha)	360	260	140	140	140	140	140
Max feeding hours in tidal cycle	122	122	8–9	8–9	8–9	8–9	8–9
Shelduck *(Tadorna tadorna)*	1900	1300	1280	2600	3400	2100	823 (81)
Oystercatcher *(Haematopus ostralegus)*	?	?	120	?	150	?	145 (24)
Ringed plover *(Charadrius hiaticula)*	50	5	?	?	?	20	51 (11)
Grey plover *(Pluvialis squatarola)*	[200]	100	80	100	46	90	121 (28)
Bar-tailed godwit *(Limosa lapponica)*	[600+]	220	75	70	30	130	108 (60)
Curlew *(Numenius arquata)*	380	290	150	280	250	300	341 (88)
Redshank *(Tringa totanus)*	1000	900	190	400	?	600	490(106)
Dunlin *(Calidris alpina)*	[15000+]	9700	6000	4000	4700	3900	990(220)

Note: Figures in square brackets are estimates; figures in parentheses are standard errors

months' notice, so that detailed studies of bird numbers and foraging behaviour could not be started until the late winter of 1972–73. Work on invertebrate abundance and bird diets had begun in 1971. Because all the higher tidal zones were lost by the form of the land claim, shorebirds suffered not only a reduction in area available for foraging but also in maximum time for feeding during a tidal cycle, to about 4 hours on either side of low water. This reduction in feeding time did not happen until spring 1974, whereas some reduction in feeding area had already occurred by autumn 1973 (Table 1). Predictions of the effects of habitat loss, made in 1973, are summarised by Evans and Pienkowski (1983).

Predictions of changes in shorebird numbers

Pienkowski (1973) measured the average duration of feeding during each daylight tidal cycle by each shorebird species, and concluded that 'difficulties can be expected for dunlin and redshank (and probably ringed plover) for much of the time [= winter]; for grey plover and bar-tailed godwit some of the time; only marginally for knot and curlew; and not at all for shelduck and oystercatcher'. Evans *et al.* (1979) measured invertebrate densities on the area of Seal Sands that was to remain after infilling and concluded that it supported insufficient macrobenthic animals to feed all the shorebirds which used to winter on the whole of Seal Sands. Evans, therefore, predicted that the species most likely to be reduced in numbers were those which fed primarily on ragworms (*Nereis diversicolor*) (namely curlew (*Numenius arquata*), bar-tailed godwit (*Limosa lapponica*) and grey plover) and on mud-snails (*Hydrobia ulvae*), the only other common 'large' invertebrate found on Seal Sands at that time. (Redshank (*Tringa totanus*) were thought to be vulnerable in this respect.) Evans and Pienkowski (1983) drew attention to the impossibility in the 1970s of attempting to calculate the severity of reductions in numbers of the different species because very little knowledge was available on the adaptability of each species in its feeding methods and preferences. Such information is more readily available today. Another uncertainty was whether birds would respond to a reduction in food resources by a reduction in the time for which they stayed at Teesmouth during the winter, rather than by a reduction in numbers settling in autumn. As documented by Evans (1978–79), the seasonal pattern of use of the estuary by each species did not change after habitat loss, except that some dunlin disappeared during a period of cold weather.

Accuracy of the predictions

Two methods were used to assess the outcome of habitat loss. Evans (1978–79) focused on changes in the numbers settling in autumn, whereas Evans and Pienkowski (1983) used mid-winter numbers in different years as the basis for comparison. The advantage of the second approach in this particular study was that accurate counts of feeding birds were not available until January 1973 in the winter immediately before loss of habitat occurred. Estimates of numbers settling in autumn 1972 had to be derived from roost counts which may not have been complete (definitely not for dunlin) and sometimes included birds feeding elsewhere on the estuary. The disadvantages of the mid-winter comparisons were that numbers of some species were affected by a period of cold weather in January 1974, during the winter after some loss of habitat had taken place, and that later studies showed that numbers of curlew and redshank always declined through the autumn and rose in late winter, even in mild conditions, as many birds moved to feed in fields near the estuary in autumn (Townshend 1981).

Table 1 includes data published by Evans (1978–79) together with additional data from Townshend (1981) and from recent detailed year-round counts covering a period of five autumns (1990–94) some 20 years after habitat loss took place (Evans, Ward & Mercer 1996).

A thorough discussion of the changes in numbers of birds settling in autumn was provided by Evans (1978–79). This included comparisons between 1972 and 1973 (loss of feeding area) and between 1973 and 1974 (loss of both feeding area and feeding time). Most of the predictions made in 1973 and outlined above of the effects of habitat loss on the different species were borne out by the counts in later years, at least in qualitative terms. In retrospect, this is somewhat surprising, as no information was available in 1973 on the scale of nocturnal feeding, so that predictions based on loss of feeding time might have been inaccurate. Also, the importance of non-tidal wetlands close to the estuary as supplementary feeding sites during high water had not been appreciated (Davidson & Evans 1986).

Longer-term effects of the method by which the intertidal land was claimed, *viz* enclosure and infilling with a slurry of dredgings, are apparent from Table 1. The marked increases in shelduck (*Tadorna tadorna*) numbers feeding on the reduced area of Seal Sands in winters 1975–76 and 1976–77 were probably the result of larger extents of fine soft muds providing excellent feeding substrates. As these sediments consolidated (and more recently as incursions of sand were deposited over the eastern parts of Seal Sands), shelduck numbers have decreased considerably. Dunlin, which also prefer feeding on muddy substrates, have also decreased in recent years, but they did not show parallel increases to those recorded for shelduck in the winters immediately after habitat loss, probably because of inadequate time for feeding. As substrates consolidated in the late 1970s and became sandier in parts, numbers of bar-tailed godwits and ringed plovers (*Charadrius hiaticula*) have also increased. Superimposed upon these sediment changes have been changes in abundance of certain invertebrates, eg colonisation of, and then disappearance from, large parts of Seal Sands by the amphipod *Corophium volutator*. Redshank numbers in autumn have varied in parallel with *Corophium* abundance in the last five years, though the correlation between bird density and prey density in different parts of Seal Sands was not significant (Evans, Ward & Mercer 1996).

Conclusions

Habitat loss at Seal Sands was on a large enough scale to allow changes in numbers of some shorebird species, resulting from loss of feeding area and/or feeding time, to be detected against the background of year-to-year variability in numbers arising from natural causes. Unfortunately, the fate of the birds that disappeared was not established, as none was marked. Predictions did not take account of the changes in substrates on the area remaining after habitat loss.

THE EFFECTS OF LOSS OF HABITAT ON THE ORWELL ESTUARY

Background

The port of Felixstowe, Suffolk, has expanded from its original coastal location into the mouth of the Orwell estuary, towards Fagbury Point (Figure 2), through a succession of southward developments from 1964 onwards. The most recent were in 1985–86, with construction of the Trinity

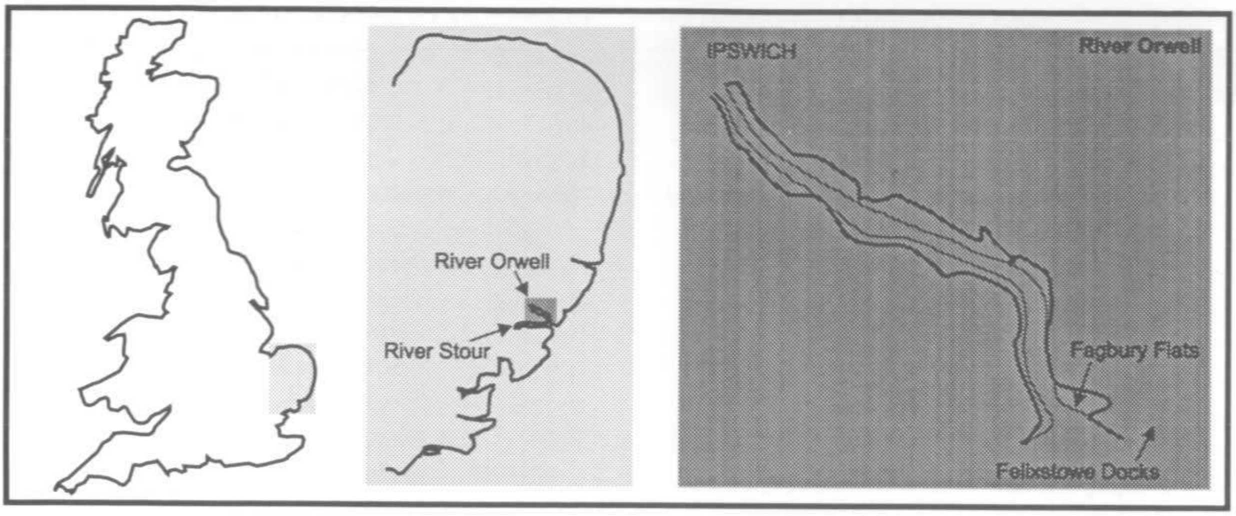

Figure 2. The Orwell estuary

Terminal, which caused some loss of intertidal habitat and deterioration of feeding conditions for shorebirds; and more particularly in the winter of 1988–89, in which a strip of land between low- and high-water marks, comprising 19 ha of the remaining 34 ha of intertidal mussel beds, mud and sandflats, was enclosed and infilled. Overspill of sediments from the infilling process altered the character of several of the 15 ha of intertidal flats that remained (Wright 1989). The significant ornithological importance of the Orwell estuary was documented by Ravenscroft (1987) and summarised by Davidson and Evans (1985), as part of an assessment of the implications for nature conservation of the (proposed) 1988–89 developments.

Counts of birds roosting at Fagbury have been made for many years as part of the Wetland Bird Survey (former Birds of Estuaries Enquiry). Unfortunately, not only birds which feed on the Orwell but also on the adjacent Deben and Stour estuaries may use the Fagbury roost; hence, it is difficult to deduce the effects of loss of feeding habitat at Fagbury Flats simply from roost counts. Accordingly, simultaneous counts at low water of birds feeding along discrete stretches of both banks of the whole Orwell estuary were made in 1984–85 and 1985–86, and again in the winter of development (1988–89) and three subsequent winters, to enable quantitative assessment of the effects of habitat loss. Additionally, more detailed and frequent counts of bird use and feeding on Fagbury Flats alone were made between 1988–89 and 1991–92 by M T Wright. These data have been made available by the Suffolk Wildlife Trust.

The situation before habitat loss

The report to the Nature Conservancy Council by Davidson and Evans (1985) was based chiefly on data from recoveries of ringed birds and on detailed observations at Fagbury and elsewhere on the Orwell of the distribution and numbers of various shorebird and wildfowl species in only one winter (1984–85), which included periods of very severe weather, early in 1985.

On the basis of the order of occupation of different sectors of intertidal land by birds feeding along the Orwell, they concluded that Fagbury Flats (which held the only mussel beds) were the preferred feeding areas on the estuary during the whole non-breeding season for oystercatchers (*Haematopus ostralegus*), ringed plovers, grey plovers and turnstones (*Arenaria interpres*), and in autumn also for dunlin, curlew and shelduck. (Most shelduck deserted the area in winter.) For four species, the percentages of the total estuary populations feeding on the Fagbury mudflats were much higher than the 6% which these flats formed of the total intertidal area on the Orwell. Up to 94% of oystercatchers fed at Fagbury, 51% of ringed plovers, 54% of grey plovers, and 45% of turnstones. These percentages varied with the date and weather conditions. During the very cold weather early in 1985, substantial influxes of oystercatchers and dunlin occurred and both numbers and proportion of the total Orwell population feeding at Fagbury increased. Davidson and Evans

(1985) suggested, therefore, that the site was particularly important during severe weather.

They predicted that loss of the Fagbury feeding areas would particularly affect oystercatchers (which fed chiefly on the mussel beds), ringed and grey plovers (which fed preferentially on firm sediments, scarce on the Orwell) and turnstones (which also fed chiefly on the mussel beds, though probably chiefly on other invertebrates found within them). They predicted that total Orwell populations of these species would decline if displaced birds were unable to settle elsewhere on the Orwell (in less preferred types of intertidal habitats). Although Fagbury was not a preferred feeding area for redshank in 1984–85 and not for dunlin in winter, studies of individuals of these species colour-marked at Fagbury showed very little movement to feeding areas elsewhere on the Orwell or on other nearby estuaries. Davidson and Evans (1985) therefore predicted that the total Orwell populations of these two species would decline if Fagbury mudflats were to be lost to dock development. A final prediction concerned the effects of severe weather: under such conditions, birds displaced from nearby estuaries or from upstream on the Orwell by ice forming over intertidal areas would not be able to settle at Fagbury, the most marine feeding site, after dock development. This was expected to lead to reductions in survival of some oystercatchers and black-tailed godwits (*Limosa limosa*) that usually feed on the Stour and of redshank from the upper reaches of the Orwell.

The validity of the predictions

Partial loss of Fagbury Flats did not take place until the winter of 1988–89. Meanwhile, during construction of the Trinity Terminal in the summer of 1985, sand slurry was discharged over part of the Flats and presumably led to a deterioration in feeding conditions, as maximum numbers of all six species (even those which did not show cold-weather influxes in February 1985) were less in winter 1985–86 than they had been in winter 1984–85 (Table 2). Disturbance from construction work may also have been a reason for the lower peak numbers in the second winter (Ravenscroft 1987). Unfortunately, further detailed counts at Fagbury did not take place until the winter of 1988–89, when 19 ha of the remaining 34 ha of intertidal land were enclosed, amid considerable disturbance. Peak winter counts for the following three winters are listed in Table 2; of these, 1990–91 was severe but the other two were mild.

Probably the most valid comparisons based on peak counts are those between the bird numbers and densities in the three milder winters of 1985–86, 1989–90 and 1991–92 (though even in 1985–86 there was a brief spell of cold weather in February 1986). In all cases, numbers in 1989–90 were lower than in 1991–92, possibly a result of destabilisation of the sediments after the intertidal land claim of 1988–89. As Table 2 indicates, numbers of ringed plovers increased between 1985–86 and 1991–92, of turnstone and grey plover scarcely changed, but of oystercatcher, dunlin and redshank decreased. Densities of feeding birds of the first three species increased, as also of oystercatcher, but of dunlin and redshank decreased. These

Table 2. Peak winter counts (Nov–Feb) of feeding shorebirds before and after habitat loss on Fagbury Flats

No. of counts	13	8		24	31	31	
Winter	1984–85	1985–86		1989–90	1990–91	1991–92	
Feeding area available (ha)		34			15		
Species	Nos	Nos	Density (nos ha^{-1})	Nos	Nos	Nos	Density (nos ha^{-1})
Oystercatcher	678(Jan)	228(Feb)	6.7	34(Feb)	74(Feb)	134(Jan)	8.9
Ringed plover	92(Feb)	24(Jan)	0.7	31(Feb)	33(Jan)	58(Feb)	3.9
Grey plover	64(Dec)	31(Nov)	0.9	27(Dec)	30(Jan)	35(Feb)	2.3
Dunlin	1565(Jan)	1530(Feb)	45.0	353(Nov)	224(Feb)	483(Dec)	32.2
Redshank	245(Jan)	117(Feb)	3.4	21(Nov)	32(Nov)	40(Nov)	2.7

Table 3. Numbers of six shorebird species at low water on Fagbury Flats in six autumns

Winter Species	1984–85	1985–86	1988–89	1989–90	1990–91	1991–92
Oystercatcher	271	95	23	4	10	22
Ringed plover	40	7	15	8	6	0
Grey plover	64	16	48	27	8	13
Dunlin	980	450	616	353	57	483
Redshank	124	103	160	21	32	40
Turnstone	40	12	22	9	9	0

changes were accompanied by a change in the nature of the surface substrate of some of the surviving 15 ha of intertidal land, from muds to sands, a result of overspill of the sandy material used to infill the enclosed land. Thus, irrespective of any changes in invertebrate densities, the habitat became more suitable for the plovers and less suitable for the two species that feed preferentially on muddy areas.

A better way to examine the effects of habitat loss at Fagbury could be to compare the numbers of each species settling there at the end of their normal autumn migration in the different years. To establish the normal migration timings, counts of the whole Orwell estuary are probably the most appropriate for examination, and these are most frequent in 1984–85. They suggest that most oystercatcher passage finished by late October, ringed plover, turnstone and redshank by late November, and grey plover and dunlin by early December (these generalisations exclude, therefore, effects of periods of cold weather).

Table 3 attempts to establish the size of the potential wintering populations that settled by choice at Fagbury in the different years, based on the timings of end of passage stated above. As may be seen, the effects on numbers settling by choice are much greater than on the peak numbers counted. This raises again the question whether the peak numbers in a winter are sustainable and suggests that the cold-weather influxes (and possibly the early spring migration influxes of certain species in mild Februaries (Table 2)) may have exceeded the instantaneous carrying capacity of the site. Table 3 also highlights that, with the exception of oystercatcher, all species settled in larger numbers in autumn 1988, before infilling and habitat loss commenced (in December) than they had done in autumn 1985. The severe reduction in numbers between autumns 1988 and 1989 is perhaps a better indication of the combined effects of loss of area and, as described by Wright (1989), major effects outside the development area, *viz* the deposition of a layer of consolidated silt over parts of the remaining intertidal land.

An important question raised by the decreases in numbers of birds feeding on Fagbury Flats is whether numbers settling on the whole estuary decreased in parallel. Table 4 summarises information on the numbers of the six species that settled on the whole estuary after autumn migration in the different years.

As may be seen by comparing Tables 3 and 4, the changes in numbers using the whole estuary from year to year were usually far

Table 4. Numbers of six shorebird species at low water on the whole Orwell estuary in six autumns

Winter Species	1984–85	1985–86	1988–89	1989–90	1990–91	1991–92
Oystercatcher	478	489	214	189	152	393
Ringed plover	234	173	204	274	152	35
Grey plover	182	206	252	193	200	122
Dunlin	12 947	8 933	9 837	8 396	5 308	8 873
Redshank	2568	1 516	1 575	1 439	1 630	1 652
Turnstone	189	166	147	191	225	97

greater than the changes in numbers feeding on Fagbury Flats, so that the decreases in numbers of all species at Fagbury between the autumns of 1988 and 1989 were masked in four cases by changes elsewhere in the estuary, for reasons unknown. Only for redshank and oystercatcher was there agreement between the size of the decline at Fagbury and on the whole estuary.

Movements of birds during the period of habitat loss in 1988–89

Birds captured and dye-marked during autumn 1988 at Fagbury were resighted throughout the winter. These sightings confirmed the detailed counts of feeding birds at Fagbury, namely that dunlin and redshank were mainly site-faithful until early and late January, respectively, several weeks after construction work began, but that grey plover stayed throughout the whole period of construction; ringed plover, however, moved around the estuary throughout the winter. When they left Fagbury in January 1989, dunlin are known to have moved to three other sectors of the river (C, D and E) but redshank only to C. The fates of these birds are unknown; none were recaptured or resighted in later winters. If 'displaced birds' had returned to the sectors to which they had moved in January 1989, increases might have been expected there, but none were detected by low-water counts in these sectors in autumn 1989.

Conclusions

Detailed observations over several winters showed that the numbers of birds settling in autumn on the remaining area of Fagbury Flats were less than had used the larger area before habitat loss. Nevertheless, the decreases were not in proportion to the loss of area, partly because of modification of the substrates of the remaining area by the land claim technique. In retrospect, it would have been instructive to have had separate counts of birds feeding on the area lost and the area remaining, before any land claim took place. The area lost (about 3% of the total intertidal area of the Orwell) and the numbers of birds involved were too small for several species to allow detection of the effects of the undoubted reductions in numbers at Fagbury on the Orwell numbers, when viewed against the background of high year-to-year variability of numbers on the whole estuary. Study of the fate of the displaced birds, by marking and recapture, also did not provide the quantity of information necessary to reach firm conclusions, even though 724 birds (679 of which were dunlin) were marked in the autumn and winter of 1988–89. This figure represents some 7% of the total shorebird numbers present in a mild winter. The man-hours required to achieve this were considerable; to have had a higher proportion of each species marked (and resighted) would have been very demanding.

PRIORITIES FOR FURTHER RESEARCH

If further examples of unavoidable habitat loss in estuaries take place with adequate advanced warning, it would be particularly valuable to obtain information on the characteristics of birds displaced, either during the land claim process if it occurs over winter, or between winters if it occurs over summer. The predictions would be that juveniles and/or smaller individuals would move, because these are the least competitive. A marking scheme enabling separation of large and small, adult and juvenile during resightings, would be valuable. If the birds excluded by habitat loss are the least capable of surviving on the estuary affected, then it seems probable that they would also be at greater risk than established birds if they tried to settle elsewhere in estuaries which were already 'full'.

Research on habitat preferences of different species would also be valuable to establish how far any preferences for feeding on particular substrates or in particular tidal zones apply to the whole of a species' non-breeding range.

ACKNOWLEDGEMENTS

I thank the many members of the Shorebird Research Group at the University of Durham for their contributions over the past 25 years; and Mick Wright and the Suffolk Wildlife Trust for allowing me to (mis-?)interpret their data from the Orwell study.

REFERENCES

Davidson, N.C. & Evans, P.R. 1985. *Implications for nature conservation of the proposed Felixstowe Dock expansion.* Report to the Nature Conservancy Council, Peterborough (Contract 2/85).

Davidson, N.C. & Evans, P.R. 1986. The role and potential of man-made and man-modified wetlands in the enhancement of the survival of overwintering shorebirds. *Colonial Waterbirds*, **9**, 176–188.

Evans, P.R. 1978–79. Reclamation of intertidal land: some effects on shelduck and wader populations in the Tees estuary. *Verhandlung ornithologische Gesellschaft Bayern*, **23**, 147–168.

Evans, P.R. & Dugan, P.J. 1984. Coastal birds – numbers in relation to food resources. In: *Coastal waders and wildfowl in winter*, edited by P.R. Evans, J.D. Goss-Custard & W.G. Hale, 8–28. Cambridge: Cambridge University Press.

Evans, P.R. & Pienkowski, M.W. 1983. Implications for coastal engineering projects of studies at the Tees estuary on the effects of reclamation of intertidal land on shorebird populations. *Water Science and Technology*, **16**, 347–354.

Evans, P.R. & Townshend, D.J. 1988. Site faithfulness of waders away from the breeding grounds: how individual migration patterns are established. *Proceedings of 19th International Ornithological Congress*, 594–603. Ottawa: University of Ottawa Press.

Evans, P.R., Ward, R.M. & Mercer, T. 1996. *An overview of the results of the monitoring programmes related to nature conservation concerns arising from the River Tees Barrage and Crossing Act 1990 for the years 1990–1994, before commissioning of the barrage.* Stockton-on-Tees: Teesside Development Corporation.

Evans, P.R., Herdson, D.M., Knights, P.J. & Pienkowski, M.W. 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and shelduck. *Oecologia*, **41**, 183–206.

Goss-Custard, J.D. 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In: *Behavioural ecology: ecological consequences of adaptive behaviour*, edited by R.M. Sibley & R.H. Smith, 169–188. Oxford: Blackwell Scientific.

Pienkowski, M.W. 1973. *Feeding activities of wading birds and shelducks at Teesmouth and some possible effects of further loss of habitat.* Report to Institute of Terrestrial Ecology, Norwich.

Ravenscroft, N.O.M. 1987. *Waders and wildfowl of the Orwell estuary 1983–86.* Ipswich: Suffolk Trust for Nature Conservation.

Schekkerman, H., Meininger, P.L. & Meire, P. 1994. Changes in the waterbird populations of the Oosterschelde (SW Netherlands) as a result of large scale coastal engineering works. *Hydrobiologia*, **282/283**, 509–524.

Townshend, D.J. 1981. *The use of intertidal habitats by shorebird populations, with special reference to grey plover and curlew.* PhD thesis, University of Durham.

Townshend, D.J. 1985. Decisions for a lifetime: establishment of spatial defence and movement patterns by juvenile grey plovers. *Journal of Animal Ecology*, **54**, 267–274.

Wright, M. 1989. *The response of wading birds to the loss of wintering habitat on the Orwell estuary.* Report to the Felixstowe Dock & Railway Company.

Saltmarsh carrying capacity and the effect of habitat loss on spring staging brent geese: two case studies using marked individuals

B Ganter & B S Ebbinge
IBN-DLO Department of Aquatic Ecology, PO Box 23, 6700 AA Wageningen, The Netherlands

SUMMARY
In this paper we synthesise two studies concerning the carrying capacity of spring staging sites for brent geese and the impact of the loss of a preferred spring staging site. First, it was shown that a large natural saltmarsh site was filled to capacity with spring staging brent geese whereas a nearby inland feeding site was not. There was evidence for mechanisms of competitive exclusion from the preferred site: young birds and males in poor body condition tended to be less likely to return to the preferred site. Second, birds that were followed after loss of a different large spring staging saltmarsh dispersed widely and appeared more often in less preferred areas than control birds. Reduction in subsequent breeding success or survival of displaced birds when compared to control birds could not be detected. These results suggest that, although some preferred natural spring staging habitats are filled to capacity and there may not be enough such areas to support the whole population in spring, numbers of dark-bellied brent geese are not currently limited by the availability of spring staging habitat.

INTRODUCTION

In order to be able to predict the effect of habitat loss and change on wetland birds, researchers must assess the importance of wetlands to individuals, local populations and overall populations of the birds. In this context, the following questions are important.

- What are the criteria for the preferential use of a wetland by birds?
- Is the carrying capacity of the wetland reached?
- Are other unused wetlands of similar quality available?
- What happens to individuals and populations of birds, immediately and in the long term, when this wetland is lost?

Ideally, studies of both carrying capacity and actual cases of habitat loss should attempt to document effects on individuals in terms of dispersal, reproductive success, and survival rates. Only by assessing the latter two parameters, which directly affect the fitness of the birds, can predictions about effects on overall populations be made.

In this paper we summarise results from long-term investigations on dark-bellied brent geese (*Branta bernicla bernicla*), concerning the carrying capacity of spring staging areas and the impact of habitat loss.

THE IMPORTANCE OF SPRING STAGING SALTMARSHES IN THE ANNUAL CYCLE OF BRENT GEESE

Dark-bellied brent geese are long-distance migrants from breeding areas in northern Siberia to staging and wintering areas in western Europe. In the spring most of them stage on saltmarshes in the Wadden Sea, where they build up body reserves very fast: body mass increases by about 30% within one month in late April and early May (Ebbinge *et al.* 1982; Ebbinge & Spaans 1995). Body condition at the time of departure in spring is an important factor influencing brent goose reproduction: individuals with a higher body mass on departure from the Wadden Sea have a higher chance of returning with young the following autumn (Ebbinge & Spaans 1995). On saltmarshes, brent geese can selectively feed on nutrient-rich plant species such as sea plantain (*Plantago maritima*) and sea arrowgrass (*Triglochin maritima*) (Prop & Deerenberg 1991), which makes the rapid mass gain possible and is therefore important for reproductive success. Brent geese show a high degree of site fidelity to their spring feeding sites on saltmarshes (StJoseph 1979; Prokosch 1984).

From the 1950s to the late 1980s, saltmarshes in the Wadden Sea have in some places been severely reduced by embankments. At the same time, the world population of dark-bellied brent geese has increased more than tenfold to around 250 000 birds in the first half of the 1990s. As a result, alternative inland feeding areas are now also used by brent geese in spring, but saltmarshes are the preferred habitat because of the higher nutritive value of saltmarsh plants (Boudewijn 1984).

The case studies summarised below address two questions related to brent geese on saltmarshes in spring.

- Are Wadden Sea saltmarshes 'filled' with brent geese so that they cannot accommodate any more of them?
- What are the consequences of the loss of a large part of saltmarsh to the brent geese that used to stage there?

COLOUR-RINGING AS A TOOL IN BRENT GOOSE RESEARCH

Since 1973, over 5000 dark-bellied brent geese have been individually marked with coded plastic leg rings that can be read in the field with a telescope at a distance of up to 300 m. Ringing has taken place in all seasons and in all parts of the range, with the main focus of the ringing activity shifting from England (1970s) to Germany and The Netherlands (late 1970s and 1980s) and, recently, to the breeding grounds in Siberia. Resightings of the ringed birds are made mainly by volunteer ring-readers in western Europe and are centrally stored, with detailed feedback to the observers provided at least once a year. Up to now, more than 130 000 resightings have been stored. About 20% of the sightings include information about relationships between birds (presence of partners and/or young). These data form the basis for numerous analyses of brent goose ecology involving individual birds. Apart from data on individual movements, analyses of environmental and demographic correlates of survival and breeding success are possible. Due to the largely non-systematic nature of data collection, there are complications for quantitative analyses of the resightings, but the large geographical scope of the colour-ringing scheme also offers many unique opportunities. The following case studies are based on various subsets of resighting data from this scheme.

CASE STUDY I: REGULATION OF BRENT GOOSE NUMBERS ON SPRING STAGING SITES

In a study of the factors governing the distribution of brent geese on their spring staging sites, Ebbinge (1992) used the recovery of the dark-bellied brent goose population and the wide annual fluctuations in breeding success as 'natural experiments' to investigate the carrying capacity of a prime spring staging site. This site, the saltmarsh of the Boschplaat Nature Reserve on the Dutch Wadden Sea island of Terschelling, was by far the most important spring staging site in The Netherlands when brent goose numbers were still low in the middle of this century. The Boschplaat was compared with an inland feeding area consisting of improved grassland on the nearby island of Texel, where brent geese did not occur in larger numbers in spring until the late 1970s. Although overall goose grazing pressure per unit area was higher on the Texel site, the Boschplaat, being a natural saltmarsh area, has vegetation of higher quality and the added advantage of a natural structure, with creeks offering shelter from predators.

Spring peak numbers in both areas were compared with the overall population size in the same years (31 years between 1958 and 1990 for the Boschplaat, 20 years between 1967 and 1990 for Texel). On the Boschplaat, spring peak numbers increased with the world population until the total population size was about 100 000 (1975–76) and then stabilised around 12 000 birds (with annual fluctuations related to environmental conditions). On Texel, however, numbers continued to increase with the world population until the end of the study in 1990; carrying capacity here was not yet reached (Figure 1). Exponential models fitted to the data for both sites confirmed that saturation on the Boschplaat was reached at a much faster rate than on Texel.

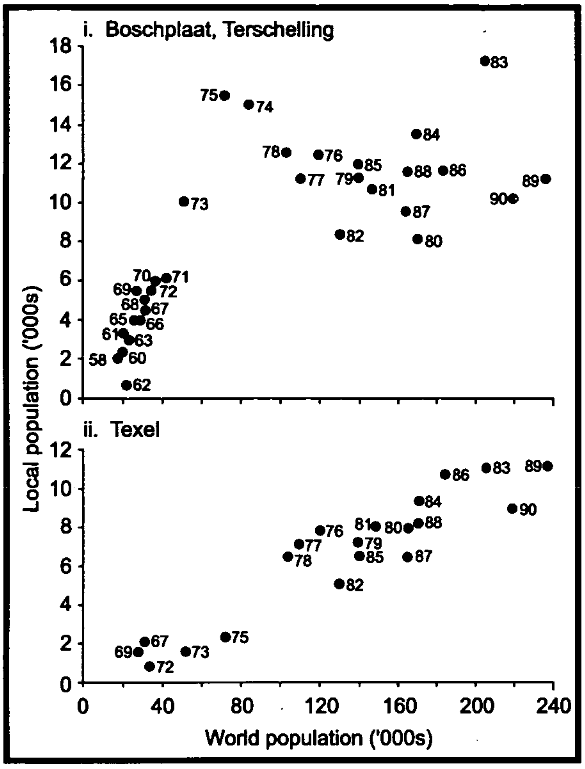

Figure 1. Spring peak numbers of brent geese on (i) Boschplaat and (ii) Texel as a function of world population size. Figures indicate years (reprinted with permission from *Ardea*, **80** (1992), 212)

Ebbinge (1992) further investigated the dynamics of immigration and emigration to and from the two areas. Annual adult survival rate was estimated to be 84%, and, because first-year birds accompany their site-faithful parents to the spring staging areas, there will be an excess of birds in those areas in springs following a successful breeding season (when the production of young exceeds adult mortality) and a deficit of birds in springs following a poor breeding season. In fact, after years with a high production of juveniles, fewer birds appeared on the Boschplaat in spring than would have been expected under the assumption of complete site fidelity, whereas there was an excess of birds on Texel. In springs following years with >30% young in the autumn population, between 4000 and 12 000 birds did not find room on the Boschplaat and had to go elsewhere. After poor breeding seasons (<1.5% young in the autumn population), there was an influx of 'foreign' birds to the Boschplaat and an efflux from Texel. This indicated that the saltmarsh area on the Boschplaat remains filled to capacity while the improved grassland site on Texel acts as a buffer that is used by brent geese when they cannot find room in more preferred areas.

The mechanisms leading to the exclusion of some birds from the preferred site were investigated by Ebbinge (1992) using colour-marked individuals. Birds were caught, marked and weighed both on the Boschplaat and on Texel, and observations of colour-ringed birds were made at both sites in subsequent years. Models fitted to the resighting data showed that, after successful breeding seasons (ie in springs with increased competition on the saturated site), heavier males had a higher probability of returning to the Boschplaat than lighter males, whereas there was no such relationship on Texel (Figure 2i). In years after a failed breeding season there was no significant effect of male body mass on probability of returning to either island (Figure 2ii). Thus, only in years with increased competition does body condition

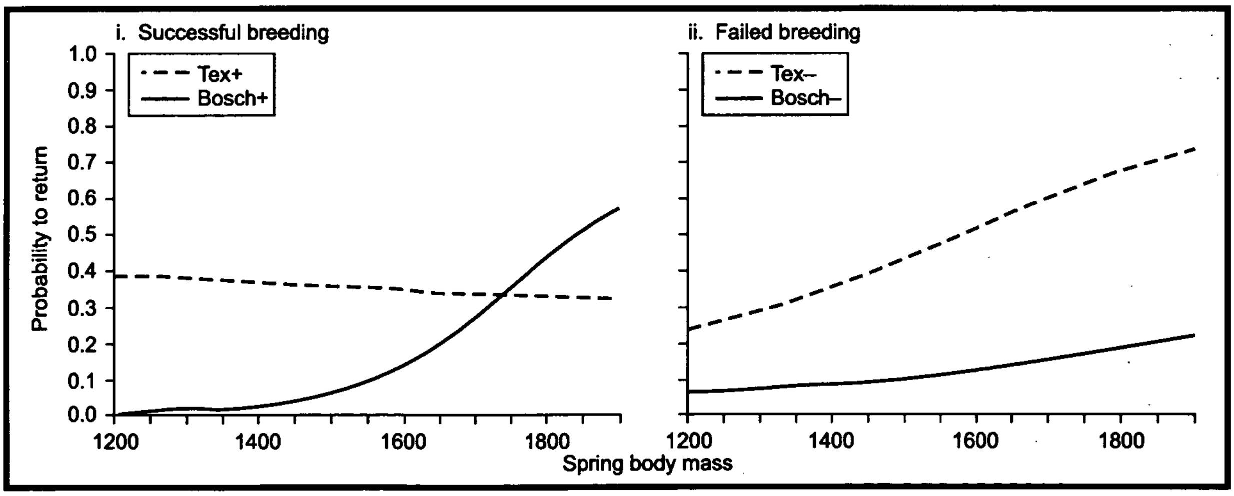

Figure 2. Predicted proportion of adult male brent geese returning in subsequent years to the same spring staging site, as a function of spring body mass, following (i) successful breeding (+) (increase in population size, and hence increased competition), and (ii) failed breeding (–) (reduced population size, and reduced competition). Bosch = Boschplaat, Tex = Texel (reprinted with permission from *Ardea*, **80** (1992), 219)

Table 1. Sightings of Rodenäs and control birds outside the ringing areas in spring, 1983–95. N = total number of individuals in analysis (ringed and resighted at any time after ringing); n = total number of individuals seen per site. For location of sites see Figure 3 (source: Ganter *et al.* (1997): reprinted with permission from *Aquatic Conservation*)

	Rodenäs birds (N=66)														Control birds (N=88)													
Year	83	84	85	86	87	88	89	90	91	92	93	94	95	n	83	84	85	86	87	88	89	90	91	92	93	94	95	n
1. Rodenäs Vorland						– ringing site –																						0
2. Sylt	10													10	2													2
3. Föhr	2	5	4	1	6	6	3							9		1	1		1									3
4. Langeneß	1											1		2								1	1	1				3
5. Gröde										1				1														0
6. Hamburger Hallig					1									1					1									1
7. Hooge									1	1				1									1					1
8. Norderoog					1									1														0
9. Pellworm	2	3	3	2				1						6	1	2	2	1									1	7
10. Nordstrandisch-moor	1													1	2													2
11. Süderoog	2													2						– ringing site –								
12. Südfall		1												1		3												3
13. Nordstrand		1			1									2						– ringing site –								
14. Eiderstedt								1				1		2						– ringing site –								
15. Neuwerk	1													1														0
16. Baltrum									1					1														0
17. Groningen coast														0					1		2		1	1	1			3
18. Schiermonnikoog			1			1								2	1	1	1											1
19. Friesland coast			1											1				1		1	1							3
20. Ameland										1	1			1								1	1					2
21. Terschelling													1	1	2	1	1				2		1	1	1	1	1	4
22. Texel	1	2	4	2			1					2		6										1				1
23. Schouwen –Duiveland		1		1	1	1	1	1	1	1				2														0
24. Veersemeer			1	1										1														0

seem to be important for males, who have a prominent role in aggressive interactions (Teunissen, Spaans & Drent 1985), when defending a spot for themselves or their families.

Another factor affecting competitive ability is age. A number of first-year birds were colour-ringed on the Boschplaat and on Texel, and those from the Boschplaat were less likely to return to the same site and more likely to be seen elsewhere than those from Texel. Young birds thus appear to have difficulties establishing themselves on the Boschplaat. In summary, the study by Ebbinge (1992) has shown that the natural saltmarsh area of the Boschplaat on Terschelling has been filled to capacity with spring staging brent geese since the mid-1970s (although the capacity fluctuates annually due to environmental factors), whereas on the man-made inland grazing area on Texel brent goose numbers have not yet reached carrying capacity. Age of birds and body mass of males are among the factors determining which birds are excluded from the saturated Boschplaat.

CASE STUDY II: CONSEQUENCES OF LOSS OF SPRING STAGING HABITAT FOR BRENT GEESE

In 1981, the Rodenäs Vorland, which was then one of the prime spring staging saltmarsh areas for brent geese in the Wadden Sea, with peak numbers of up to 18 000 birds, was lost through embankment. Shortly afterwards, the area was completely deserted by brent geese. The fate of close to 100 birds that were colour-marked at the Rodenäs Vorland at the time of embankment was analysed by Ganter, Prokosch and Ebbinge (1997) and compared with a similar-sized control group of birds marked in the same spring in nearby areas. The analysis covered a period of 13 years after the embankment.

In subsequent springs, both displaced and control birds were seen at numerous sites other than their ringing sites, both in nearby areas and in areas which were a long distance away (Table 1, Figure 3). However, long-distance movements occurred more frequently in the displaced birds, especially during the first years after the habitat loss. Interestingly, the displaced birds moved more often to Texel, a 'buffer' site where carrying capacity has not yet been reached (see above), and less often to Terschelling, a preferred site that is filled to capacity, than did control birds.

Much more meaningful than the mere description of dispersal after habitat loss are the parameters actually affecting the fitness of birds after such an event, namely reproductive success and survival rates. Ganter *et al.* (1997) examined both these parameters, again using the same groups of colour-ringed displaced and control birds. No significant difference was found between reproductive success (measured as the proportion of ringed adults accompanied by first-year birds in autumn) of displaced and control birds, although there was a tendency towards lower breeding success in displaced birds. Survival could not be estimated from spring resighting data because of the very unequal distribution of observer effort, but resighting rates from Great Britain and France in winter could be used for this purpose, assuming that displaced and control birds were equally likely to be spotted in these countries in winter. Again, the resighting rate of displaced and control birds did not differ significantly, but there was a tendency for displaced birds to be resighted less often. For both analyses, sample sizes were rather small and statistical power was low. The

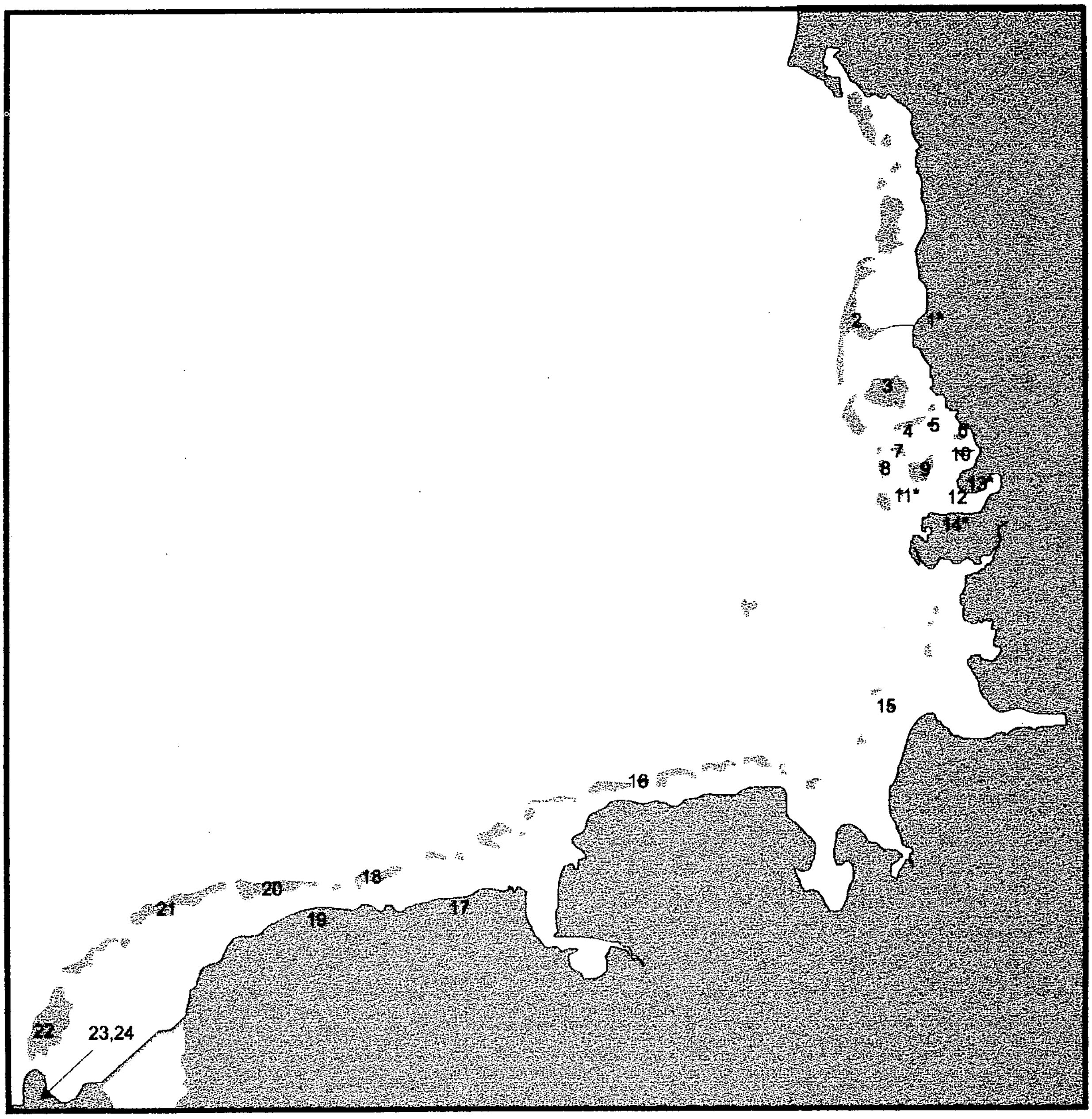

Figure 3. Sites where Rodenäs and/or control birds were resighted in spring. For names of sites see Table 1. * = ringing sites (source: Ganter *et al.* 1997: reprinted with permission from *Aquatic Conservation*)

absence of statistical significance does not, therefore, exclude the possibility of biologically meaningful effects which are too small to be detected with the limited sample size available.

Even though the results of this study concerning the actual effects of habitat loss on fitness parameters, and thus on the population, are rather inconclusive, the study exemplifies the approaches needed to assess those effects. In order to reach firm conclusions about the impact of habitat loss or change on long-lived animals such as geese, large numbers – larger than in the study of Ganter *et al.* (1997) – of marked individuals must be followed and their fitness assessed systematically over a long period of time.

CONCLUSIONS

The studies we have summarised here demonstrate the use of different approaches to questions of carrying capacity and effects of habitat loss. They show how marked individuals can (and should) be used in a meaningful assessment of the impact of habitat loss or change.

The results from the brent goose spring feeding site on the saltmarsh of the Boschplaat show that this natural area is filled with Brent to the point that it cannot accommodate any additional birds: carrying capacity has been reached. This does not necessarily mean that all saltmarshes of equivalent quality in the Wadden Sea are equally filled to capacity, but there are similar indications from other sites as well (Prokosch 1984). Alternative areas, which may be less preferred by the birds because of factors such as food quality, disturbance, or predators, are available, and numbers of birds here have not yet reached carrying capacity. Birds that have been forced out of a preferred area because of habitat loss appear to have difficulty establishing themselves in another preferred area, but can establish themselves successfully elsewhere. By contrast, birds that move 'voluntarily' (presumably good competitors) have been observed as immigrants at preferred sites.

So far, no disadvantages, in terms of survival or reproduction, of staging in less preferred areas could be demonstrated in brent geese. Although there may still be effects which are too slight to be detected by the methods used so far, these results lead to the tentative conclusion that the population of dark-bellied brent geese may not be currently limited by the availability of spring feeding areas. This agrees with recent results from research on the arctic breeding grounds, where observations of brent goose breeding success and the interactions with predators suggest that breeding habitat for brent geese is limited by the activities of predators and that the population may now have reached its maximum, as determined by conditions on the breeding grounds (B S Ebbinge & B Spaans, unpublished data).

It must be pointed out that the lack of negative effects of saltmarsh loss to the population size of dark-bellied brent geese does not mean that there are no negative effects concerning brent geese overall. The ability of brent geese to switch from their preferred spring grazing habitat on natural saltmarshes to inland feeding areas has already resulted in considerable agricultural conflict in parts of the flyway. Further loss of saltmarshes will exacerbate this conflict.

REFERENCES

Boudewijn, T. 1984. The role of digestibility in the selection of spring feeding sites by brent geese. *Wildfowl,* **35,** 97–105.

Ebbinge, B.S. 1992. Regulation of numbers of dark-bellied brent geese *Branta bernicla bernicla* on spring staging sites. *Ardea,* **80,** 203–228.

Ebbinge, B.S. & Spaans, B. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b. bernicla* in the high Arctic. *Journal of Avian Biology,* **26,** 105–113.

Ebbinge, B.S., StJoseph, A., Prokosch, P. & Spaans, B. 1982. The importance of spring staging areas for arctic-breeding geese, wintering in western Europe. *Aquila,* **89,** 249–258.

Ganter, B., Prokosch, P. & Ebbinge, B.S. 1997. Dispersal and fitness parameters of dark-bellied brent geese after loss of their spring staging saltmarsh habitat. *Aquatic Conservation.* In press.

Prokosch, P. 1984. Population, Jahresrhythmus und traditionalle Nahrungsplatzbindung der Dunkelbäuchigen Ringelgans (*Branta b. bernicla* L. 1758) im Nordfriesischen Wattenmeer. *Ökologie der Vögel,* **6,** 1–99.

Prop, J. & Deerenberg, C. 1991. Spring staging in brent geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia,* **87,** 19–28.

StJoseph, A.K.M. 1979. The seasonal distribution and movements of *Branta b. bernicla* in western Europe. *Proceedings of the First Technical Meeting on Western Palearctic Migratory Bird Management, Paris, 1977.* Slimbridge: International Waterfowl Research Bureau.

Teunissen, W., Spaans, B. & Drent, R. 1985. Breeding success in brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. *Ardea,* **73,** 109–119.

The concept of carrying capacity and shorebirds

J D Goss-Custard & A D West

Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset BH20 5AS, UK

SUMMARY

This paper discusses the term 'carrying capacity', defined in terms of the 'one-in, one-out rule'. On this definition, capacity is reached when, for every additional bird that arrives, another one either dies or emigrates, so that numbers in a locality cannot increase and the habitat is fully occupied. Simulations with an individuals-based and physiologically structured model showed that this definition is appropriate for wintering oystercatchers eating mussels, a system in which interference between foraging birds occurs; as the numbers of recruits settling on the mussel beds in September increased to very high levels, the number remaining by spring reached a plateau. Whether birds were assumed to remain on the estuary until they died at some point during the winter or whether they emigrated before they starved made no difference to the predicted capacity of the mussel beds. Carrying capacity in this system could also be defined in terms of the total bird-days per winter because this quantity likewise tended to plateau as the numbers of recruits settling in September increased. However, the plateau was less clearly defined and it took a very much higher number of September recruits for capacity defined this way to be reached.

Further simulations showed that, without interference, the numbers of autumn recruits could be increased to the point at which no birds remained on the mussel beds by spring because food density had been depleted to below the levels required for even the most efficient birds to balance their energy budget. The relationship between numbers remaining by March and the numbers settling the previous September was thus dome-shaped. In systems with little or no interference, therefore, carrying capacity may only be measured as the total number of bird-days per winter. However, without interference, the carrying capacity measured in bird-days per winter depends critically on the numbers of birds that arrive in September. Defining carrying capacity in terms of bird-days per winter rather than in terms of the numbers remaining in March does not solve the difficulties of defining and measuring capacity in systems without interference. In such systems, measuring capacity in bird-days per winter – as is so often done – provides a poor prediction because the total number of bird-days depends on the numbers that arrive in autumn.

Whether carrying capacity is actually reached depends on there being a sufficiently large number of potential recruits to the estuary in autumn; in the oystercatcher–mussel system, it required 8000 recruits in September for the carrying capacity of *ca* 3200 to be achieved. In many species and localities, there may not normally be enough recruits for the capacity of a locality to be reached. However, this should not be taken to mean that a reduction in food supplies through habitat loss or change would not affect local numbers. If competition for food is sufficiently intense for the rates of emigration and/or mortality to be density-dependent, a reduction in the food supply would lead to increased rates of emigration and/or mortality, and so to a reduction in local bird numbers. This was confirmed by simulations which showed that winter habitat loss caused local mortality or emigration to increase in oystercatchers long before carrying capacity was reached.

INTRODUCTION

No other concept in our area of science seems to provoke as much ambivalence as to its use as does the notion of 'carrying capacity'. Some authors put the term inside quotes, as if they are uncertain about the wisdom of using it but are unable to find another notion that encompasses as adequately what it is they want to say.

Others use the term without defining it, as if its meaning was understood and accepted by everyone, but then draw implications that many others would not accept. A particularly unfortunate tendency is for some authors to imply that habitat loss will only affect population size if the carrying capacity of the area has already been reached. It is this dangerous misunderstanding in particular which makes it timely once again to discuss the definition of the concept, how capacity might be measured and the implications of its use for managing wetland birds.

The useful idea that the term 'carrying capacity' incorporates is that there must be a limit to the numbers of birds that an area can support, given the abundance of resources and enemies that are present. But – as with the term 'carrying capacity' itself – the word 'limit' brings with it connotations that can differ between scientists. In population equilibrium theory, it means that something, such as disease or accidents, reduces the rate of increase of the population and thus lowers the equilibrium population size – at which, on average, birth and death rates are equal – to a level below that at which it would otherwise have been (Sinclair 1989; Goss-Custard 1993; Sutherland 1996a). A limiting factor also affects the rate with which the population returns to equilibrium after it has been perturbed. Used in this sense, a limiting factor can be exerting its downward pressure on numbers even though the population is still increasing. In the context of carrying capacity, however, the word 'limit' implies that no further increase in numbers is possible. Another way of saying this is that capacity is reached when, for every additional bird that arrives, one bird either emigrates or dies (Goss-Custard 1985) – the so-called 'one-in, one-out' definition of carrying capacity. An example is when all the available breeding territories are occupied because, under the prevailing levels of competition, territory size cannot be squeezed any further.

When used in this sense, the concept of carrying capacity is best applied in migratory birds to the maximum numbers that can live in a particular locality at a particular time of year; for example, the numbers of territorial breeding pairs. It is not appropriate to apply the term to the equilibrium size of the 'global' (or 'greater' or 'meta') population. Were this to be done, we would find ourselves arguing that the capacity of the wintering grounds was influenced by processes on the breeding grounds, and *vice versa*, because global equilibrium population size in migratory populations depends on processes operating during both the breeding and non-breeding seasons (Fretwell 1972; Goss-Custard 1993; Sutherland 1996b). Were it to be applied at this scale, much of the useful commonsense value of the concept would be lost (Goss-Custard 1993). In any case, it seems most unlikely that capacity can actually be reached everywhere throughout the global range. The increasing density-dependent resistance to further population increase would prevent the population from ever reaching the size at which, throughout a species' range, one animal dies for every additional one that is born (Goss-Custard 1993; Goss-Custard *et al.* 1997; Sutherland 1996a). As model simulations below will demonstrate, the supply of recruits must be very high indeed if capacity is to be reached, and this seems likely only to arise at the local scale (Goss-Custard 1993).

This article, therefore, discusses the concept of carrying capacity in the context of the numbers of birds that can be supported in a particular locality at a particular time of year. By simulations with a model describing an intensively studied system, the article explores some of the factors and processes that determine capacity and discusses how it might be measured. It also re-emphasises the frequently misunderstood, yet vital, point that habitat loss can reduce local bird numbers even before the capacity of the area has been reached. When predicting the effect of habitat loss, the key issue is whether density-dependent processes are already operating, or will operate after the habitat is lost, and not whether the area is already at capacity (Goss-Custard *et al.* 1995).

FACTORS AND PROCESSES DETERMINING OVERWINTER CARRYING CAPACITY

The simulation model was constructed to capture what we believe to be the important features of the interaction between populations of oystercatchers (*Haematopus ostralegus*) and mussels (*Mytilus edulis*); here, we use simulations from version 2 of the model, as detailed by Clarke and Goss-Custard (1996).

Model of the Exe estuary mussel beds

The model is individuals-based and physiologically structured. It uses empirically determined responses of individual oystercatchers to each other and to their common food supply obtained on the Exe estuary, SW England. It calculates the biomass of mussels consumed each day by every individual oystercatcher in the model population and works out the resulting depletion through the winter of the mussel food supply on each of 12 mussel beds. Overwinter mussel losses due to other mortality agents and the weather-related decline in the flesh content of individual mussels are also included. The model therefore tracks daily through the winter the changing biomass density of the food supply on each mussel bed.

Individual oystercatchers in the model open mussels either by stabbing or hammering, because birds using the two methods have different average foraging efficiencies and are subject to different levels of interference (Goss-Custard & Durell 1988). Age-related changes in feeding method and dominance – which affect a bird's susceptibility to interference – are included in the age-structured model. In order to calculate the mussel bed on which each individual bird feeds over each low-water period, the model first calculates, from a functional response relating intake rate to the biomass density of large (>30 mm long) mussels, the interference-free intake rate of a bird of average efficiency for each of the mussel beds. The rate a particular individual would actually achieve on each bed then depends on its own foraging efficiency and dominance – two components of competitive ability which vary between birds independently of each other – and on the current density of oystercatchers on the bed. Next, each individual is selected each day in random order to choose, within its empirically determined ability to discriminate, the mussel bed where it achieves the highest gross intake rate at that time. The model is therefore based on game theory in that the choices made by one competing individual as to where to feed over a low-tide period are contingent on those made by its competitors. Many birds – particularly the subdominant ones – continually change their feeding site as the relative quality of the mussel beds changes over the winter through differential rates of prey depletion and as other birds change their foraging location, or die. Changes in bed area associated with the fortnightly neaps/springs cycle are included because oystercatcher densities, and thus interference competition, are much higher on neaps. It is assumed the rates of feeding are the same during night and day low-water periods.

The model tracks the feeding location and intake rate of each bird on each day from September to March. It also tracks their body condition. Each bird is given fat reserves in September drawn at random from the empirically determined distribution of weights for each age class. Energy requirements for each day are calculated from Kersten and Piersma (1987), using the average air temperature for that day on the Exe. The birds are assumed to be inactive at roosts for 12 hours each day; this is the only time when additional thermoregulation costs below the thermo-neutral temperature are likely to be incurred. Once an individual has assimilated its daily existence energy requirements, any surplus energy consumed is stored as fat, deposited with an empirically determined efficiency (Kersten & Piersma 1987), up to a maximum rate of 5% of current body weight per day (Zwarts *et al.* 1990). Each bird attempts during autumn and winter to accumulate fat at the mean rate observed by its age class on the Exe. The reserves maintain the bird on days when it fails through foraging to meet its current daily requirements. An individual dies if its fat reserves fall to zero for one day.

Carrying capacity and the departure decision rules used

When oystercatchers arrive on the estuary in autumn from the breeding grounds, the carrying capacity of the mussel beds could be achieved almost immediately, by one bird leaving for every additional one that arrives, or later, by one bird starving at some point during the winter, or by both. As we do not know the relative contribution played by emigration and mortality in determining how many birds overwinter successfully, we ran simulations using a number of alternative decision rules which birds may use. Having arrived on the Exe in autumn, each individual was assumed to:

- remain until spring, unless it died first because its fat reserves fell to zero;

- emigrate if, at any time before March, its fat reserves fell to a level equivalent to 8% of its body weight, the point at which oystercatchers leave the Wadden Sea in severe weather (Hulscher 1989, 1990); or
- emigrate if its weight fell for five days in succession at any time before 31 December, it being assumed that it would be too risky to seek a new wintering area any later in the winter.

Birds of all ages and feeding methods were assumed in these simulations to make any of these three decisions. However, as birds may only be flexible in their choice of wintering estuary during their immaturity, a fourth series of simulations were run in which only the immature birds were allowed to leave the estuary if their weight fell for five days in succession.

In order to determine the carrying capacity of the mussel beds, the numbers of oystercatcher recruits to the estuary in autumn was varied between *ca* 0.1 and five times the numbers that overwinter on the Exe at present. In the first instance, each simulation was run for one winter. Plotting the numbers of oystercatchers remaining the following March as a function of the number of recruits the previous September revealed that the number of 'survivors' levelled off at *ca* 3200 birds when the number of recruits had reached *ca* 8000 (Figure 1). From then on, one bird emigrated or died for every additional recruit that arrived in autumn. The numbers remaining in March could not rise any higher so carrying capacity had been reached. This shows that the 'one-in, one-out' definition of carrying capacity is applicable to the oystercatcher–mussel system, at least over the range in the numbers of September recruits employed.

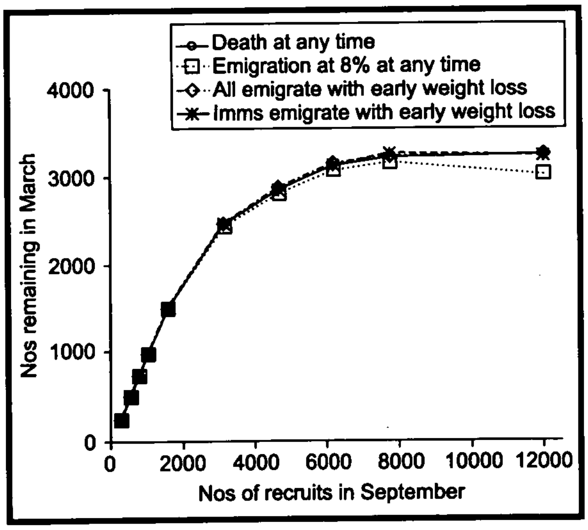

Figure 1. Model predictions for the numbers of oystercatchers remaining on the Exe estuary mussel beds at the end of winter (March) as a function of the numbers settling there during the previous September. Four decision rules were used to eliminate individual birds: a bird of any age (i) died if its fat reserves fell to zero at any time during the winter, (ii) emigrated if its fat reserves fell at any time to 8% of its body mass, or (iii) emigrated if its fat reserves fell for five successive days at any time before 31 December, after which it remained on the estuary and may have died. In (iv), only immature birds (1st–4th winter) emigrated if their fat reserves fell for five successive days before 31 December, after which they remained on the estuary and may have died

Predicted capacity was the same for all four decision rules employed (Figure 1). The reason is that, when large numbers of recruits arrived in autumn, the interference competition was so intense that many birds could not feed fast enough to survive, let alone to increase their body weight, even at this time of year when food was abundant and the birds' temperature-related energy requirements were rather low. It did not matter whether model birds opted to emigrate or remained until they died because a bird that lost weight for five days in succession was destined to die shortly anyway. Many birds disappeared more-or-less immediately, irrespective of the decision rule they used (Figure 2). Accordingly, much of the strongly density-dependent overwinter decrease in bird numbers (inset to Figure 2) - which was, of course, the demographic process responsible for capacity being achieved – occurred early on, when large numbers of recruits arrived. In contrast, when smaller numbers of recruits arrived in September, rather few birds lost weight before the end of December so that many of the losses occurred late in the winter with all four decision rules. It thus made little difference to the predicted value of carrying capacity whether we assumed that capacity was achieved through starvation or emigration.

Model outputs (A D West, unpublished) revealed that the decision rule used made little difference to the other main conclusions reached by Goss-Custard *et al.* (1996) on the process by which capacity was achieved.

- Although with high numbers of

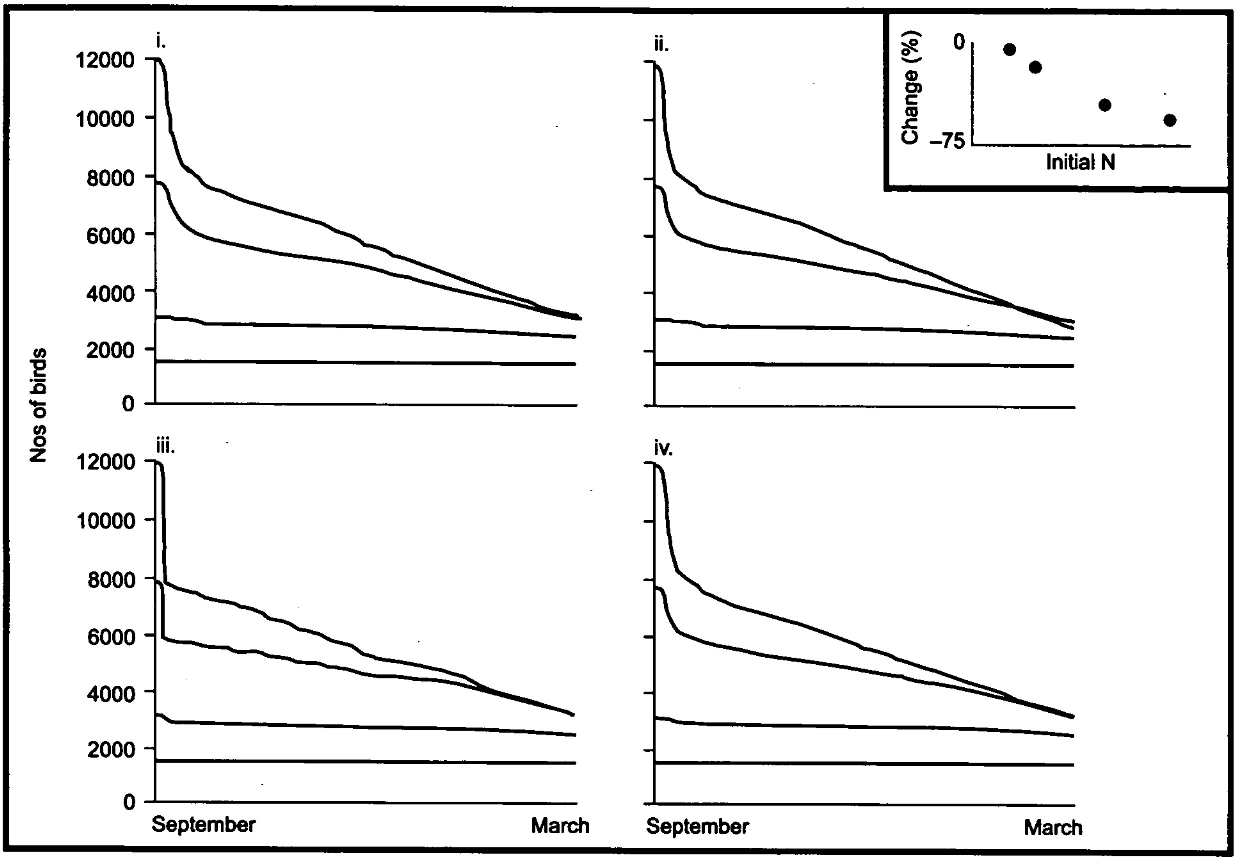

Figure 2. Model predictions for the numbers of oystercatchers remaining on the mussel beds at each stage of the winter using the four decision rules (i–iv) given in Figure 1. The four lines in each graph show the change in numbers with 12 000, 8000, 3000 or 1750 oystercatchers settling on the mussel beds in September. The inset shows the numbers remaining in March as a percentage of the numbers settling in September in relation to the numbers recruiting in September

September recruits many birds died or emigrated early in autumn, carrying capacity was only finally determined in late winter. It depended on the rate of overwinter mussel loss due to both depletion by oystercatchers and other mortality agents, to the overwinter decline in the flesh content of individual mussels, and to the higher temperature-related energy requirements of the birds.

- The disappearance of birds peaked during neap tides when interference competition was intensified by the reduced area of mussel beds exposed at low tide and, in some simulations, the low flesh content of the upshore mussels exposed on neap tides.
- Whether a bird died or emigrated depended on both its dominance and its foraging efficiency.

The decision rule used did not make any difference to the distribution of oystercatchers over the 12 mussel beds. These comparisons further confirmed that uncertainty about the actual decision rule used by oystercatchers when responding to competition for food made little difference to our understanding of the way in which carrying capacity was achieved.

Food supply, interference competition and carrying capacity

The two feedback processes that dictate the carrying capacity of the mussel beds are mussel depletion – in which the more efficient foraging oystercatchers are at an advantage – and interference competition – in which the socially dominant oystercatchers have the advantage. The respective influence of these two processes in determining carrying capacity – measured as the numbers surviving the winter – was explored by independently varying mussel abundance and the intensity of interference competition.

Food abundance was varied by increasing or decreasing the September mussel biomasses on each mussel bed by multiples (range 0.3–1.7) of the average biomass recorded during the eight years of the study, but retaining the present level of interference. A clear carrying capacity was achieved across a wide range of mussel abundance (Figure 3i). As might have been expected, for capacity to be reached, a greater number of recruits was required in September when food supply was large than when it was small; compared with the number of recruits required at present-day levels of food abundance, some 50% more were required for capacity to be reached with the largest food abundance used. As would also be expected, capacity increased sharply with mussel abundance, but not in proportion to the increase in the food supply (Figure 3ii) because interference competition intensified as numbers increased.

Interference was varied in two ways. First, simulations were run in which it was assumed that all the oystercatchers recruited in September consisted entirely of stabbers, amongst which interference is low, or of hammerers, in which interference is high (Goss-Custard & Durell 1988). Second, the strength of interference experienced by birds of a given social rank in populations containing both stabbers and hammerers was reduced using the procedure detailed in Goss-Custard *et al.* (1995). The intensity of interference was reduced either to half its present level or removed altogether; in the latter case, birds were able to feed together at extremely high densities without the intake rate of the subdominants being affected.

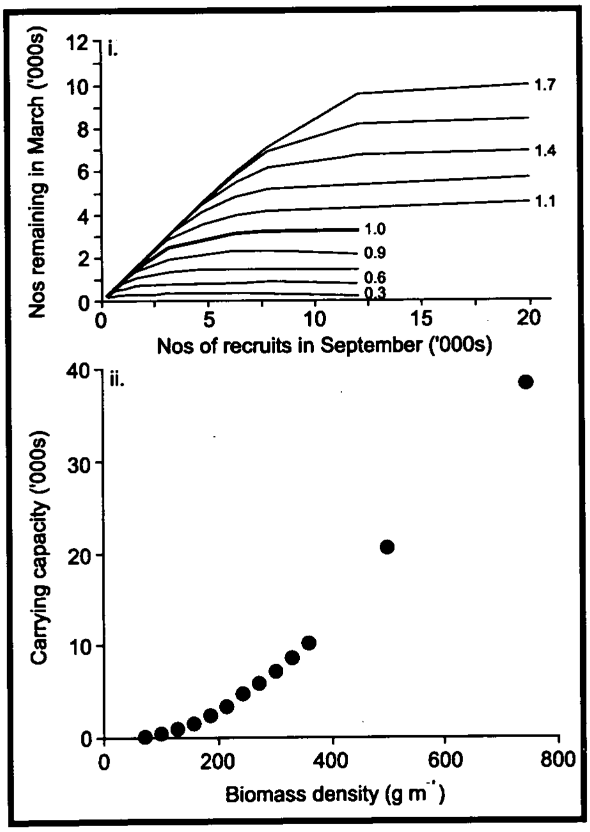

Figure 3. Model predictions for the numbers of oystercatchers remaining on the Exe estuary mussel beds at the end of winter (March) in relation to the abundance of mussels present on the 12 beds in the previous September. Mussel biomass is expressed in multiples of the average mussel biomass recorded on all the beds over eight years. The heavy line represents simulations using the average mussel biomass

i. The numbers of oystercatchers remaining in March as a function of the numbers settling the previous September, with each line referring to one level of mussel abundance
ii. The relationship between carrying capacity – the level of the plateaux in (i) – and food abundance in September

Reducing or removing interference changed the shape of the relationship between the numbers remaining in March and the numbers recruited the previous September from being a curve with a decelerating rise to a clearly identifiable plateau to one which was dome-shaped (Figure 4). Whereas the numbers of birds remaining in March in a population of only interference-prone hammerers remained level across a wide range of numbers of recruits in September – even with 20 times present-day numbers – the numbers remaining in a stabber-only population reached a peak before falling towards zero at high numbers of recruits (Figure 4i). In the simulations in which interference was reduced by half in populations of mixed hammerers and stabbers, the numbers remaining in March again reached a peak, rather than a plateau (Figure 4ii). The dome-shaped pattern was even more pronounced with no interference (Figure 4iii). In many of the simulations with reduced or no interference, no oystercatchers remained at the end of the winter after very large numbers had been recruited the previous September.

The reason for the change from a plateau to a dome-shaped curve, of course, is that, with reduced or no interference, large numbers of recruits quickly reduced food abundance to such low levels that only the most efficient foragers – if any – could feed by the end of the winter at the rate required to survive. In these circumstances, if carrying capacity were to be defined as the numbers remaining at the end of the winter, capacity would usually be zero! With little or no interference occurring, carrying capacity can only be measured in terms of the total

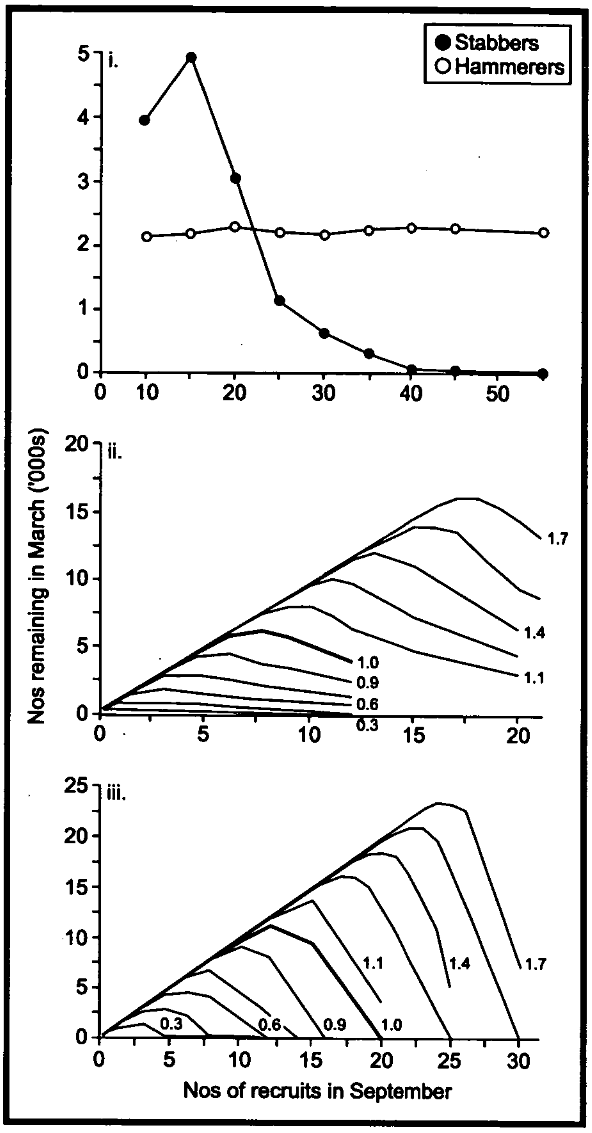

Figure 4. Model predictions for the numbers of oystercatchers remaining on the Exe estuary mussel beds at the end of winter (March), as a function of the numbers settling there during the previous September, according to the intensity of the interference between foraging birds

i. The recruits in September consist entirely of birds that open mussels either (i) by stabbing, and so experience low levels of interference, or (ii) by hammering, and experience high levels of interference
ii. Using the procedure detailed in Goss-Custard *et al.* (1995), the interference levels are set at half those observed on the Exe, with birds of both feeding methods occurring in the simulated population in the proportions observed in nature
iii. As (ii), but with no interference allowed

In both (ii) and (iii), the numbers of oystercatchers of both feeding methods remaining on the mussel beds at the end of winter (March) are shown in relation to the abundance of mussels present on the 12 beds in the previous September, with mussel biomass expressed as in Figure 3

bird-days over the winter, and not as the numbers remaining at the end of winter.

To explore the effect of measuring capacity in terms of bird-days per winter, the relationships between the numbers of recruits, initial food abundance and bird-days per winter for selected simulations are shown in Figure 5. With present-day levels of interference at three representative levels of food abundance, the total number of bird-days per winter tended to plateau as the numbers of September recruits increased (Figure 5i). Bird-days were calculated only from 1 October onwards; otherwise, the calculation was inflated by the sometimes large numbers of birds that, despite having a zero intake rate because of the intense interference, lived for several days into September on the fat reserves they were assumed – probably unrealistically – to carry when they arrived. However, the curves in Figure 5i show two important differences from those shown in Figure 1, in which capacity was measured in terms of the numbers of survivors in March. With capacity measured in bird-days per winter, the plateaux are less clearly defined. It also takes approximately ten times more September recruits for capacity to be reached. Although in systems with strong interference one therefore has the option of measuring carrying capacity either in terms of the numbers of birds remaining at the end of the winter or as the numbers of bird-days per winter, the two definitions differ in the clarity with which plateaux can be identified and give very

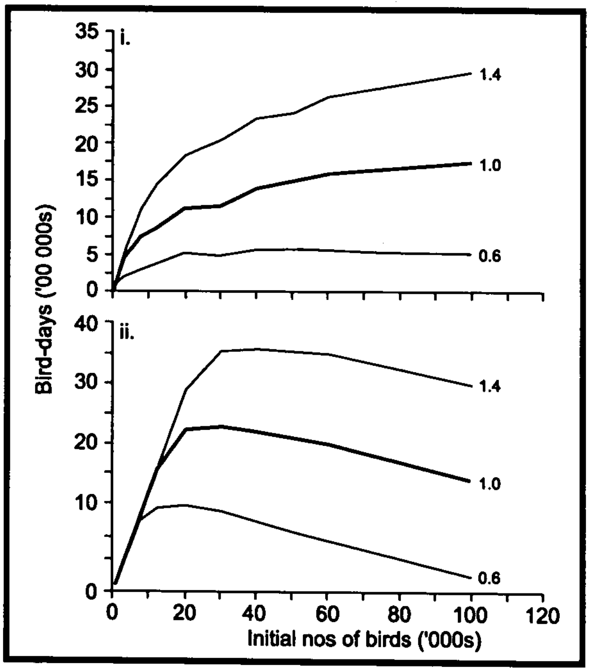

Figure 5. Model predictions for the total number of oystercatcher bird-days from October to March, as a function of the numbers settling there during the previous September, at three levels of mussel abundance on the 12 beds in September, with mussel biomass expressed as in Figure 3

i. With present-day levels of interference
ii. With no interference

different predictions as to the number of September recruits that are required for them to be reached.

When no interference between foraging birds was assumed to occur, no plateaux were reached (Figure 5ii); rather, the relationships were dome-shaped as before, although substantially flatter (compare Figures 5ii and 4iii). This means that, without interference, the predicted carrying capacity measured in bird-days per winter depends critically on the numbers of birds that arrive in September. The reason again is that, when large numbers arrive in September, the food supply is rapidly reduced and, because of the non-linear shape of the functional response that relates intake rate to food abundance and because of individual variations in foraging efficiency, the consequences for intake rate and thus bird survival later in the winter are not simple. We conclude that defining carrying capacity in terms of bird-days per winter rather than in terms of the numbers remaining in March does not solve the difficulties of defining and measuring capacity in systems without significant interference. In such systems, simply measuring capacity in bird-days per winter – as is so often done – may provide only a poor prediction because the total number of bird-days per winter depends on the numbers that arrive in autumn.

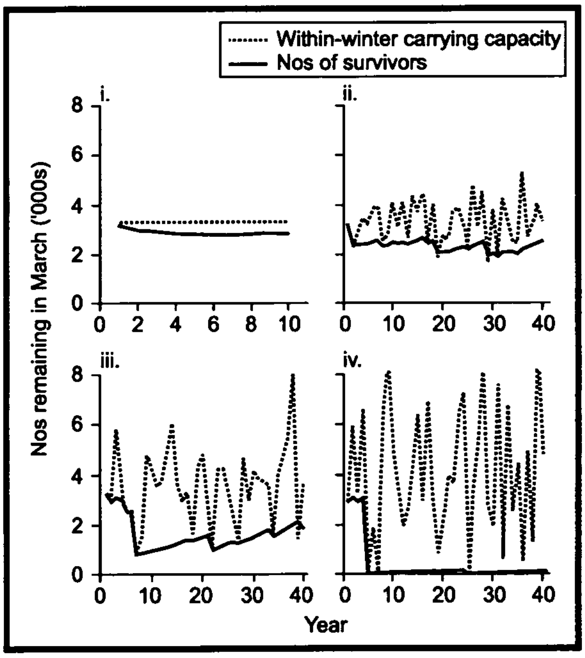

Figure 6. Model predictions for the numbers of oystercatchers remaining (solid line) on the mussel beds at the end of a series of successive winters in which the food supply present in September (i) does not vary between years, or varies at random within the range of (ii) one, (iii) two, and (iv) three standard deviations of the annual variation that was actually observed on the estuary over eight years. The dashed line shows the potential carrying capacity of each winter

Capacity and annual variability in food supply

A striking feature of the simulations with present-day levels of interference was that it required over 8000 recruits in September for the carrying capacity of 3200 to be reached (Figure 1). Far more recruits than can be supported at capacity are needed if the full capacity is to be realised. As a result, the carrying capacity of an area may not be reached on many occasions simply because the supply of recruits available falls below the number needed to exploit the area fully (Goss-Custard *et al.* 1996).

One of several mechanisms preventing enough recruits arriving in an area is annual variation in the feeding conditions (Goss-Custard *et al.* 1996). Figure 6 shows the effect of varying the combined biomass of mussels on the 12 mussel beds around the long-term observed average by using multiples of the observed standard deviation in the annual biomass recorded over eight Septembers to calculate the annual fluctuations in the food supply. Each year, the adults that survived the winter returned the following September with 0.5 juveniles per adults. The potential capacity of the mussel beds in each winter, given the mussel biomass present at the start, was obtained from the plateaux shown in Figure 3.

With no annual variation in mussel biomass, the numbers of oystercatchers surviving each winter – although declining – remained close to carrying capacity (Figure 6i). But as the annual variation in mussel biomass increased from one to three times the observed level, the numbers remaining in March fell increasingly far below the potential capacity of the mussel beds in each winter because, after numbers had fallen sharply in the first winter of food scarcity, too few juveniles arrived in subsequent Septembers for the carrying capacities of later winters to be reached (Figures 6ii–iv). Figure 7 summarises the widening discrepancy as the annual variability in food abundance increased between the mean numbers remaining in March and the average capacity of the mussel beds. With large annual variations in the

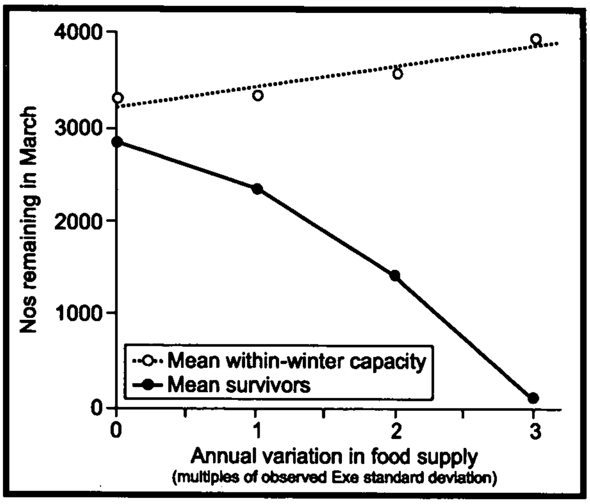

Figure 7. Model predictions for the numbers of oystercatchers remaining in March (solid line) as a function of the annual variation in the mussel food abundance, measured as described in Figure 6. The dotted line shows the numbers that could have remained on the estuary had the supply of recruits in September been sufficient for the potential carrying capacity of the mussel beds to have been realised

feeding conditions, capacity may only be reached in sites which, each year, attract large numbers of oystercatchers from other potential wintering sites (Goss-Custard *et al.* 1996).

CARRYING CAPACITY AND DENSITY DEPENDENCE

These results do suggest that, in many species and localities, carrying capacity often may not be reached in nature, even in systems where interference is strong. The model predicts that the carrying capacity of the Exe estuary mussel beds exceeds the *ca* 2500 oystercatchers that winter on them at present, a conclusion that is consistent with trends in mussel and oystercatcher abundances on the estuary since 1976 (Goss-Custard *et al.* 1997). This finding should not be taken to mean, however, that reducing the quantity or quality of the food supply in a locality, through habitat loss and change, would not affect the numbers of birds remaining in that locality. If competition for food is already sufficiently intense for the rates of emigration or mortality to be density-dependent, reducing the food supply – and thus intensifying competition between birds – through habitat loss and change will reduce local numbers (Goss-Custard 1977; Goss-Custard *et al.* 1995). If birds already emigrate or die because they cannot compete successfully for food, increasing the intensity of competition still further by reducing the food supply is bound to increase the numbers of birds that have to emigrate or die, and this may happen at levels of competition that are well below the very high levels that occur when capacity has been reached.

Indeed, simulations with the oystercatcher–mussel model show that a locality may be very far below capacity yet numbers would still be reduced by habitat loss and change. Figure 8i shows the density-dependent emigration and/or mortality functions at different biomasses of mussels derived from the model: these graphs show the numbers of birds that disappeared before March rather than the numbers that remained, which are shown in Figure 3. At the present-day levels of mussel biomass, the rates become density-dependent when *ca* 1000 recruits arrive in September. As the biomass of food on the 12 mussel beds is changed from being very high (the lowest

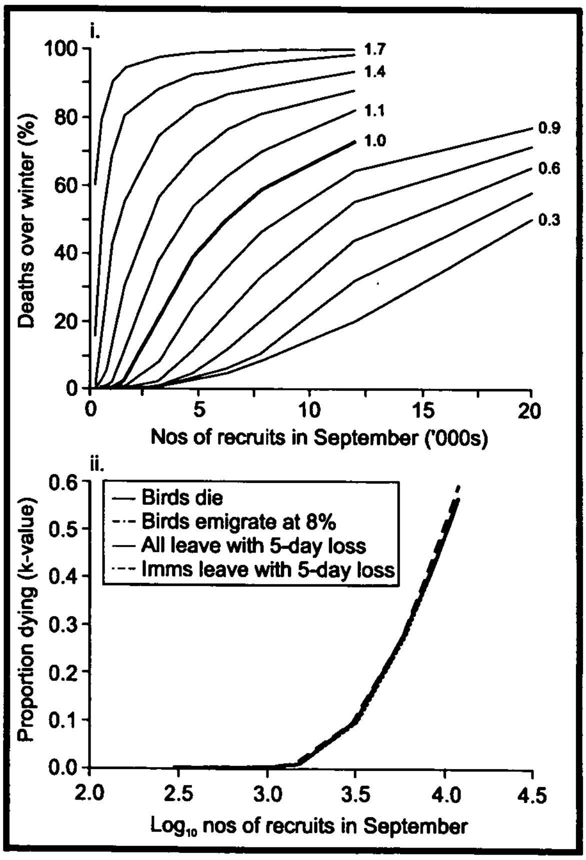

Figure 8. Model predictions for the proportion of oystercatchers starving between September and March, as a function of the numbers settling there during the previous September

i. Mortality rate in relation to the abundance of mussels present on the 12 beds in September, with mussel biomass expressed as in Figure 3

ii. Mortality rate expressed as a k-value, and plotted against the logarithm of the September numbers line) to very low (the topmost line), density dependence starts at an ever lower number of recruits and becomes steeper. In Figure 8ii, the overwinter mortality and emigration rates at the present-day mussel biomass are expressed as k-values (Varley & Gradwell 1960). As discussed in Goss-Custard (1980, 1993), with this formulation, carrying capacity is reached when the slope of k-value against the logarithm of the number of September recruits is 1; this is when one bird dies or leaves for every additional recruit. With the present-day mussel biomass, this occurs at *ca* 8000 recruits (3.9 on the $\log_{10}$ scale). At less than *ca* 1000 recruits, emigration and mortality are broadly independent of density. Therefore, mortality and/or emigration are density-dependent over the range 1000–8000 September recruits before the mussel beds reach capacity. Were the food supplies to be reduced at a time when the numbers of recruits fell within this range, more birds than at present would leave or die because of increased competition for food. Local oystercatcher numbers would therefore be lower than they would have been had the food supplies not been reduced.

The effect of food abundance on the range over which mortality and/or emigration are density-dependent before capacity is reached is explored in Figure 9, in which oystercatcher numbers are expressed as densities. The range over which rates are density-dependent, but the mussel beds are below carrying capacity, expands as the food supply increases, and can be very wide. It would therefore be incorrect to argue that a reduction in food supply through habitat loss or change will not reduce local bird numbers, unless the area is at capacity; a reduction will happen well before the numbers of recruits are high enough for capacity to have been reached.

DISCUSSION

As oystercatcher densities reach densities of 25 birds ha^{-1} very widely in Europe, Figure 9 might be used to argue that the removal of any mussel bed is likely to increase the rates of emigration or mortality. However, this would be a premature conclusion. Version 2 of the model contains some functions that are now being revised and this is expected to have the effect of increasing the densities at which competition begins seriously to affect oystercatcher emigration and survival rates. For example, interference is now known to reduce intake rates only at higher oystercatcher densities than was assumed in Version 2 (Stillman *et al.* 1997). Similarly, the opportunity for oystercatchers to compensate for low consumption rates on mussels at low tide by feeding at high tide on alternative food supplies upshore of the mussel beds and in fields around the estuary was represented in Version 2 by a single value for all population sizes, which is certainly unrealistic. We suspect that recent improvements in the parameterisation of the model will increase the predicted carrying capacity of the mussel beds and the densities at which mortality and emigration become density-dependent.

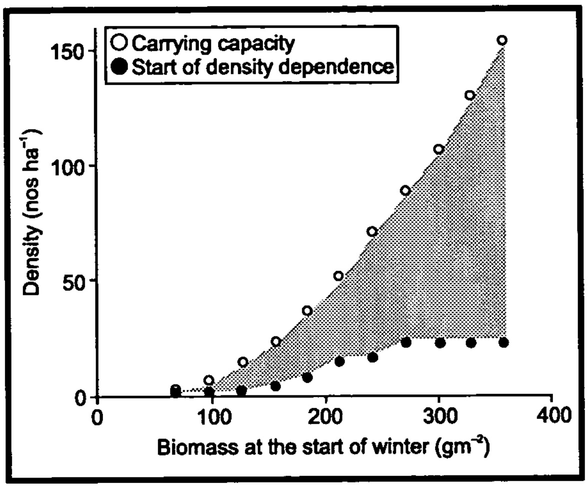

Figure 9. The density of oystercatchers in September in relation to the biomass density of mussels on the 12 mussel beds in September:

i. at which the subsequent overwinter mortality rate becomes density-dependent (●)
ii. at which the carrying capacity is reached (o)

On the other hand, this preliminary version of the model has enabled us to explore the concept of carrying capacity and to take further the earlier attempts to investigate the effect that the presence of interference has on the way in which it might be thought about and measured (Goss-Custard & Charman 1976). When interference amongst birds is strong, capacity can be defined in terms of the number remaining at winter's end because, as the numbers of September recruits increased, the numbers remaining by spring reached a plateau. When the birds were assumed not to experience interference, however, the simulations showed that the numbers of autumn recruits could be increased to the point at which no birds remained by spring because food density had been reduced to below the levels required for all the birds – however efficient they were – to survive. In systems with little or no interference, therefore, carrying capacity can only be defined in terms of the total number of bird-days per winter. However, the simulations showed that the relationship between bird-days per winter and the number of September recruits is still dome-shaped; the predicted carrying capacity therefore still depends critically on the numbers of birds that arrive in September. Defining carrying capacity in terms of bird-days per winter rather than in terms of the numbers remaining in March does not solve the difficulties of defining and measuring capacity in systems without interference. In such systems, measuring capacity in bird-days per winter – as is so often done – may provide only a poor prediction because the total number of bird-days per winter depends on the numbers that arrive in autumn, and this is not normally taken into account. Such predictions may therefore best be regarded only as approximations of the actual ability of an area to support birds.

REFERENCES

Clarke, R.T. & Goss-Custard, J.D. 1996. The Exe estuary oystercatcher–mussel model. In: *The oystercatcher: from individuals to populations,* edited by J.D. Goss-Custard, 389–392. Oxford: Oxford University Press.

Fretwell, S.D. 1972. *Populations in a seasonal environment.* Princeton: Princeton University Press.

Goss-Custard, J.D. 1977. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology,* **14**, 721–739.

Goss-Custard, J.D. 1980. Competition for food and interference among waders. *Ardea,* **68**, 31–52.

Goss-Custard, J.D. 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In: *Behavioural ecology: ecological consequences of adaptive behaviour,* edited by R.M. Sibly & R.H. Smith, 169–188. Oxford: Blackwell Scientific.

Goss-Custard, J.D. 1993. The effect of migration and scale on the study of bird populations: 1991 Witherby lecture. *Bird Study,* **40**, 81–96.

Goss-Custard, J.D. & Charman, K. 1976. Predicting how many wintering waterfowl an area can support. *Wildfowl,* **27**, 157–158.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit. 1988. The effect of dominance and feeding method on the intake rates of oystercatchers, *Haematopus ostralegus,* feeding on mussels, *Mytilus edulis. Journal of Animal Ecology,* **57**, 827–844.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell S.E.A. le V. dit, Urfi, A.J. & West, A.D. 1995. Consequences of habitat loss and change to populations of wintering migratory birds: predicting the local and global effects from studies of individuals. *Ibis,* **137**, S56–66.

Goss-Custard, J.D., West, A.D., Caldow, R.W.G., Clarke, R.T., Durell, S. E.A. le V. dit. 1996. The carrying capacity of coastal habitats for oystercatchers. In: *The oystercatcher: from individuals to populations,* edited by J.D. Goss-Custard, 326–351. Oxford: Oxford University Press.

Goss-Custard, J.D., Ross, J., McGrorty, S., Durell, S.E.A. le V. dit & Caldow, R.W.G. 1997. Locally stable numbers in a migratory shorebird where carrying capacity has not been reached. *Ibis.* In press.

Hulscher, J.B. 1989. Sterfte en overleving van Scholeksters *Haematopus ostralegus* bij strenge vorst. *Limosa,* **62**, 177–181.

Hulscher, J.B. 1990. Survival of oystercatchers during hard winter weather. *Ring,* **13**, 167–172.

Kersten, M. & Piersma, T. 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea,* **75**, 175–187.

Sinclair, A.R.E. 1989. Population regulation in animals. In: *Ecological concepts: the contribution of ecology to an understanding of the natural world,* edited by J.M. Cherrett, 197–241. Oxford: Blackwell Scientific.

Stillman, R.A., Goss-Custard, J.D., Clarke, R.T. & Durell, S.E.A. le V. dit. 1997. Shape of the interference function in a foraging vertebrate. *Journal of Animal Ecology.* In press.

Sutherland, W.J. 1996a. *From individual behaviour to population ecology.* Oxford: Oxford University Press.

Sutherland, W.J. 1996b. Predicting the consequences of habitat loss for migratory populations. *Proceedings of the Royal Society of London B,* **263**, 1325–1327.

Varley, G.C. & Gradwell, G.R. 1960. Key factors in population studies. *Journal of Animal Ecology,* **29**, 339–401.

Zwarts, L., Ens, B.J., Kersten, M. & Piersma, T. 1990. Moult, mass and flight range of waders ready to take off for long-distance migration. *Ardea,* **78**, 339–364.

Numbers of breeding herons in relation to ecological changes in the reed belt of Neusiedler See, Austria

A Grüll[1] & A Ranner[2]

[1] *Biological Station Neusiedler See, A-7142 Illmitz, Austria*
[2] *BirdLife Österreich, Museumsplatz 1/10/8, A-1070 Wien, Austria*

SUMMARY

Changes in numbers of breeding great white egrets and purple herons, as well as other population parameters, such as colony number, size and distribution, are discussed with regard to ecological factors. The results suggest that water depth at the colony site is not a limiting factor for the numbers and distribution of breeding pairs. Rather, the heron populations seem to be regulated by the supply of feeding habitats and their water levels.

THE PROBLEM

The reed belt of the Neusiedler See in Austria is one of the most important breeding sites for large wading birds in Europe. It is where the great white egret (*Casmerodius albus*) occurs at the westernmost point of its European range and, with more than 600 pairs (1996), the area supports about half of the European population, excluding Russia and the Ukraine. In addition, the numbers of the purple heron (*Ardea purpurea*) attain the 1% level of the whole population of Europe (J van Vessem, pers. comm.). Herons in particular depend on specific aspects of hydrology or hydrography, and are therefore potential indicators of change in these fundamental characteristics of an aquatic ecosystem (Voisin 1991; Kushlan 1993). For the reed belt of Neusiedler See, there is evidence of a significant increase in silting up of reed beds through the deposition of reed peat caused by eutrophication over the last 25 years, so that today there are large parts of the reed belt which dry out when water levels are low (Csaplovics 1989; Herzig 1990). This drying out could have a serious effect on the numbers and distribution of reed-dwelling wading birds because their colony sites in reed beds seem usually to be associated with constant flooding to a water depth of at least 10 cm, but mostly more than 30 cm (eg Bauer & Glutz von Blotzheim 1966; Cramp & Simmons 1977; Van der Kooij 1991; Voisin 1991). Our study tested whether low water depths or the drying out of colony sites when water levels are low are already acting as limiting factors. We restrict the analysis to the period 1981–95, for which annual and systematic counts by the Biological Station Neusiedler See are available.

METHODS

The common reed (*Phragmites australis*) covers 180 km^2 of the lake forming a belt up to 5 km wide. Almost all colonies are situated near the edge of this reed belt, mostly at a distance of less than 1 km from the water's edge, or on a large reed island. The details of the aerial survey methods used for measuring the size of colonies will be published elsewhere. The position of single colonies identified from the air in some uniform reed sections varied between years by distances of

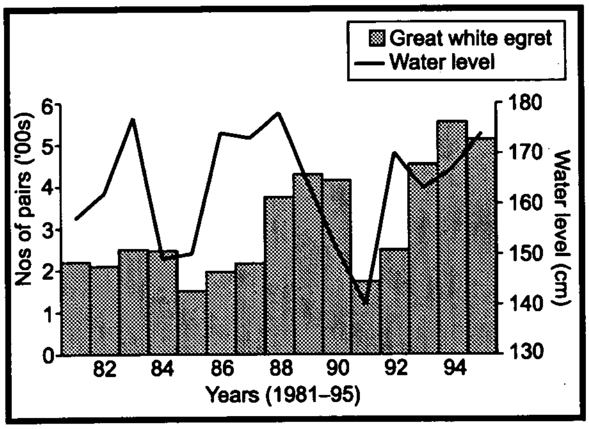

Figure 1. The size of the breeding population (pairs) of the great white egret (columns) in relation to water level (line) at Neusiedler See, 1981–95

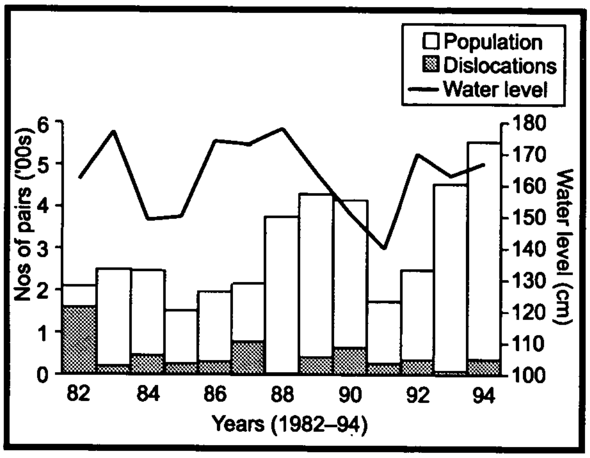

Figure 2. The size of the breeding population (columns) and number of 'dislocations' (shaded) in the great white egret in relation to the water level of the lake. 'Dislocations' are calculated as the yearly number of newly established pairs which may have come from other colonies on the lake; these increases in numbers are thus matched by declines in other colonies in the same year

more than 1 km. As the counters as well as the maps used for colony location changed several times during the census period, it was not possible to clarify whether this variability was real or artefactual. To counter this problem, we defined clusters of colonies with a diameter of less than 800 m as a 'colony site', an area within which identifiable colonies were located over a period of years. On this definition, almost all recorded breeding sites were clearly separated from neighbouring colonies by larger distances. Based on a geodetic survey of the ground profile of the Neusiedler See by Csaplovics (1989), the water depth under each individual colony was calculated for every water level. The average of all colonies within one site was then calculated for every colony site. As the ground profiles within the colony sites were mostly uniform, errors in exact location of the colonies during census work should be negligible. Statistical analysis was performed with the computer software package StatView 512+. All correlations are calculated as Spearman Rank correlation coefficients (rs).

POPULATION PARAMETERS IN RELATION TO ECOLOGICAL FACTORS

Population development in relation to the water level of the lake

Sufficient material for this analysis is only available for the great white egret. During the dry periods of 1984–85 and 1990–91, when water levels fell below 150 cm, a marked decline in the entire population took place. In both cases, the decline occurred not in the first but in the second year of the drought (1985 and 1991 respectively), one year after the drop in water level (Figure 1). The emigration of potential breeders during dry periods therefore seems to be less determined by the spring water levels in the year in question than by water levels in the previous year. To test whether, in response to changes in water level, breeding pairs moved between colony sites within the lake, we calculated the yearly number of dislocations. Dislocations are calculated as the yearly number of newly established pairs which may have come from other colonies on the lake; these increases in numbers are thus matched by declines in other colonies in the same year. Figure 2 provides no evidence that pairs changed colonies more in dry years. Low water levels thus do not seem to induce any splitting or dissolving of colonies.

Colony number and size in relation to the entire population

Average colony size in the great white egret, but not the number of colonies, increases with the size of the entire population (Figure 3), and it does so simultaneously in all areas of the reed belt (Figure 4). Population increases thus primarily result in a more or less uniform growth in the size of the colonies in all areas of the reed belt. We have no evidence which suggests that there are preferred areas which are occupied first

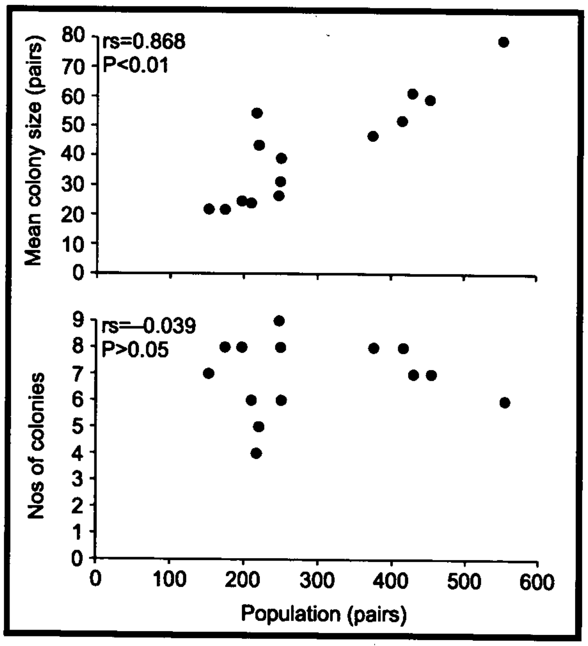

Figure 3. Mean colony size (top) and number of colonies (bottom) in relation to entire breeding population in the great white egret

and within which population size subsequently fluctuates only within narrow limits.

Colony size in relation to water depth at colony site

In the great white egret there is a weak positive correlation between water depth and colony size (Figure 5). The diagram shows that smaller colonies may be located in entirely dried-up areas.

'Quality' of a colony site in relation to water depth

As a measure of site quality, the total number of all broods identified at one colony site over the entire course of observation was calculated. The total number of broods does not correlate with the average depth of water at the colony site in either the great white egret or the purple heron (Figure 6).

FACTORS LIMITING DISTRIBUTION AND POPULATION

The study aims to identify the factors which could be crucial in controlling the distribution of colonies and limiting population size. For the following reasons, the results suggest that the water regime at a colony site is not critical for colony selection, and thus does not determine or limit the numbers and distribution of breeding herons.

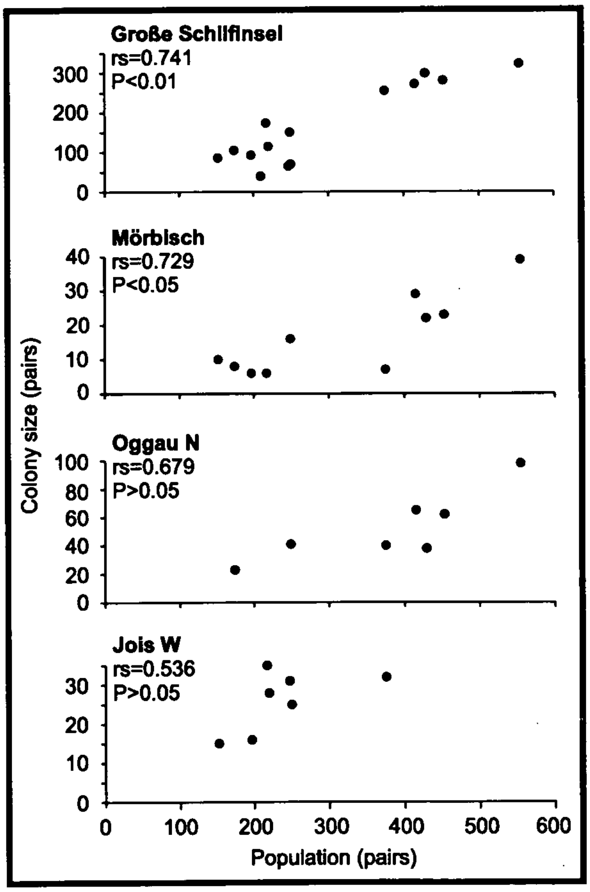

Figure 4. Colony size in four different parts of the reed belt in relation to entire breeding population in the great white egret

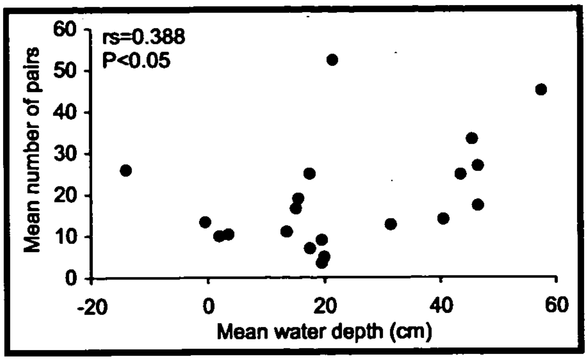

Figure 5. Mean number of breeding pairs per year in relation to the water depth at colony sites of the great white egret (one extreme high value omitted)

- The delayed response of the great white egret to low water levels indicates that settling birds do not react to the water depth in the reed belt *per se*, but to some correlates which may exert their effect during the first breeding season of a drought.

- In the great white egret, colony size fluctuates more or less in synchrony in all parts of the reed belt, despite considerable differences in water regime; we have no evidence that there are optimal areas which are colonised preferentially.

- Fluctuations in water level do not induce an increase in the number of pairs changing colony, as would be expected if water depth is critical for settlement.

- Finally, the total number of broods at a colony site is not determined by the average depth of water.

We therefore have no indication that hydrographic factors at nesting sites limit population size. Suitable nest sites seem to be in excess of needs and are therefore not critical for the formation of a colony. It is more likely that the numbers and distribution of breeding pairs at Neusiedler See are regulated in the feeding habitats within the catchment area of the colonies (eg Fasola & Barbieri 1978; Gibbs *et al.* 1987; Fasola & Alieri 1992; Kelly, Pratt & Green 1993). In the case of the great white egret, the critical factor limiting prey availability, and therefore breeding success, could be the

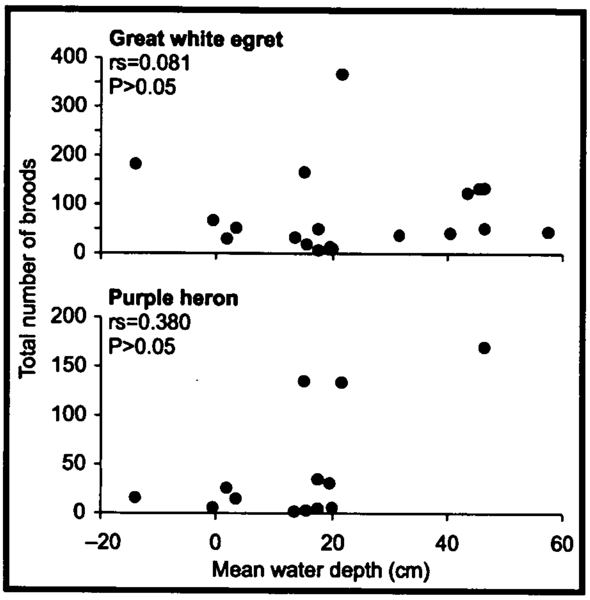

Figure 6. Total number of broods and mean water depth at colony sites of the great white egret and purple heron (two extreme values are omitted for both species)

water level in the feeding areas (eg Maddock & Baxter 1991). But, if so, why do the settling birds react to a severe reduction in water level only after a delay of one year? The Hungarian results of Warga (1938) are interesting in this respect. He found that starvation in egret nestlings in dry years only took place when these years coincided with low vole densities; in other years, they switched over to this terrestrial prey and had normal breeding successes in spite of low water levels. As great white egrets at Neusiedler See in spring eat many voles that are taken from arable land, this terrestrial food supply may compensate for low water levels and allow the birds to start breeding during the first year of drought. Later in the season, however, the growth of the crop may prevent the birds from catching enough voles for rearing the young. The birds might therefore change breeding site the following year at the start of the next breeding season.

We have some evidence that the shallow and very eutrophic pools of open water within the reed belt may play an important role for feeding aggregations of great white egrets (E Nemeth, pers. comm.). Further indications of this come from the relationship between the depth of water and colony size, as well as from a positive correlation between the total number of broods in the great white egret and the width of the reed belt (Figure 7). These correlations may imply that the flooded reed areas have a certain importance as a source of food supply.

CONCLUSIONS FOR PROTECTION AND FURTHER RESEARCH

Considering the protection of the wading birds in the National Park Neusiedler See – Seewinkel, our study has shown that long-term population trends cannot obviously be explained by the silting up of the reed belt. Given the high plasticity in choice of nesting site, it seems unlikely that this factor will limit populations in the foreseeable future. The limiting factors must be sought in the feeding habitats within the catchment areas of the colonies. The challenge for researchers is therefore to redirect their interest from the breeding colonies to the more extensive feeding habitats. Finding out the most important feeding resources and measuring the relationships between them and breeding success over space and time will form the first task (eg Gibbs *et al.* 1987). To understand these complicated associations, we suggest that the conspicuous and increasingly numerous great white egret is an ideal subject for study. The recent shift to agrarian feeding habitats as well as the new tradition of overwintering in our study area in this species leads us to expect valuable insights into population regulation and limiting factors.

ACKNOWLEDGEMENTS

First of all we are grateful to our pilot Robert Klein, who navigated our aerial counts from 1981 to 1995, as well as to our colleagues counting wading birds for longer or shorter periods: Dr E Csaplovics, B Kohler, E Lederer, Dr H Metz, Dr Ch Müller, Dr G Rauer, DI Th Zuna-Kratky and Dr E

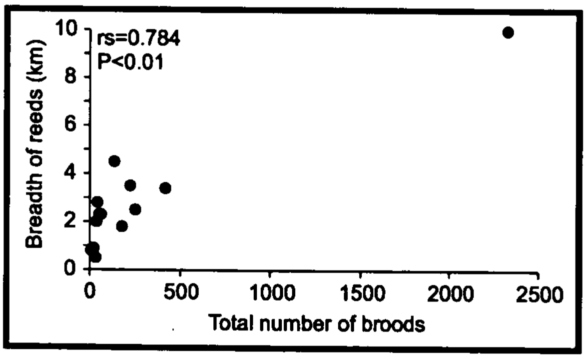

Figure 7. Total number of broods at a colony site in relation to the width of the reed belt in the great white egret. Correlation without the extreme value is also significant (rs=0.725; P<0.01)

Zwicker. All flights were supported by Biologische Station Neusiedler See/Amt der Burgenländischen Landesregierung. Furthermore, we want to thank Dr E Csaplovics and DI H Kanonier for calculating the water depth in the breeding colonies.

REFERENCES

Bauer, K. & Glutz von Blotzheim, U.N. 1966. *Handbuch der Vögel Mitteleuropas,* **1**. Frankfurt am Main: Akademie Verlagsges.

Cramp, St. & Simmons, K.E.L. 1977. *Handbook of the birds of Europe, the Middle East and North Africa,* **1**. Oxford: Oxford University Press.

Csaplovics, E. 1989. Die geodätische Aufnahme des Bodens des Neusiedler Sees. *Wissenschaftliche Arbeiten aus dem Burgenland,* **84**.

Fasola, M. & Alieri, R. 1992. Conservation of heronry Ardeidae sites in north Italian agricultural landscapes. *Biological Conservation,* **62**, 219–228.

Fasola, M. & Barbieri, F. 1978. Factors affecting the distribution of heronries in northern Italy. *Ibis,* **120**, 537–540.

Gibbs, J.P., Woodward, S., Hunter, M.L. & Hutchinson, A.E. 1987. Determinants of great blue heron colony distribution in coastal Maine. *Auk,* **104**, 38–47.

Herzig, A. 1990. Zur limnologischen Entwicklung des Neusiedler Sees. In: *International Symposium Schutz und Entwicklung großer mitteleuropäischer Binnenseelandschaften. Bodensee – Neusiedler See – Balaton,* edited by Arbeitsgemeinschaft Gesamtkonzept Neusiedler See, 91–98. Eisenstadt.

Kelly, J.P., Pratt, H.M. & Greene, P.L. 1993. The distribution, reproductive success, and habitat characteristics of heron and egret breeding colonies in the San Francisco Bay area. *Colonial Waterbirds,* **16**, 18–27.

Kushlan, J.A. 1993. Colonial waterbirds as bioindicators of environmental change. *Colonial Waterbirds,* **16**, 223–251.

Maddock, M. & Baxter, G.S. 1991. Breeding success of egrets related to rainfall: a six-year Australian study. *Colonial Waterbirds,* **14**, 133–139.

Van der Kooij, H. 1991. Nesthabitat van de Purperreiger *Ardea purpurea* in Nederland. *Limosa,* **64**, 103–112.

Voisin, C. 1991. *The herons of Europe.* London: Poyser.

Warga, K. 1938. Phaenologische und nidobiologishe Daten aus der Kolonie von *Egretta a. alba* (L.) am Kisbalaton. *Proceedings of the International Ornithological Congress,* **8**, 655–663.

Latitudinal patterns in the structure of coastal wader assemblages and associated implications of habitat loss

P A R Hockey & K N Barnes[1]

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa 7701
[1]Present address: Avian Demography Unit, Dept of Statistical Sciences, University of Cape Town, Rondebosch, South Africa 7701

SUMMARY

This study analyses large-scale patterns in the ecological structure of wader assemblages at wetlands along the east Atlantic seaboard. Species richness and foraging densities increase, and average mass decreases, on a north–south axis. We derived a species packing index based on morphological attributes and relative abundance as a crude measure of interspecific niche overlap within assemblages. Species packing was maximal in the tropics, decreasing symmetrically towards higher latitudes. Species packing was strongly correlated with species evenness and also with the proportion of obligate visual foragers (plovers) in the assemblage. The analyses of assemblage structure show that the impacts of habitat loss will vary considerably with latitude. Numerical impacts per unit of habitat area lost will be greatest at south temperate latitudes, but the impacts on diversity will be greatest in the tropics. We discuss reasons why estimates of carrying capacity are inadequate for the accurate prediction of the effects of habitat loss and suggest directions for future research that may help improve our understanding about the relationship between wader populations and their resource bases.

INTRODUCTION

Waders (Charadrii) have a worldwide distribution, and many migrate thousands of kilometres between continents and hemispheres during their annual cycles, spending as much as 75% of their lives away from their breeding grounds (Burger 1984). Hayman, Marchant and Prater (1986) recognise 214 species within the suborder Charadrii. This diversity, coupled with interspecific differences in migratory movements, has confounded the search for general patterns of wader distribution (eg Morrison 1984). A plethora of data exist which describe numbers and species composition in wader assemblages (eg Prater 1981; Lane 1987; Morrison & Ross 1989; Smit & Piersma 1989), but limited attempts have been made to synthesise these data. Rather, many students of waders have adopted a reductionist approach and have concentrated their efforts on describing in detail the distribution and dispersal patterns of individual species (eg Myers, Maron & Sallaberry 1985; Piersma & Davidson 1992). Such an approach provides important insights into wader biology at the autecological level, but limited insight into the causes of broad-scale variation in the ecological structure of wader assemblages.

In the search for an ecological understanding of wader distribution, we focused our attention on the coastal wetlands of the east Atlantic. Spanning a wide range of latitudes, there are several sites where wader numbers have been counted and where the intertidal area is known (Hockey *et al.* 1992). As measures of ecological community structure we investigated how patterns of species richness, body size, foraging mode and species packing (see Methods) varied with latitude. We set out to answer the following key questions.

- Do community-level attributes of wader assemblages in the boreal winter vary predictably with latitude?

- If such patterns exist, can they be explained by environmental variables?

- Can such analyses assist in predicting the effects of habitat loss over large spatial scales?

METHODS

Latitudinal patterns in species richness of waders (residents and migrants combined) during the boreal winter at 31 coastal wetlands in the east Atlantic were sourced from Appendix A of Hockey *et al.* (1992) and from Schepers and Marteijn (1994) for Baie de Corisco, Estuaire du Gabon and Baie du Cap Lopez (Gabon). Body weights were obtained from Johnsgard (1981) and the proportional abundance of wader species at each site was used to calculate an average body mass for the site. For classifying foraging mode, all plovers (*Vanellus*, *Pluvialis* and *Charadrius*) were assumed to be obligate visual foragers: all other species were conservatively considered as facultative visual/tactile foragers.

Habitat, food type and time (in order of importance) are the principal axes along which organisms can partition themselves in multidimensional niche space (Holt 1987). Species packing can be defined as the proximity of species' resource utilisation functions along a resource continuum. It is a relative concept: at high levels of species packing, species utilisation functions are closer together on the selected resource continuum and niche overlap is correspondingly high. In markedly three-dimensional habitats, habitat structural complexity is often of paramount importance in structuring bird communities (eg Wiens 1989). Estuaries, by contrast, are an essentially two-dimensional environment and we identified food as the resource variable likely to have the greatest influence on wader community structure during the boreal winter.

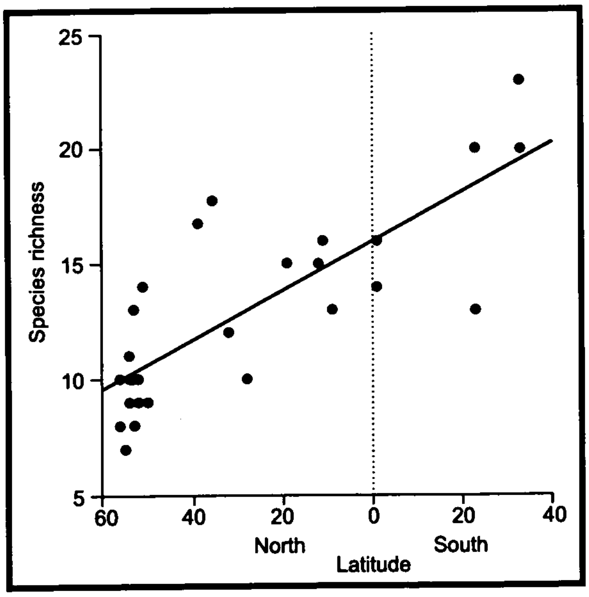

Figure 1. Species richness in east Atlantic wader assemblages during the boreal winter as a function of latitude: species richness includes both resident and migrant species

We used morphological characters to assess the potential for ecological overlap between co-occurring wader species (data from Cramp & Simmons 1983; Maclean 1993). Three variables were used to calculate a Bray–Curtis measure of similarity for all possible pairs of species. These variables were:

- bill length, which determines the range of depths in the substratum over which birds can capture prey;
- tarsal length, which influences the range of water depths in which waders can forage and the distances over which they can detect prey; and
- body mass, which is an index of the size of prey that birds can handle.

To derive a species packing index for each site, the relative proportions of each species present were calculated. For each pair of species occurring at a site, a packing value was calculated from the Bray–Curtis similarity measure for that pair using the formula:

$$P_{ik} = S_{ik}\ \mathrm{Min}\ (F_{ij};F_{kj})$$

where:

P_{ik} = the packing value for the species pair,

S_{ik} = the Bray–Curtis similarity coefficient for species *i* and *k*,

F_{ij} = the proportional abundance of species *i* at site *j*, and

F_{kj} = the proportional abundance of species *k* at site *j*.

The index is directly dependent on the proportional abundance of the rarer of the two species at the site. The community packing index was calculated as:

$$P_j = \sum_{i=1}^{n-1} \sum_{k=i+1}^{n} P_{i,k}$$

The behaviour of the index P_j was investigated using hypothetical wader assemblages containing even and uneven spreads of either very similar, or very dissimilar, species. This indicated that the theoretical upper and lower limits to P_j were approximately 0.1 and 2.5.

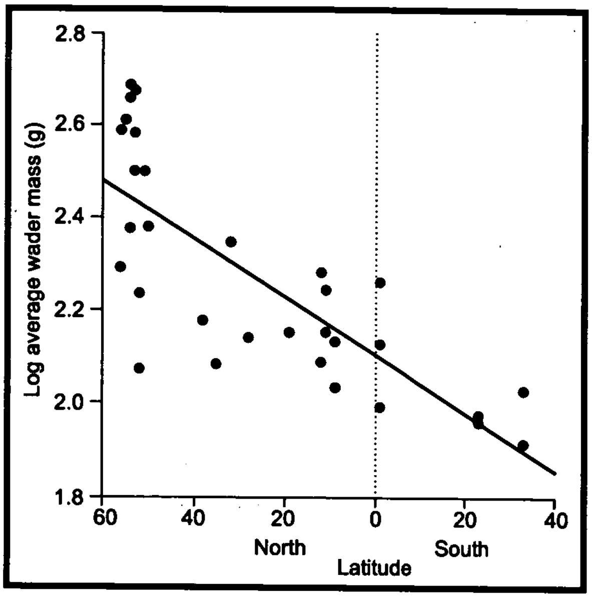

Figure 2. The mass of the 'average' wader during the boreal winter at different latitudes in the east Atlantic

RESULTS AND DISCUSSION

Wader species richness increases linearly from north to south (r_{29}=0.79, P<0.0001; Figure 1), and average bird mass (calculated from all individuals of all species) decreases logarithmically along the same axis (r_{29}=0.78, P<0.001; Figure 2). In terms of foraging mode (all individuals of all species), facultative visual/tactile foragers numerically dominate estuarine wader assemblages at both temperate and tropical latitudes, but obligate visual foragers become increasingly prevalent, in terms of both species richness and numbers, towards the tropics (Figure 3).

The latitudinal pattern of species packing is parabolic and approximately symmetrical about the Equator (Figure 4). Rather than attempting to fit a (biologically meaningless) mathematical expression to the data, we compared mean species packing indices between four latitude bands: tropical (0–15°), subtropical (15–30°), temperate (30–45°) and cold temperate (45–60°). Average species packing is significantly different between these bands (one-way ANOVA, $F_{3,27}$=24.3, P<0.0001). Differences between individual latitude bands were compared using a Student–Newman–Keuls Multiple Range Test. There is no significant difference between average species packing in cold temperate (mean P_j=0.66) and temperate (mean P_j=0.69) latitudes. At subtropical latitudes (mean P_j=1.15) and tropical latitudes (mean P_j=1.75), species packing is higher. Average indices of species packing in temperate, subtropical and tropical latitudes are all significantly different from one another.

Species packing indices are linearly correlated with species evenness:
(J)=H/lnS
where:

$$H = \sum_{i=1}^{s} P_i \ln P_i,$$

S = species richness, and
P_i is the number of individuals of species *i*, expressed as a proportion of the total number of birds (r_{29}=0.82, P<0.0001; Figure 5).

This result shows that proportional species abundance becomes increasingly uneven towards temperate latitudes; ie at high latitudes assemblages are numerically dominated by progressively fewer species.

The above indicates the existence of the following broad-scale patterns. Species richness during the boreal winter increases from north to south, approximately doubling between 56°N and 33°S. At cold temperate latitudes north of 45°N there is little predictability as to whether wader assemblages will be dominated by large or small species. In more mesic climates small species tend to dominate, this trend becoming increasingly pronounced further south. On the basis of species packing alone, there are structural changes in wader assemblages moving from temperate to tropical latitudes,

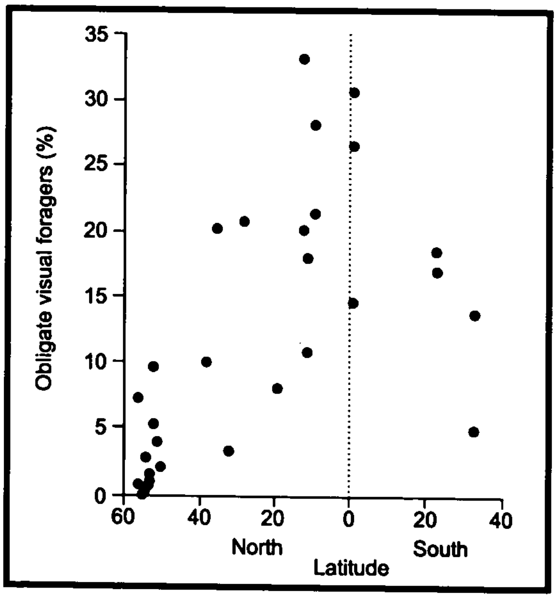

Figure 3. Latitudinal variation in the proportion of obligate visual foragers in wader assemblages in the east Atlantic during the boreal winter

and the patterns north and south of the Equator are mirror images of one another. Tropical assemblages are characterised by having relatively high species packing and evenness and a higher numerical proportion and diversity of visual foragers than found elsewhere.

Based on the premise that an increase in bird diversity will lead to the most 'efficient' use of a resource spectrum, a correlation could be predicted between species packing and species richness. This is not the case here, however, as rare taxa have little influence on the species packing index for a site. In ecological terms it is the common species that characterise a community and the existence of a positive relationship between species packing and evenness is a far more significant result than is the lack of a relationship between species richness and packing. The sensitivity of our packing index to the former rather than the latter provides support for its having ecological meaning.

Short-billed obligate visual foragers (plovers) are morphologically constrained to catching their prey at or on the substratum surface. The increasing preponderance of visual foragers towards the tropics suggests that the availability of surface-active prey is greatest at low latitudes. In cold temperate regions of the north, ambient temperatures are low during the winter residence period of waders and several of their bivalve and polychaete prey migrate deeper in the substratum at this time of year to avoid low surface temperatures, forcing birds to obtain their prey by probing (Hulscher 1996). Pienkowski (1979) documented an increasing proportion of plovers in wader assemblages between north-western Europe and Mauritania. He also noted that, as ambient temperatures decreased, the feeding rate of plovers started to decrease before that of scolopacids, suggesting that the former became energy-stressed more frequently at low temperatures (because of their reliance on surface-active prey). Concomitant with their potentially more precarious energy budgets, plovers at cold northern latitudes carry larger winter fat reserves than do scolopacids (Pienkowski 1979). Cold-induced vertical migration of invertebrates is very unlikely to occur in the temperate latitudes of the south-east Atlantic during the austral summer residence period of waders; waders at these latitudes do not deposit fat reserves other than in the pre-migration period (Summers & Waltner 1979). Nevertheless, the proportion of plovers in wader assemblages on temperate south-east Atlantic coasts is smaller than at subtropical and tropical latitudes.

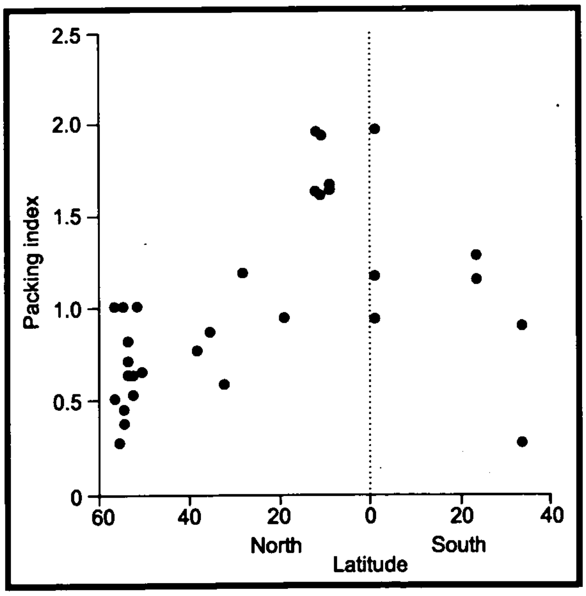

Figure 4. Species packing in wader assemblages of the east Atlantic during the boreal winter as a function of latitude

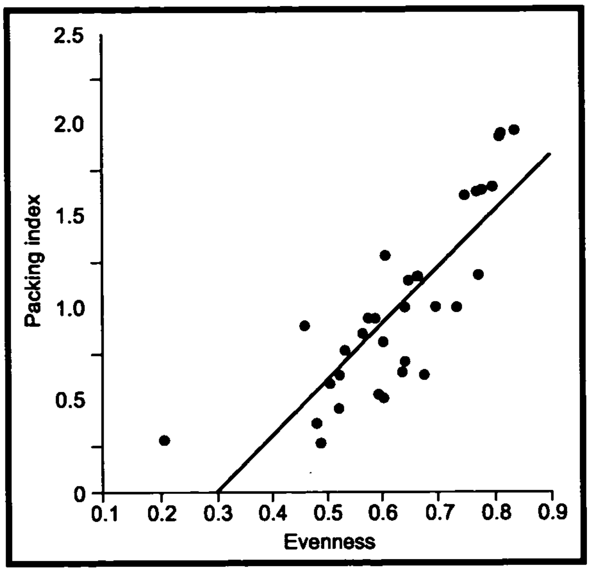

Figure 5. The relationship between the species packing index and evenness in wader assemblages of the east Atlantic during the boreal winter

In contrast to temperate situations, tropical and subtropical mudflats are often characterised by high densities of crabs at the mud surface, especially where mudflats are associated with mangrove woodlands (eg Schepers & Marteijn 1994). Crabs are eaten extensively by waders at many tropical and subtropical sites. For example, fiddler crabs (*Uca* spp.) are the dominant prey species of all plovers on the mudflats of Guinea–Bissau (Zwarts 1985).

Comparative analyses of community structure at large spatial scales are experimentally intractable, but a comparison of two equivalent-sized estuaries at the same latitude in South Africa supports our contention that the proportional abundance of plovers is environmentally linked to the availability of surface-active prey, rather than being a simple, phylogenetically linked consequence of migration distance. At the Berg River estuary on the cool Atlantic coast (33°S), polychaetes are the dominant prey of most waders (Kalejta 1993). At the Swartkops River estuary on the warm Indian Ocean coast (34°S) the dominant prey is the estuarine mudprawn (*Upogebia africana*), many of which come to the surface at low tide, where they crawl about conspicuously: this behaviour is geographically localised and possibly parasite-induced (Martin 1991). Based on multiple January counts (Martin & Baird 1987; Velasquez, Kalejta & Hockey 1991), plovers account for 32% of waders at the Swartkops estuary and only 7% of waders at the Berg estuary. This natural experiment indicates that, even at temperate latitudes, atypical conditions (in this case the abundance of surface-active mudprawns at the Swartkops estuary) can result in a 'tropical' wader assemblage at a temperate site. The Swartkops estuary is the only estuary in temperate southern Africa which regularly supports more than 20 greater sand plovers (*Charadrius leschenaultii*) – a predominantly tropical species during the non-breeding season (Hockey & Douie 1995).

CONSERVATION AND RESEARCH IMPLICATIONS

Because there are marked differences in the structure of wader assemblages at different latitudes, the effects of habitat loss will be latitude-specific not only in terms of the species and numbers of birds affected, but also in terms of the foraging guilds that are impacted. The number of birds impacted per unit area of habitat loss is predicted to be greatest at south temperate latitudes where foraging densities are highest (Hockey *et al.* 1992), but the diversity impacted at these sites will be low relative to more tropical latitudes where species' abundances are more even.

Predicting, or even interpreting, the effects of habitat loss is hampered by unknowns (eg Evans 1978–79). Spacing patterns of obligate visual foragers and facultative visual/tactile foragers are different: given species of approximately equal size, obligate visual foragers will usually be more widely spaced than other birds (Goss-Custard 1985). Ultimately, densities of facultative foragers are likely to be energy-limited, whereas obligate visual foragers may be limited to relatively low densities by their own foraging behaviour.

A priori predictions of the effects of the loss of wader habitats on the non-breeding grounds ultimately depend on an understanding of the relationship between population density, energy demand and the carrying capacity of the habitat in question. Population densities may be limited behaviourally or energetically. At present, there is an unexplained disparity between energy production by invertebrates and energy consumption by waders. On the one hand, habitat loss does lead to population decreases (this volume), yet on the other hand energy consumption rates of waders at coastal wetlands generally fall far below invertebrate production rates, although production and consumption rates apparently track one another (Hockey *et al.* 1992). The disparity between food production and consumption rates may reflect the activities of non-avian predators such as fishes or may simply be a consequence of the relationship between prey production and availability to birds. However, the difference generally is so large that even a knowledge of both production and consumption seems to give us little ability to predict quantitative effects of habitat loss on wader populations. A poor understanding of the natural mortality rates (eg senescence) of estuarine invertebrates undoubtedly exacerbates the problem (Hockey *et al.* 1992). An exception to this generalisation is a model developed by Goss-Custard *et al.* (1995) for a single predator–single prey situation. It should be noted, however, that the construction of this model relied on information about individual differences in foraging performance/behaviour – a luxury unlikely to be available in most situations.

The concept of carrying capacity is well established in the literature and is intuitively appealing. With some exceptions (eg Goss-Custard *et al.* 1995), however, it is rather loosely applied to communities rather than to components of that community. To assume that all species within a community are at the same point relative to their species-specific carrying capacity is simplistic – at any one site, numbers of any one species can vary considerably from year to year, dependent to a large extent on the size of the regional population (eg Underhill 1987). That vacant niches also exist is a reality, as evidenced by extensions in range and abundance of red knots (*Calidris canutus*) and bar-tailed godwits (*Limosa lapponica*) in temperate southern Africa during the last 50 years (Hockey & Douie 1995): there is no evidence that colonisation by these species resulted in displacement of species already present. Our analyses of species packing imply that vacant niches are probably least available in the tropics, where species packing and evenness are both high. A prediction stemming from this is that tropical wader assemblages are more saturated, and hence less susceptible to invasion, than are temperate assemblages.

We suggest that the question of why species packing should increase at low latitudes requires further research. A link with prey type diversity is possible, but considered unlikely: on sandy beaches, invertebrate species richness decreases towards the tropics (Hockey *et al.* 1983). It may simply be that the high degree of prey selectivity by obligate visual foragers, relative to facultative foragers, allows the co-existence of a greater diversity of morphologically similar species. Some light may be shed on this by a tropical–temperate comparison of the links between invertebrate and bird body size–frequency distributions. This would also help answer the question of whether resource use by tropical wader assemblages is more 'efficient' than that by temperate assemblages. If this is indeed the case, it would again point to the potential vulnerability of tropical wader assemblages to habitat loss.

Our predictive abilities are hampered by a lack of general paradigms which may stem in part from an autecological bias to wader studies. We suggest that a broader-scale view of the problem is required, with a basis in the extensive body of available and emergent ecological theory. We should not be wary of regional and global-level multi-species analyses as a means of generating testable hypotheses about the causes of wader distribution patterns and the consequences of habitat loss.

ACKNOWLEDGEMENTS

This work was funded by research grants to Hockey from the South African Foundation for Research Development and the University of Cape Town's Research Committee. We thank the British Trust for Ornithology for access to unpublished data, Rene Navarro for assistance with statistical analyses and Tracey Phillips for assistance with Figure preparation.

REFERENCES

Burger, J. 1984. Abiotic factors affecting migrant shorebirds. In: *Behaviour of marine mammals, vol. 6. Shorebirds: migration and foraging behaviour,* edited by J. Burger & B.L. Olla, 1–72. New York: Plenum Press.

Cramp, S. & Simmons, K.E.L., eds. 1983. *The birds of the western Palearctic, vol. 3.* Oxford: Oxford University Press.

Evans, P.R. 1978–79. Reclamation of intertidal land: some effects on shelduck and wader populations in the Tees estuary. *Verhandlungen der Ornithologischen Gesellschaft in Bayern,* **23,** 147–168.

Goss-Custard, J.D. 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In: *Behavioural ecology: ecological consequences of adaptive behaviour,* edited by R.M. Sibly & R.H. Smith, 169–188. Oxford: Blackwell Scientific.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T. & West, A.D. 1995. Deriving population parameters from individual variations in foraging behaviour. II. Model tests and population parameters. *Journal of Animal Ecology,* **64,** 277–289.

Hayman, P., Marchant, J. & Prater, A.J. 1986. *Shorebirds.* London: Christopher Helm.

Hockey, P.A.R. & Douie, C. 1995. *Waders of southern Africa.* Cape Town: Struik Winchester.

Hockey, P.A.R., Navarro, R.A., Kalejta, B. & Velasquez, C.R. 1992. The riddle of the sands: why are shorebird densities so high in southern estuaries? *American Naturalist,* **140,** 961–979.

Hockey, P.A.R., Siegfried, W.R., Crowe, A.A. & Cooper, J. 1983. Ecological structure and energy requirements of the sandy beach avifauna of southern Africa. In: *Sandy beaches as ecosystems,* edited by A. McLachlan & T. Erasmus, 507–521. The Hague: W. Junk.

Holt, R.D. 1987. On the relation between niche overlap and competition: the effect of incommensurable niche dimensions. *Oikos,* **48,** 110–114.

Hulscher, J.B. 1996. Food and feeding behaviour. In: *The oystercatcher: from individuals to populations,* edited by J.D. Goss-Custard, 7–29. Oxford: Oxford University Press.

Johnsgard, P.A. 1981. *The plovers, sandpipers and snipes of the world.* Lincoln: University of Nebraska Press.

Kalejta, B. 1993. Diets of shorebirds at the Berg River estuary, South Africa: spatial and temporal variation. *Ostrich,* **31,** 385–393.

Lane, B. 1987. *Shorebirds in Australia.* Melbourne: Nelson.

Maclean, G.L. 1993. *Roberts' birds of southern Africa.* Cape Town: John Voelcker Bird Book Fund.

Martin, A.P. 1991. *Feeding ecology of birds on the Swartkops estuary, South Africa.* PhD thesis, University of Port Elizabeth.

Martin, A.P. & Baird, D. 1987. Seasonal abundance and distribution of birds at the Swartkops estuary. *Ostrich,* **58,** 122–134.

Morrison, R.I.G. 1984. Migration systems of some New World shorebirds. In: *Behaviour of marine animals, vol. 6. Shorebirds: migration and foraging behaviour,* edited by J. Burger & B.L. Olla, 125–202. New York: Plenum Press.

Morrison, R.I.G. & Ross, K. 1989. *Atlas of Nearctic shorebirds on the coast of South America.* Ottawa: Canadian Wildlife Service.

Myers, J.P., Maron, J.L. & Sallaberry, M. 1985. Going to extremes: why do sanderlings migrate to the Neotropics? *Ornithological Monographs,* **36,** 520–535.

Pienkowski, M.W. 1979. Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. *Verhandlungen der Ornithologischen Gesellschaft in Bayern,* **23,** 105–124.

Piersma, T. & Davidson, N.C., eds. 1992. The migration of knots. *Wader Study Group Bulletin,* **64,** Supplement.

Prater, A.J. 1981. *Estuary birds of Britain and Ireland.* Calton: Poyser.

Schepers, F.J. & Marteijn, E.C.L., eds. 1994. *Coastal waterbirds in Gabon, winter 1992.* (Report no. 41.) Zeist: WIWO.

Smit, C.J. & Piersma, T. 1989. Numbers, midwinter distribution and migration of wader populations using the east Atlantic flyway. In: *Flyways and reserve networks for waders,* edited by H. Boyd & J.-Y. Pirot, 24–63. (IWRB Special Publication no. 9.) Slimbridge: International Waterfowl Research Bureau.

Summers, R.W. & Waltner, M. 1979. Seasonal variations in the mass of waders in southern Africa, with special reference to migration. *Ostrich,* **50,** 21–37.

Underhill, L.G. 1987. Waders (Charadrii) and other waterbirds at Langebaan Lagoon, South Africa, 1975–1986. *Ostrich,* **58,** 145–155.

Velasquez, C.R., Kalejta, B. & Hockey, P.A.R. 1991. Seasonal abundance, habitat selection and energy consumption by waterbirds at the Berg River estuary, South Africa. *Ostrich,* **62,** 109–123.

Wiens, J.A. 1989. *The ecology of bird communities, vol. 1. Foundations and patterns.* Cambridge: Cambridge University Press.

Zwarts, L. 1985. The winter exploitation of fiddler crabs *Uca tangeri* by waders in Guinea–Bissau. *Ardea,* **73,** 3–12.

Response of migratory coastal bird populations to the land claim in the Nordstrand Bay, Germany

H Hötker

Forschungs- und Technologiezentrum Westküste der Universität Kiel, Hafentörn, 25761 Büsum, Germany

SUMMARY

Extensive counts before and after a land claim of 33 km^2 in the Nordstrand Bay on the German coast of the Wadden Sea allowed us to check the predictions that were made to assess the impact on coastal bird populations of habitat loss. As predicted, the numbers of barnacle geese and wigeons feeding in the embanked area increased, whereas the numbers of brent geese, shelducks and most wader species decreased. Species that could make only little use of the embanked area showed population declines, even though the populations in the Wadden Sea of Schleswig-Holstein increased over the same period. The results suggest that the population sizes of knot, bar-tailed godwit, spotted redshank, redshank and greenshank had been close to carrying capacity before the habitat loss occurred.

INTRODUCTION

The Wadden Sea of Denmark, Germany and The Netherlands is one of the key wetlands in the east Atlantic flyway system (Smit & Wolff 1983; Boyd & Pirot 1989). About 10–12 million coastal birds visit the Wadden Sea during various stages of their annual cycles, mostly on passage (Meltofte *et al.* 1994). Land claims have been one of the major threats to the habitats of these birds; large areas of mudflats and saltmarshes have been claimed over the last few centuries (Abrahamse, Joenje & van Leeuwen-Seelt 1976). The last major land claim on the coast of Schleswig-Holstein was undertaken in the Nordstrand Bay where 33 km^2 of mudflats, saltmarshes and tidal creeks were embanked in 1987.

Habitat losses like those in the Nordstrand Bay are known to affect populations of coastal birds on a local scale (Evans *et al.* 1979; Laursen, Gram & Alberto 1984; Schekkerman, Meininger & Meire 1994; Wolff *et al.* 1976). The question of under what conditions the total population can be affected by large-scale embankments and other habitat losses is still under consideration (Goss-Custard *et al.* 1995a; Ens, Goss-Custard & Weber 1996). An impact of habitat loss on waterbird populations would only be expected if the rates of either survival or reproduction, or both, are density-dependent (Goss-Custard *et al.* 1995a), the effect being particularly severe the closer the affected area is to carrying capacity (Goss-Custard & West, this volume, pp52–62). According to Schekkerman *et al.* (1994), the following would be expected if bird numbers were close to carrying capacity prior to the habitat changes being made.

- Bird numbers decline after the habitat loss.
- The decline is a local event that is unrelated to changes in the size of the total population.
- The differing responses of individual species can be understood in the light of their distribution and/or diet.

Before large parts of the Nordstrand Bay were embanked, the possible impacts on bird populations of the land claim had been assessed. Based on extensive counts of waterfowl and waders in 1979 and on published and unpublished data from other reclaimed sites on the Wadden Sea coast, Schultz (1980, 1981) predicted the changes that would be expected to occur to wetland bird populations in the Nordstrand Bay. Now, several years after the new dike was constructed, regular counts of birds in the embanked site and in adjacent parts of the Wadden Sea allow us to review the quality of the very simple, non-mathematical predictions that had been derived without any explicit modelling approach.

This paper has three aims:

i. to check whether the predictions of Schultz (1980) have been fulfilled;
ii. to review the impact of the land claim in the Nordstrand Bay on the populations of coastal birds, both locally and in the surrounding Wadden Sea; and
iii. to use the criteria of Schekkerman *et al.* (1994) to evaluate if numbers of individual species have been close to carrying capacity prior to the land claim.

STUDY SITE

Before the land claim took place, the Nordstrand Bay was one of the largest bays on the coast of Schleswig-Holstein, with a comparatively high diversity of habitats including extensive (sheep-grazed) saltmarshes, mudflats, sandflats and some permanently flooded tidal channels (Minister für Ernährung, Landwirtschaft und Forsten des Landes Schleswig-Holstein (MELF) 1981). The land claim comprised about 1% of the mudflats and as much as 10% of the saltmarshes of the mainland coast of Schleswig-Holstein (MELF 1987). The new 8.9 km sea dike, which was constructed from 1985 to 1987, crosses the bay between the mainland and the peninsula of Nordstrand. It has embanked all saltmarshes and most of the silty parts of the bay. Extensive sandy mudflats were left in front of the dike.

Since the end of the construction works, the embanked area – named Beltringharder Koog – has largly been managed for nature conservation. The central part of the reserve consists of a saltwater lagoon of *ca* 800 ha. Two sluices in the new dike allow considerable water exchange with the sea. Under normal circumstances, the water level in the lagoon is allowed to rise and fall by up to 40 cm within a tidal cycle, resulting in the exposure of up to 160 ha of intertidal flats.

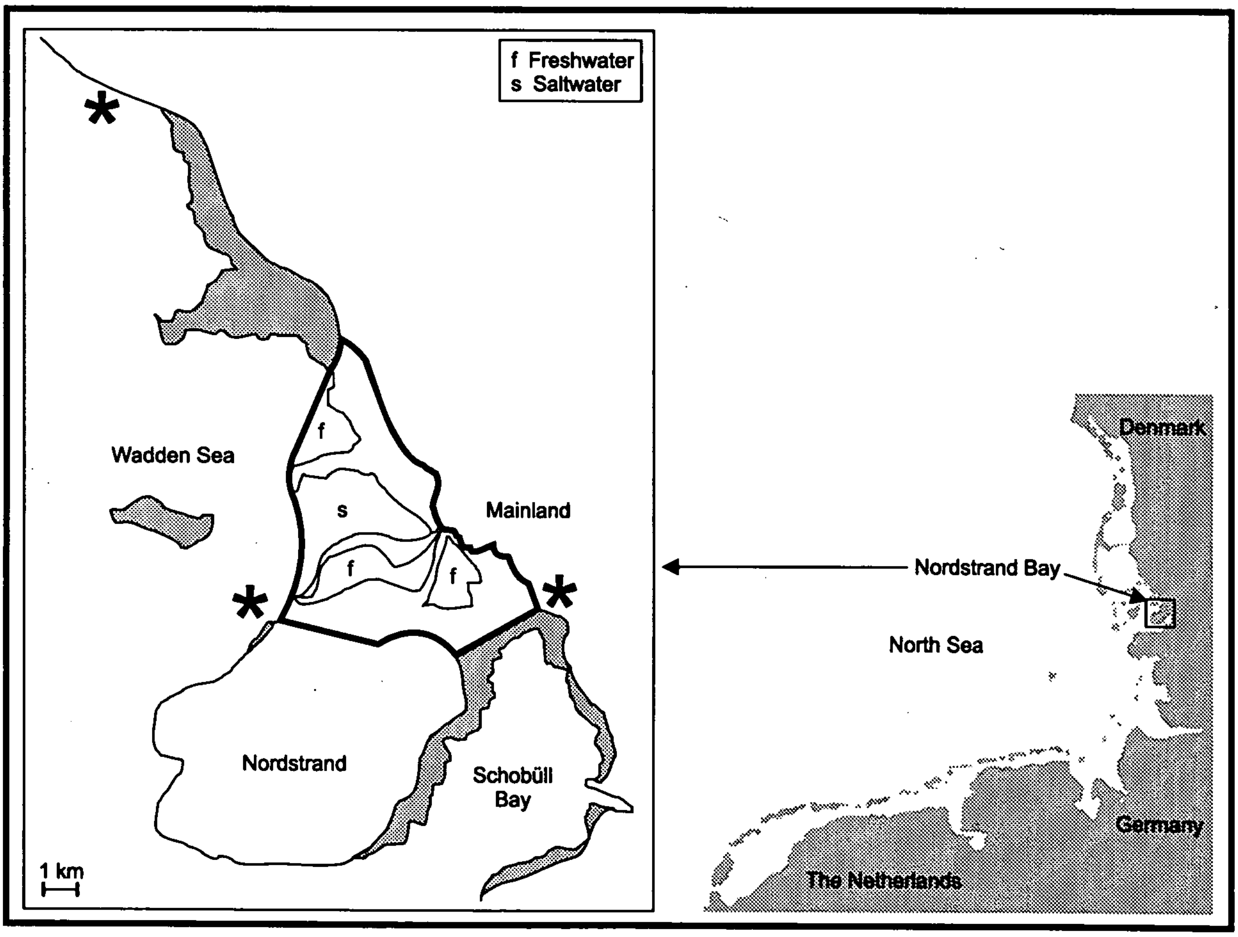

Figure 1. The Nordstrand Bay after the land claim. The embanked area, the Beltringharder Koog, is surrounded by a bold line. The edges of the coastline of the greater Nordstrand Bay are marked by asterisks. Dotted areas show the remaining saltmarshes. f = freshwater lakes; s = saltwater lagoon

Table 1. Most important migratory waterbird species in the Nordstrand Bay in 1979. Maximum counts in 1979, predictions of population development after the land claim and actual population development after the land claim. +/– stable population, – population decrease 10% to 90%, - -: severe population decrease >90% (modified from Schultz 1980, 1981)

Species	Maximum count in 1979	Prediction for the number of birds feeding in the embanked area	Prediction for the number of birds roosting in the embanked area	Population development in the embanked area, roosting birds	Population development in the greater Nordstrand Bay	Population development in the Wadden Sea, numbers of significant trends per season[1]	% of birds in the embanked area at low tide
Barnacle goose (*Branta leucopsis*)	80	+	+	+	+	0	78
Brent goose (*Branta bernicla*)	4720	- -	- -	-	+	1x increase	75
Shelduck (*Tadorna tadorna*)	7034	- -	-	-	+	1x decrease	70
Wigeon (*Anas penelope*)	8995	+	+	+	+	3x increase	85
Oystercatcher (*Haematopus ostralegus*)	7391	- -	-	-	+	0	42
Avocet (*Recurvirostra avosetta*)	486	-	-	+	+	1x increase	78
Grey plover (*Pluvialis squatarola*)	3526	- -	-	+/-	+/-	3x increase	20
Knot (*Calidris canutus*)	7349	- -	-	-	-	1x increase	9
Dunlin (Calidris alpina)	15613	-	-	+/-	+/-	2x increase	35
Bar-tailed godwit (*Limosa lapponica*)	4169	- -	-	-	-	1x increase	22
Curlew (*Numenius arquata*)	6491	-	+/-	+/-	+	2x increase	36
Spotted redshank (*Tringa erythropus*)	1201	-	+/-	-	-	2x increase	30
Redshank (*Tringa totanus*)	2584	-	-	-	-	3x increase	48
Greenshank (*Tringa nebularia*)	411	- -	-	-	-	0	28

[1] Source: Rösner 1994

The benthic communities in the saltwater lagoon resembled those of the Wadden Sea with, however, lower densities of most species (Thiel *et al.* 1990, 1991). The remaining parts of the reserve consist of non-tidal, mostly very shallow, freshwater bodies with predominantly unvegetated and muddy shores. In the northern part of the reserve, the land areas are grazed by sheep and cattle whereas, in the south, grazing ceased in order to allow a natural succession of vegetation. Public access to the reserve is limited to a road connecting the mainland and the new dike and to the dikes surrounding the reserve.

METHODS

Complete and regular counts of coastal birds in the study site were available for the following years: 1979, 1986–95. Two to five persons counted simultaneously from 0130 h before to 0130 h after high tide. Counts in 1979 took place every fortnight. Thereafter, they were made on spring tides, every 14–16 days. Besides the high-tide counts, low-tide counts were carried out from July 1987 to June 1991, usually on the same days as the high tide counts. Time activity budgets of shelducks (*Tadorna tadorna*) and waders were monitored between July 1987 and February 1992. Spring-tide counts of coastal

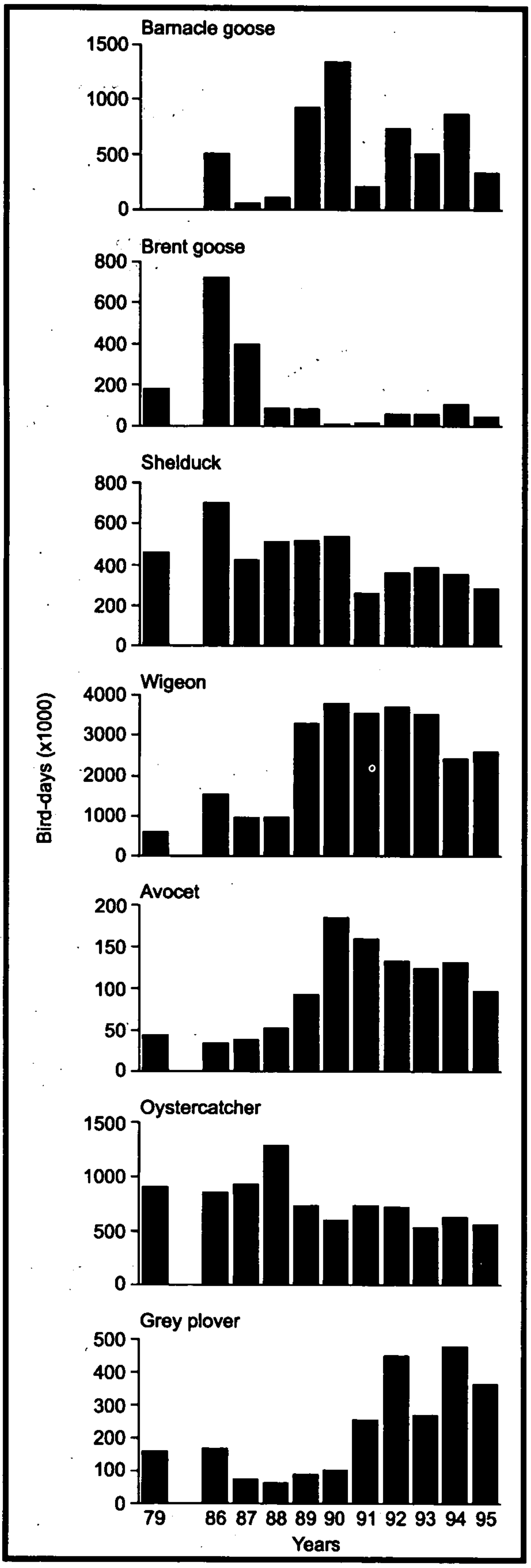

Figure 2i. Population changes of coastal bird species in the Nordstrand Bay. Numbers of bird-days (x1000) in the years 1979 and 1986–95

birds of the greater Nordstrand Bay, which includes the claimed area and the remaining bay up to the Hauke-Haien-Koog 15 km north of the reserve (Figure 1), were available for the years 1979 and 1986–91. In order to analyse population trends of coastal birds, I used the annual sum of bird-days. For details of methods, see Hötker and Kölsch (1993), Hötker (1994), Hötker (1995).

THE PREDICTIONS

The counts of coastal birds in 1979 revealed that 14 species were represented in the study area by at least 1% of their geographical flyway population (Table 1; data on flyway population sizes based on information available in early 1980). The predictions for the effect of habitat loss on these 14 species were based on information on:

- habitat selection, especially the species' abilities to use inland freshwater habitats;
- management plans of the embanked area;
- data from other reclaimed sites, in particular the Grevelingenmeer (Wolff *et al.* 1976), the Lauwersmeer (Prop & van Eerden 1981) and the Hauke-Haien-Koog (Kelm 1977).

The predictions were expressed verbally and qualitatively in Schultz (1980). I transferred the predictions into a semi-quantitative system by assuming that 'heavy reduction' means a decrease in numbers of more than 90%.

RESULTS

In general, there was good agreement between predicted and observed trends (Table 1). With respect to the high-tide counts, most of the few exceptions can be explained.

In brent geese (*Branta bernicla*), the immediate response to the land claim was as strong as predicted. In the autumn migration period following the final closure of the dike in May 1987, the number of brent goose days in the site dropped to less than 10% of the numbers reached during previous autumn migration periods. Since 1992, brent geese have started to feed on the slowly expanding saltmarsh vegetation in the reserve and on the dikes. The numbers of brent geese visiting the site increased with the improving conditions in the feeding sites (Figure 2). Many of the brent geese which had been expelled from their original habitats occurred on feeding sites surrounding the Beltringharder Koog in the spring migration periods. Of the 277 brent geese marked before the land claim, 43 individuals have been sighted in May of one or more of the following years. Only nine of them have been reported from the ringing site itself. Thirteen brent geese were in The Netherlands on the date on which they had been ringed in the Nordstrand Bay in one of the years before, and 22 were sighted on saltmarshes surrounding the Beltringharder Koog (Figure 3).

The avocet (*Recurvirostra avosetta*) population increased, mainly due to an increase in the numbers breeding. The migratory population, which could not easily be distinguished from the breeding population, probably decreased after 1993 (personal observations), as predicted by Schultz (1980).

The numbers of grey plover (*Pluvialis squatarola*) and dunlin (*Calidris alpina*) at high tide did not decrease as predicted because, since 1991, the high-tide roosts in the Beltringharder Koog attracted many birds feeding in the adjacent Schobüll Bay. Such a large exchange of birds between the Schobüll and the Nordstrand Bay had not been noticed before the embankment took place.

Predictions of how the numbers of birds feeding in the enclosed area would change were even more accurate than those made for the numbers of birds roosting at high tide. As predicted, only the herbivores barnacle goose (*Branta leucopsis*) and wigeon (*Anas penelope*) were able to profit from the land claim. The numbers of avocets present were strongly influenced by the breeding birds which foraged mainly within the Beltringharder Koog. In all other species, only relatively few individuals could be seen feeding in the enclosed area at low tide after the area had been embanked. At low tide, the numbers of birds in the enclosed Beltringharder Koog were generally much lower than at high tide (Table 1) and, moreover, the birds in the embanked area showed less feeding activity than their conspecifics in the surrounding Wadden Sea habitats (Hötker 1994). Only redshanks used the Beltringharder Koog for extensive extra feeding at high tide.

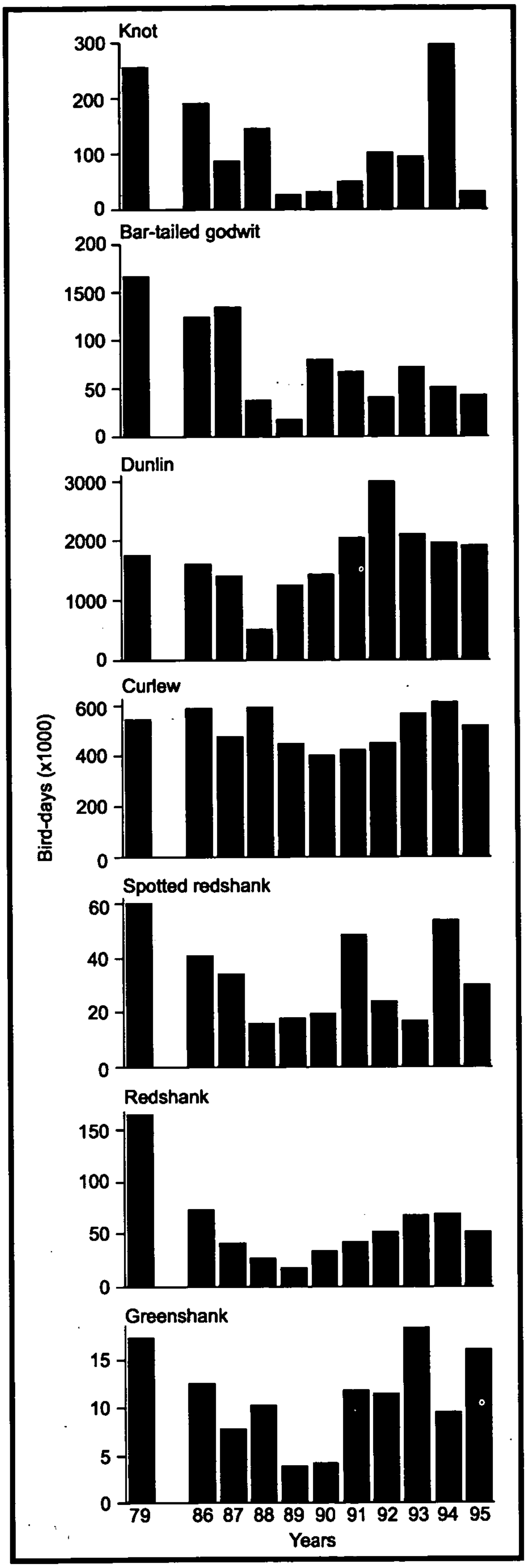

Figure 2ii. Population changes of coastal bird species in the Nordstrand Bay. Numbers of bird-days (x1000) in the years 1979 and 1986–95

How did the local population changes in the enclosed area influence the populations in the greater Nordstrand Bay? Most of the species under consideration experienced increases in the Schleswig-Holstein part of the Wadden Sea from 1986 to 1994 (Rösner 1994, see Table 1). These increases were mirrored by decreases of some species in the greater Nordstrand Bay. Most notably, the population size of those species which were least able to feed in the embanked area decreased in the greater area. In the group of species whose numbers increased in the greater area, significantly higher percentages of birds used the embanked area at low tide compared with the group of species whose population sizes in the greater area were stable or decreasing (Mann–Whitney U-test: P=0.004, z=8.265). For knot (*Calidris canutus*), bar-tailed godwit (*Limosa lapponica*), spotted redshank (*Tringa erythropus*), redshank (*T. totanus*), and greenshank (*T. nebularia*), the lost feeding opportunities due to the land claim could not be compensated in the immediate surroundings of the study site.

DISCUSSION

The predictions on population change in waterbirds in the Nordstrand Bay after the land claim (Schultz 1980) were realised remarkably well. The knowledge of the species' habitat requirements and the experience gained with earlier land claims obviously had been sufficient to produce a reliable prediction for the bird life in the embanked area itself.

One reason for the success of the predictions was surely their simplicity. The predictions were qualitative or semi-quantitative and they were restricted to the affected area itself. Schultz (1980) and his co-workers did not try to assess the consequences of the habitat losses in the Nordstrand Bay for the total Schleswig-Holstein Wadden Sea populations or even for the total flyway populations. Indeed, even the extensive counts of waterbirds both in the Nordstrand Bay and in the whole Schleswig-Holstein Wadden Sea which have taken place since Schultz's report was written have not been able to provide any conclusive data on whether population size over the whole region was affected. There are several reasons for the difficulties of interpreting the results of counts in the Wadden Sea.

- *Severity of the winter*. Populations of coastal birds are known to be very sensitive to the severity of the winter weather (Ridgil & Fox 1990; Meltofte *et al.* 1994). The eastern part of the Wadden Sea, in particular, may be nearly completely vacated by coastal birds in severe winters (Meltofte *et al.* 1994; Hötker & Kölsch 1993). In this study, all winters in the baseline years before the land claim took place had been especially severe, whereas the winters following the land claim were much milder.
- *Scale of loss in relation to remaining habitat* versus *accuracy and completeness of counts*. Although the land claim in the Nordstrand Bay was huge, it comprised less than 2% of the total area of the Schleswig-Holstein Wadden Sea. Complete counts of the Wadden Sea which would have been able to show post-habitat loss changes in population sizes were too infrequent, too incomplete and too imprecise to detect the rather subtle changes which could have been induced by the loss of a comparatively small loss of habitat.
- *Transitoriness of bird populations*. Most bird populations in the Wadden Sea are transitory. Changes in numbers of birds counted do not necessarily reflect a change in the number of birds visiting the site, but could also be the result of changed staging times and, hence, a changed turn-over rate.

In view of all these difficulties, it seems very unlikely that even improved counts of birds in the Wadden Sea could provide sufficient data to answer the question of whether a loss of habitat, such as in the Nordstrand Bay, has affected overall population sizes. Counts will at best show local effects. For assessing the impact of habitat losses on a Wadden Sea scale or on the flyway level, data on the population biology of the species have to be considered (Goss-Custard *et al.* 1995a; Ens *et al.* 1996).

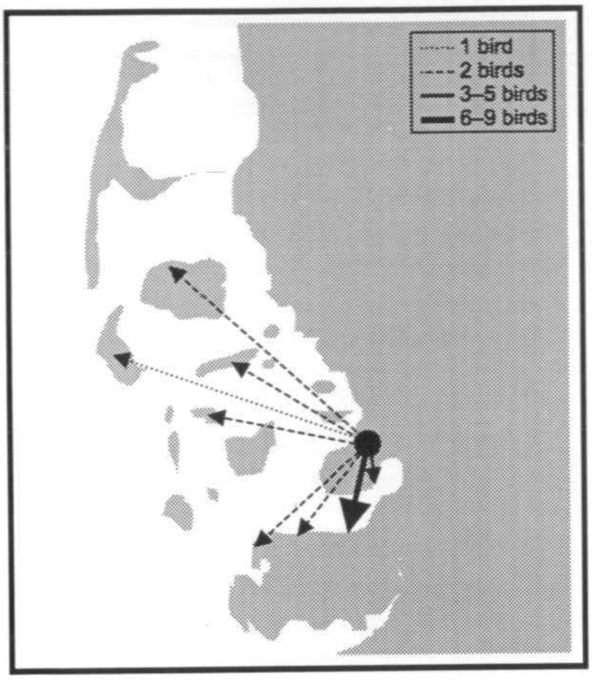

Figure 3. Dispersal of brent geese after the land claim. The dot marks the site where 277 brent geese had been colour-ringed

The low numbers of birds feeding in the embanked area (Table 1) clearly show that even quite sophisticated management of a tidal saltwater lagoon could not restore the feeding grounds for shelducks and waders to their original value (for details see Hötker 1994). The Beltringharder Koog, however, has attracted more waders and shelducks to its high-tide roosting sites than did the saltmarshes of the unclaimed Nordstrand Bay. The high-tide roosts in the Beltringharder Koog were situated on islands, which were inaccessible to man and ground predators. These islands were never flooded, not even during storm tides, and they offered protection against the wind. Special attention was paid to minimising disturbance in the embanked area. Hunting ceased and access was forbidden to large parts of the area. Thus, quite obviously, the quality of the Beltringharder Koog for roosting has increased. Habitat loss through embankments of coastal habitats may, in particular, affect the availability of high-tide roost sites. In contrast to feeding sites, relatively little is known about the roost site requirements of waders. Safe high-tide roosts are vital elements of the daily home ranges of waders. Although they may not limit wader populations as often as the availability of food, the availability of high-tide roosts should more often be considered in impact assessment procedure.

Following the criteria of Schekkerman *et al.* (1994), the numbers of knot, bar-tailed godwit, spotted redshank, redshank and greenshank had been close to carrying capacity prior to the land claim. All of these species have declined in the greater Nordstrand Bay, all have had positive trends in the whole Wadden Sea of Schleswig-Holstein (although greenshank not significantly), and all, with the exception of redshank, could make very little use of the embanked area in terms of feeding.

ACKNOWLEDGEMENTS

My thanks go to all colleagues who helped collecting the data used for this analysis, in particular Holger A Bruns. I am grateful to Bart Ebbinge and Peter Prokosch for providing their brent geese ringing and sighting data. Wilfried Knief and Peter Prokosch who were involved in writing the first reports on the birds of the Nordstrand Bay (Schultz 1980, 1981) kindly commented on an earlier version of the manuscript. I also thank John Goss-Custard for his valuable comments and final improvements to the manuscript.

REFERENCES

Abrahamse, J., Joenje, W. & van Leeuwen-Seelt, N. 1976. *Wattenmeer.* Neumünster: Wachholtz.

Boyd, H. & Pirot, J.Y., eds. 1989. *Flyways and reserve networks for water birds.* (IWRB Special Publication no. 9.) Slimbridge: International Waterfowl Research Bureau.

Ens, B.J., Goss-Custard, J.D. & Weber, T.P. 1996. *Effects of climate change on bird migration strategies along the East Atlantic Flyway.* (Research Report 96/1.) Wageningen: IBN-DLO.

Evans, P.R., Herdson, D.M., Knight, P.J. & Pienkowski, M.W. 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and shelduck. *Verhandlungen der Ornithologischen Gesellschaft in Bayern,* **41**, 183–206.

Goss-Custard, J.D. & West, A.D. 1997. The concept of carrying capacity and shorebirds. In: *Effect of habitat loss and change on waterbirds,* edited by J.D. Goss-Custard, R. Rufino & A. Luis, 52–62. (ITE symposium no. 30.) London: The Stationery Office.

Goss-Custard, J.D., Caldow, R.W.G, Clarke, R.T., Durell, S.E.A. le V. dit, Urfi, J. & West, A.D. 1995a. Consequences of habitat loss and change to populations of wintering migratory birds: predicting the local and global effects from studies of individuals. *Ibis,* **137**, S56–S66.

Goss-Custard, J.D., Clarke, R.T., Briggs, K.B., Ens, B.J., Exo, K.-M., Smit, C., Beintema, A.J., Caldow,

R.W.G., Catt, D.C., Clark, N.A., Durell, S.E.A. le V. dit, Harris, M.P., Hulscher, J.B., Meininger, P.L., Picozzi, N., Prys-Jones, R., Safriel, U. & West, A.D. 1995b. Population consequences of winter habitat loss in a migratory shorebird. I. Estimating model parameters. *Journal of Applied Ecology*, **32**, 320–336.

Hötker, H. 1994. Wadden Sea birds and embankments – can artificial wetlands compensate for losses due to land claims? *Ophelia Supplement*, **6**, 279-295.

Hötker, H. 1995. Aktivitätsrhythmus von Brandgänsen (*Tadorna tadorna*) und Watvögeln (Charadrii) an der Nordseeküste. *Journal für Ornithologie*, **136**, 105–126.

Hötker, H. & Kölsch, G. 1993. Die Vogelwelt des Beltringharder Kooges. Ökologische Veränderungen in der eingedeichten Nordstrander Bucht. *Corax*, **15**, Supplement, 1–145.

Kelm, H.-J. 1977. *Hauke-Haien-Koog-Bericht 1977*. Schlüttsiel. Unpublished report.

Laursen, K., Gram, I. & Alberto, L.J. 1984. Short-term effect of reclamation on numbers and distribution of waterfowl at Højer, Danish Wadden Sea. *Proceedings of the third Nordic Congress of Ornithology*, 97–118.

Minister für Ernährung, Landwirtschaft und Forsten des Landes Schleswig-Holstein (MELF). 1981. *Gutachten zur geplanten Vordeichung der Nordstrander Bucht*. Schriftenreihe der Landesregierung Schleswig-Holstein 12, Kiel.

Minister für Ernährung, Landwirtschaft und Forsten des Landes Schleswig-Holstein (MELF). 1987. *Küstenschutz Nordstrander Bucht*. Kiel: Faltblatt.

Meltofte, H., Blew, J., Frikke, J., Rösner, H.U. & Smit, C.J. 1994. Numbers and distribution of waterbirds in the Wadden Sea. (IWRB Publication no. 34.) *Wader Study Group Bulletin 74, Special issue*, 1–192.

Prop, J. & van Eerden, M.R. 1981. Het voorkomen van trekvogels in het Lauwerszeegebied vanaf de afsluiting in 1969 tot en met 1978. *Limosa*, **54**, 1–16.

Ridgil, S.C. & Fox, A.D. 1990. *Cold weather movements of waterfowl in western Europe*. (IWRB Special Publication no. 13.) Slimbridge: International Waterfowl Research Bureau.

Rösner, H.-U. 1994. Population indices for migratory birds in the Schleswig-Holstein Wadden Sea from 1987 to 1993. *Ophelia Supplement*, **6**, 171–186.

Schekkerman, H., Meininger, P.L. & Meire, P.M. 1994. Changes in the waterbird populations of the Oosterschelde (SW Netherlands) as a result of large-scale coastal engineering works. *Hydrobiologia*, **282/283**, 509–524.

Schultz, W. 1980. *Forschungsvorhaben "Vogelkundliche Bedeutung der Nordstrander Bucht"*. Institut für Haustierkunde der Universität Kiel, Staatliche Vogelschutzwarte Schleswig-Holstein, Kiel. Unpublished report.

Schultz, W. 1981. *Forschungsvorhaben "Vogelkundliche Bedeutung der Nordstrander Bucht"*. Institut für Haustierkunde der Universität Kiel, Staatliche Vogelschutzwarte Schleswig-Holstein, Kiel. Unpublished report.

Smit, C.J. & Wolff, W.J. 1983. Birds of the Wadden Sea. In: *Ecology of the Wadden Sea*, edited by W.J. Wolff. Rotterdam: Balkema.

Thiel, H., Hagge, A., Hinz, V. & Leling, A. 1990. *Hydrobiologische Untersuchungen im Beltringharder Koog und den vorgelagerten Wattgebieten*. Jahresbericht 1989, University of Hamburg.

Thiel, H., Hagge, A., Hinz, V. & Leling, A. 1991. *Hydrobiologische Untersuchungen im Beltringharder Koog und den vorgelagerten Wattgebieten*. Jahresbericht 1990, University of Hamburg.

Wolff, W.J., Haperen, A.M.M., van Sandee, A.J.J., Baptist, H.J.M. & Saeijs, H.L.F. 1976. The trophic role of birds in the Grevelingen estuary, The Netherlands, as compared to their role in the saline Lake Grevelingen. In: *Proceedings of the 10th European Symposium on Marine Biology*, Vol. 2, 673–689. Wetteren: Universal Press.

Use of a spatial decision support system for analysis of habitat use by wintering northern pintails

C W Jeske[1], W Ji[1], P C Chadwick[1], W Norling[1] & M C Finley[2]

[1] *National Biological Service, National Wetlands Research Center, 700 Cajundome Boulevard, Lafayette, Louisiana 70506, USA*
[2] *Johnson Controls World Services, 700 Cajundome Boulevard, Lafayette, Louisiana 70506, USA*

SUMMARY
A multi-functional spatial decision support system (SDSS) was developed at the spatial analysis branch of the National Wetlands Research Center, and the wildlife analysis module of the system was used to study habitat use by wintering pintail. We instrumented female pintails at Catahoula Lake, Louisiana, in October of 1992–94 and located the instrumented birds weekly through the following March. Using the SDSS developed in an ARC/INFO geographical information system (GIS) environment, we were able to visualise movements of instrumented pintails over varied environmental conditions and landscape features to determine habitat use. Weather data were used to determine factors important in the timing of movements. The analyses indicated that female pintails dispersed from Catahoula Lake, Louisiana, in three general patterns, based upon wetland conditions. Timing of movements coincided with periods of precipitation or disturbance, primarily hunting. Pintails which arrived at Catahoula Lake in October and November remained in the agricultural areas of Louisiana and Arkansas, with very limited movements to the coastal marshes or westward into the agricultural areas of Texas. Northward movements into Arkansas occurred whenever there was substantial rainfall in the agricultural regions, and northward movements generally stopped at the frost-line. No differences in adult or juvenile female movement patterns were apparent.

INTRODUCTION

Declines in northern pintail (*Anas acuta*) breeding population indices in North America have increased interest in pintail biology. Habitat availability and use by pintails are areas of particular interest as factors which may have contributed to the decline because of the relation between winter wetland conditions and recruitment the subsequent spring (Raveling & Heitmeyer 1989). Pintails are thought to be highly nomadic with frequent long-distance movements to utilise ephemeral habitats. Our study was initiated to determine movement patterns and environmental factors influencing movements of pintails wintering in Louisiana.
For this objective, pintail datasets needed to integrate with habitat and other environmental datasets for analysis. Therefore, a powerful computer-based tool that is able to perform spatial and temporal analyses on integrated datasets was strongly needed.

A multi-functional SDSS was developed at the spatial analysis branch of the National Wetlands Research Center. The system includes special functions for modelling and information synthesis in wetland restoration planning, wetland permit analysis, and wildlife analysis (Ji 1993, 1996; Ji & Johnston 1994, 1995; Ji & Mitchell 1995). The wildlife analysis module of the system was enhanced and used in this study to determine movement patterns of northern pintails in response to habitat changes through the winter.

METHODS

Pintails were captured using bait traps and rocket nets at Catahoula Lake in late October and early November 1992, 1993, and 1994. In 1992, 50 after-hatch year (AHY) and 39 hatch year (HY) females were instrumented with backpack radio-transmitter packages (Dwyer 1972) with a mortality sensor and 180-day expected lifespan. Forty-five and 52 AHY females, and 41 and 50 HY females were instrumented in 1993 and 1994, respectively.

Instrumented females were located weekly from aircraft. Weekly flights covered south-west, central, and north-eastern Louisiana, and eastern Arkansas. In late winter, aerial coverage included western Mississippi. Irregular flights covered south-eastern Louisiana and western Texas. In March, flights extended into southern Missouri and western Tennessee. Altitude for most flights was from 4000 to 6500 feet above ground level. At this altitude, reception distance was up to 40 miles. When a bird was contacted, ground location was determined as precisely as possible and latitude and longitude were recorded using a global positioning system (GPS) receiver or US Geological Survey topographic maps. Data on each bird and latitude and longitude for each location were recorded and stored in electronic format. The pintail data were then converted into the point coverages (maps) of the ARC/INFO GIS format, with specially designed attributes, and loaded into the SDSS.

Multiple environmental GIS datasets were obtained from the GAP analysis program and previous project databases, and loaded into the decision support GIS to form an ecosystem database.

This database includes boundary coverages of the lower Mississippi valley region, satellite (advanced very high resolution reflectometry, AVHRR) images of wet and dry seasons during multiple years, and habitat data such as wildlife refuges, forests, and major lakes in the region. These pintail and environmental datasets were integrated by linking each data layer to a specially customised interface menu of the system.

The data integration approach with the SDSS allowed simultaneous analysis of the impacts of multiple environmental factors on pintail movement. For example, overlaying pintail location data on AVHRR images of different seasons allowed us to determine surface water conditions over a large region in order to evaluate habitat use and availability. The SDSS also allowed analytical visualisation of the movement of specific pintail groups over specific environmental conditions by using specific analytical criteria, such as pintail sex and age, specific geographical regions, and time ranges (year, month, or week). Associated attribute information of the pintails could also be queried interactively. With the aid of the SDSS, we had a better understanding of the movement patterns of pintail populations in relation to major landscape features, water resources, forests, and refuge boundaries in the study area in the context of habitat uses.

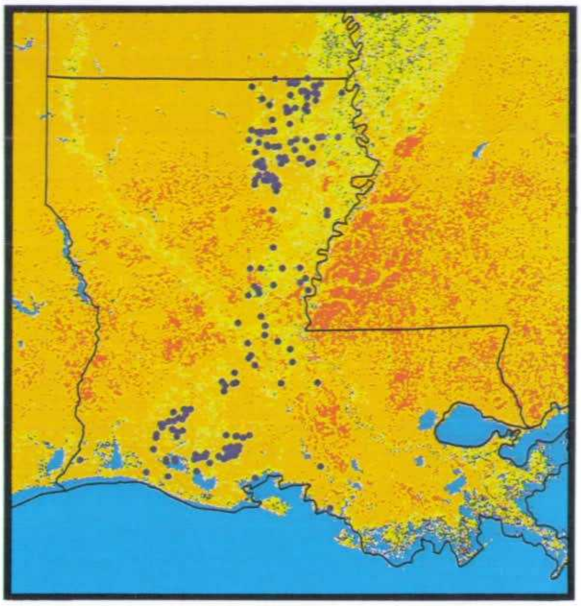

Figure 1. Example of overlaying locations of instrumented northern pintails and advanced very high resolution reflectometry (AVHRR) to determine patterns of habitat use

RESULTS

Integration of satellite imagery (Figure 1) in the SDSS helped us to visualise the following patterns of the pintail movement. Pintails remained in the vicinity of Catahoula Lake until mid-November. In mid-November, the hunting season opened and the disturbance dispersed the birds if other wetland habitats were available. For example, AVHRR imagery suggested that few other wetlands were available for the disturbed birds to disperse to in November 1992. Few instrumented pintails left the vicinity of Catahoula Lake during the month. This is compared with conditions in November 1993, when AVHRR imagery suggested abundant wetlands in the region and most instrumented birds dispersed from the vicinity of Catahoula Lake in response to the hunting disturbance. Locations of instrumented pintails were almost always in agricultural areas, with little movement to the coastal marshes of Texas or Louisiana, and little movement westward to the agricultural areas of Texas. When wetland conditions permitted, instrumented birds responded to hunting disturbance by moving in a northward direction to north-east Louisiana, where the instrumented birds primarily used flooded rice fields. In late December, when fields flooded in Arkansas, further northward movements were observed. A gradual northward movement in Arkansas was observed until mid-March, when increased ambient temperatures thawed wetlands north of Arkansas. After the start of January, few instrumented pintails responded to cold ambient temperatures by returning to more southerly locations, as they often did when cold ambient temperatures occurred in December.

DISCUSSION

Use of the SDSS allowed visualisation of movement patterns of instrumented pintails through the winter period. The ability to access habitat data, such as the AVHRR imagery, rapidly and to overlay bird locations provides an effective method for visualising how birds are responding to different conditions. The ability to query the databases to customise output enables researchers and managers to access individual data points quickly, and then identify ancillary data. For example, individual national wildlife refuges can be identified in one database, and the number of times instrumented pintails were located at that refuge can be calculated for any particular year or for all years. This information can be further refined by asking for all adult females in an individual month. As additional databases are included in the SDSS, other relations may be developed, such as the occurrence of other species at an area, if the data are available.

The SDSS is still being developed to add spatial statistical capabilities. These preliminary analyses are based upon visual interpretation of the data; continued development will add the capability to compare statistically use and availability measures, such as the use of refuge areas with the availability of refuges.

Additional databases, primarily satellite images, are being collected for additional analyses. These additions will provide the capability to model pintail response to habitat alterations, such as potential effects on pintail distribution resulting from changing agricultural practices from a rice/soybean/crayfish rotation to sugar cane, and the resulting loss of wetland habitats.

ACKNOWLEDEGEMNTS

Elijah Ramsey and Dal Chappell provided the AVHRR imagery for use in this project. Scott Wilson assisted with production of the Figure. Jimmy Johnston and Steve Hartley provided substantial support in collecting the spatial datasets.

REFERENCES

Dwyer, T.J. 1972. An adjustable radio-package for ducks. *Bird-Banding,* **43,** 282–284.

Ji, W. 1993. Integrating a resource assessment model into ARC/INFO GIS: a spatial decision support system development. In: *Proceeding of the ASPRS Annual Convention,* edited by A. Lewis, 159–166. New Orleans, Louisiana.

Ji, W. 1996. Ecosystem management: a decision support GIS approach. *Proceedings of 1996 International Geoscience and Remote Sensing Symposium,* 2225–2227.

Ji, W. & Johnston, J.B. 1994. A GIS-based decision support system for wetland permit analysis. *Proceedings of GIS/LIS '94.*

Ji, W. & Johnston, J.B. 1995. Coastal ecosystem decision support GIS: functions and methodology. *Marine Geodesy,* **18,** 229–241.

Ji, W. & Mitchell, L.C. 1995. Analytical model-based decision support GIS for wetland resource management. In: *Wetland and environmental applications of GIS,* edited by J.G. Lyon & J. McCarthy, 31–47. New York: Lewis Publishers.

Raveling, D.G. & Heitmeyer, M.E. 1989. Relationships of population size and recruitment of pintails to habitat conditions and harvest. *Journal of Wildlife Management,* **53,** 1088–1103.

Predicted impacts of the Shenzhen River regulation project on waterfowl in Deep Bay, Hong Kong

D S Melville, S McChesney[1], C Anderson[2] & P J Leader[3]

WWF Hong Kong, GPO Box 12721, Hong Kong
Present address:
[1]Binnie Consultants Ltd, 11/F New Town Tower, Shatin, New Territories, Hong Kong
[2]ERM-HK Ltd, 6/F Hecny Tower, 9 Chatham Road, Kowloon, Hong Kong
[3]1D, 1/F, Mai Po Tsuen, New Territories, Hong Kong

SUMMARY

Deep Bay lies in the north-west corner of Hong Kong on the border with the People's Republic of China. Part of the Inner Bay is a Ramsar site, and supports internationally important waterbird populations. A cross-border environmental impact assessement (EIA) study was undertaken to assess potential impacts of a river 'training' programme on the ecology of the Inner Bay. Information from exclosure experiments and simple energetics calculations indicates that Deep Bay may be approaching carrying capacity for benthic-feeding waterfowl during the late winter/spring period. Based on the results of model studies of hydrodynamics, sediment transport and water quality, it is not anticipated that there will be major impacts on benthic invertebrates and waterfowl during either the construction or operation phases of the river training project. Changes in sedimentation may, however, affect benthos as well as increase the rate of mangrove encroachment over the tidal flats, thus reducing feeding areas for waterfowl. In view of current and anticipated changes resulting from other construction projects in the bay, which were not known at the time when the model was developed and thus were not included, the study results and subsequent ecological predictions may be open to question and require re-evaluation.

INTRODUCTION

Deep Bay lies in the north-west corner of Hong Kong on the border with the Shenzhen Special Economic Zone (SEZ), People's Republic of China (Figure 1). It covers an area of 115 km^2 and nowhere is deeper than 6 m. With an average depth of 2.9 m, and a tidal range of 2.8 m, *ca* 2700 ha of mudflats are exposed at low tide (S McChesney, unpublished).

The upper margins of the Inner Bay are covered by mangrove, dominated by *Avicennia marina* and *Kandelia candel*, comprising the sixth largest area of mangrove remaining in China. Landward of the mangroves are shrimp ponds (*gei wais*) and fish ponds. Increasingly, fish ponds on both sides of the bay have been infilled for urban residential and industrial development, infrastructure and open storage.

The Shenzhen and Shan Pui Rivers flow into the head of the bay (Figure 1). Due to the extensive urbanisation of the lower parts of the catchments of these rivers, flooding is now a serious problem. Average annual rainfall is about 1900 mm, and occasionally over 200 mm falls in a day.

Deep Bay is an internationally important site for waterfowl. Numbers of wintering waterfowl have increased over the past 16 years from 13 000 in 1979 to a maximum of 68 000 in January 1996. The area is also an important staging area for migrant shorebirds, with up to 15 000 being present in spring. Internationally important (>1%) numbers of four species of waterfowl occur in the area, including *ca* 24% of the world population of black-faced spoonbill (*Platalea minor*) and *ca* 10% of the world population of spotted greenshank (*Tringa guttifer*). The area is also the type locality for over 20 species of invertebrate new to science (Lee 1993; University of Hong Kong, unpublished).

The conservation importance of Deep Bay has recently been recognised by the Hong Kong Government which declared it a Wetland of

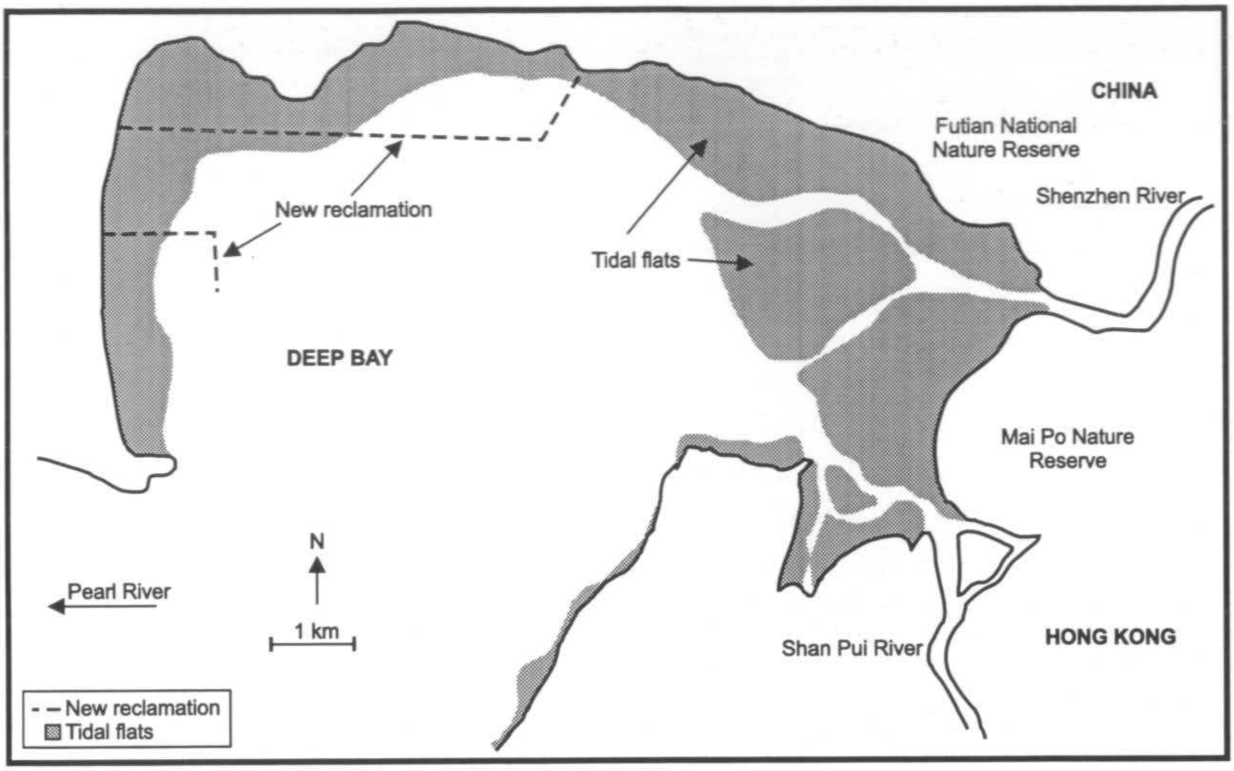

Figure 1. Location of Deep Bay

International Importance under the Ramsar Convention in September 1995. In March 1996 it was designated a Network Reserve under the East Asia/Australasia Flyway Network Agreement.

The Hong Kong and Chinese Governments are now undertaking river training projects to reduce flooding and, in the case of the Shenzhen River, to improve navigation. The Shenzhen River regulation project will result in the widening, deepening and straightening of the river. The work is expected to be completed by 1999.

Work on the Shan Pui River began without a comprehensive environmental impact assessment (EIA) being undertaken. However, a cross-border EIA study was conducted for the Shenzhen River Project. The study started in December 1993 and was completed in March 1995 (Peking University 1995). This paper summarises the findings of the study, together with those of recent post-graduate research (Anderson 1994; McChesney 1997), with respect to potential impacts of the project on waterbirds, and highlights continuing problems.

HYDRODYNAMICS, SEDIMENT TRANSPORT AND WATER QUALITY

As part of the EIA study, Peking University (1995) developed a series of computer models to simulate the following: hydrodynamics in the river and Inner Deep Bay; sediment transport, erosion and deposition; and water quality.

Sediment dynamics in Deep Bay are still poorly understood, but it appears that considerable quantities of sediment enter the bay from the Pearl River estuary on flood tides and that much of this settles out in Deep Bay. At the head of the bay, however, the relative importance of input from the Pearl River and the two local rivers remains uncertain. ^{210}Pb analysis of sediment cores from Inner Deep Bay suggests that there may have been a doubling in sedimentation rates since the mid-1980s (Peking University 1995). This increase is probably due largely to runoff from the many unprotected infill sites in the catchment. Increased sedimentation correlates in time with rapid urban development of the Shenzhen Special Economic Zone.

The Peking University model results indicate that there will be an increase in sedimentation in Inner Deep Bay during construction – in some areas sedimentation rates may increase by some 52%. Following completion of the works, sedimentation levels are predicted to be some 25% lower than current levels, but a depositional environment will persist.

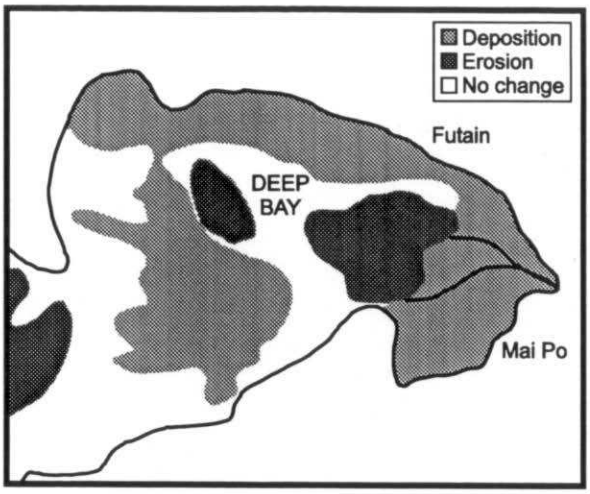

Figure 2. Areas of deposition and erosion in Deep Bay (source: Peking University 1995)

Present deposition in the Inner Bay is resulting in a rise in the elevation of the mudflats. Sediment deposition, however, is not resulting in any increase in areal extent of the flats as they are constrained by drainage channels and the fact that there is a large erosion basin immediately seaward of the flats (Figure 2). The increasing elevation of the flats is facilitating the seaward spread of mangroves, with the result that the extent of intertidal flats is decreasing in Inner Deep Bay.

During construction the additional release of contaminants from sediments could potentially adversely affect both mangroves and benthos. The model results, however, indicate that any effects will be restricted to the river mouth and these will be mitigated through sediment traps constructed in the river bed and appropriate timetabling of the works. Water quality in Deep Bay is very poor and the project is not predicted to result in any significant change following completion.

MANGROVES

Stable isotope analysis (N and C) of foodchain components revealed that mangroves contribute little to the overall productivity of the bay (with the exception of certain specialist mangrove litter-feeders, such as the crab *Parasesarma* cf. *bidens*) (C Anderson, unpublished). The majority of nutrients (>60%) driving the Deep Bay foodweb are from sewage and livestock waste.

The project will result in the loss of some 10 ha of mangrove along the River channel (*ca* 5% of the total intertidal mangrove in Inner Deep Bay). The loss of mangroves is not expected to result in any significant impact on the overall nutrient dynamics of the Bay.

The expected increase in sediment deposition during construction is likely to result in an increase in the rate of mangrove spread over the upper tidal flats, thus reducing the area available to waterfowl. Following completion of the project, the rate of sedimentation is predicted to be reduced, and hence the rate of mangrove encroachment might be reduced, but it is anticipated that it will be seven years after completion of the works before there is a net reduction in sediment deposition.

BENTHOS

The benthic community of Inner Deep Bay is species-poor, due to highly enriched waters and sediments which result from years of heavy organic pollution. However, as is frequently the case in biostimulated habitats, there is a high biomass of benthos (Pearson & Rosenberg 1978).

A gradient of pollution, from the Shenzhen River out into the bay, is reflected in the benthos. The river channel sediments support no benthos. Around the river mouth there are high densities of capitellid polychaetes and pollution-tolerant oligochaetes. Further away from the river a more diverse benthic assemblage occurs.

The bay has the highest biomass of polychaetes, and the highest proportion of biomass comprised by polychaetes, of all mudflat areas reported by Piersma, de Goeij and Tulp (1993), which undoubtedly contributes to the importance of the site for waterfowl. The proportion of abundance and biomass contributed by polychaete worms is much higher on the upper mudflat compared to the lower mudflat.

The lower intertidal benthos includes larger bivalves (>2 mm) *Sinonovacula* sp., *Theora* sp. and *Macoma* sp. The upper mudflats support fewer of these species, but very high densities of the small (<2 mm) bivalve *Pseudopythina maipoensis* occur.

The standing crop biomass of benthic invertebrates on the Mai Po mudflats ranges between 10.2 and 101.9 g dry wt m^{-2}. Total annual benthic invertebrate production of the Mai Po flats is estimated at 41.5 g ash-free dry mass (AFDM) m^{-2} (McChesney 1997).

Model results indicate that there are unlikely to be major impacts on benthos resulting from the predicted long-term changes in either water quality or sedimentation. If water quality does deteriorate further over the tidal flats, as may happen at times during construction, this could result in a reduction in benthic biomass as larger polychaetes and other species die out and smaller, pollution-tolerant species such as capitellids increase.

The impacts of such a reduction in standing crop biomass are hard to assess as much will depend on the timing of such an event. Summer is the recruitment period for most benthic invertebrate species (McChesney 1997) but, being also the wet season, any pollutant discharge is more likely to be diluted.

WATERFOWL

Deep Bay is used as a wintering ground by up to 60 000 ducks, waders and gulls, and as a staging area for migrating waders, with up to 15 000 present at one time. Inner Deep Bay is of importance to migrating waders as a 'refueling' point, along the East Asia/ Australasia flyway (Melville 1995; Minton 1995, 1996; Tulp, McChesney & de Goeij 1994). Curlew sandpiper (*Calidris ferruginea*) and red knot (*C. canutus*) departing Hong Kong in autumn are thought to carry sufficient energy reserves to reach north-west Australia (Young & Melville 1993; Barter 1992). In spring, curlew sandpipers depart at lower weights, and probably can only reach the Bo Hai in north-east China (Young & Melville 1993). In the past ten years waders have also started using Deep Bay as a moulting ground in autumn – apparently in response to the availability of high-tide roost sites created at the Mai Po Nature Reserve.

Detailed feeding studies are lacking, but recent work (Peking University 1995; P J Leader, unpublished) has shown that both ducks and waders feed mostly along the tide edge during both flood and ebb. At times of low water there is relatively little feeding activity. Birds are also known to feed at night along the tide-line, although this has not been studied in detail.

Waterfowl consumption of benthos

It was not possible to determine food intake rates/consumption patterns directly for waterfowl using the bay. An estimate of the total monthly energy consumption for those species which feed principally on benthic invertebrates was made using the equation developed by Meire, Schekkerman and Meininger (1994). This initial assessment indicated that total energy requirements for those waterfowl which are thought to consume benthic invertebrates primarily total 256 588 kg AFDM per year. The estimated monthly consumption (kg AFDM) by ducks, waders and gulls is shown in Figure 3.

No adjustments were made for variations in daily energy expenditure within the annual cycle due to physiological processes, such as deposition of energy stores for migration (spring and autumn), and increased requirements for new feather growth during moult (spring and late summer/autumn). The formula for estimating daily energy expenditure (DEE) is based on work conducted in temperate areas of Europe and North America, and thus may be rather high for 'tropical' Deep Bay. Klaassen, Kersten and Ens (1990) found that shorebirds wintering in tropical west Africa had lower maintenance metabolic rates than congeners wintering in Europe. Wiersma and Piersma (1994) reported that, in red knot, maintenance energy expenditure in Mauritania was *ca* 0.5 times that in the Wadden Sea. Similarly, Treca (1993) determined that daily food requirements for ducks and shorebirds wintering in Senegal were significantly less than those in the western Palearctic.

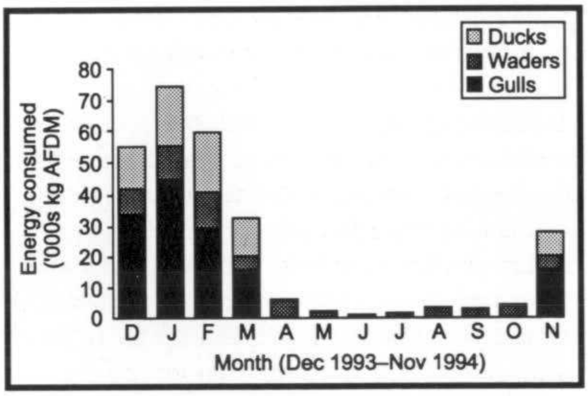

Figure 3. Estimated monthly consumption of benthos (kg ash-free dry mass)

Table 1. Estimated total consumption (kg AFDM) of benthic production on Mai Po mudflats by waterbirds* in Deep Bay

	Monthly estimated consumption by waterfowl	Estimated production of Mai Po flats**	% total production of Mai Po flats
January	74 089	74 500	99.4
February	59 314	44 000	134.8
March	32 381	67 000	48.3
April	6 190	32 000	19.3
May	1 660	52 000	3.2
June	615	41 000	1.5
July	626	22 000	2.8
August	1 602	38 000	4.2
September	2 575	68 000	3.8
October	8 240	ND	–
November	25 754	87 000	29.6
December	43 542	73 000	59.6
TOTAL	256 588	(598 500)	41.5***

* Ducks, waders, gulls

** Source: S McChesney, unpublished

*** Mean for all months except October

Although Hong Kong lies within the tropics, it experiences a subtropical climate with an exceptionally cool winter for such a latitude – 22°20'N (Dudgeon & Corlett 1994). Thus the work of Klaassen *et al.* (1990) and Wiersma and Piersma (1994) on energy requirements conducted in Mauritania (*ca* 20°N) may be less relevant to Hong Kong than the similarity in latitude might suggest. Unfortunately, calibration of the model for local conditions would have required extensive experimentation, which was beyond the scope of the study.

While the figures generated in this exercise cannot be taken as precise estimates of energy requirements by waterfowl in Deep Bay, they do, nonetheless, provide a basis for interspecific and seasonal comparisons, and a preliminary review of estimated consumption for comparison with estimated productivity (S McChesney, unpublished).

Table 1 compares estimated total monthly consumption in the period December 1993–November 1994, with estimated production on the Mai Po mudflats in 1992–93 (more recent productivity data were unavailable). Over the course of the year it appears that waterfowl could be removing up to 41.5% of total production from the Mai Po mudflats, with monthly figures ranging from 1.5% to 134.8%.

The annual total figure lies at the upper end of the range of values recorded at temperate estuaries (Table 2). However, it is likely to be an overestimate as waterfowl are known to feed to some extent in other areas of the bay in addition to the Mai Po mudflats, although the Mai Po flats support proportionately more birds than elsewhere in the bay. Benthic production figures for the Chinese side are unavailable.

Predator exclusion experiments on the Mai Po flats measured a 50–55% reduction in the standing stock of bivalve molluscs by bird predators in February and April (Peking University 1995; S McChesney, unpublished). Meire *et al.* (1994) recorded bird predation of 30–37% of the autumn standing stock (excluding large bivalves) in the Oosterschelde, The Netherlands. When engineering works there resulted in loss of habitat, bird densities did not increase, thus suggesting that carrying capacity may have been reached (Schekkerman, Meininger & Meire 1994).

The results of the present study, albeit crude, suggest that current levels of predation on benthos may be near a maximum over the winter and in spring. Inner Deep Bay may be near carrying capacity at these times.

IMPACTS OF THE SHENZHEN RIVER REGULATION PROJECT ON WATERBIRDS

Because it is estimated that up to 41.5% of total annual productivity of benthic invertebrates on the Mai Po mudflats may be consumed by waterfowl, and exclosure experiments indicate higher levels of predation in spring, the greatest impacts of the project on waterfowl in Deep Bay are most likely to result from changes in food quantity, quality, distribution and availability.

Construction phase

During construction there will be a loss of mangroves and intertidal areas along the river channel but these will not affect waterfowl adversely.

The increase in sediment deposition in Inner Deep Bay may adversely affect benthos if it is heavily polluted and oxygen depletion occurs, as may a reduction in water quality.

Such impacts could result in reduced productivity and food availability, but are likely to be relatively short term.

There is expected to be an increase in the rate of spread of mangrove over the upper tidal flats thus reducing the total area available for waterbird foraging. Mangrove encroachment also may potentially reduce the time available for feeding as most foraging takes place around the tide edge and loss of the upper flats to mangroves will reduce the distance which the tide travels over the flats. This problem may be further exacerbated as a result of current Government plans to plant mangroves on the tidal flats to compensate for those being lost to engineering works along the river channel.

Operational phase

In the long term, the project is not expected to affect water quality significantly, and hence benthic invertebrates should not be significantly affected. There will continue to be a release of pollutants through the resuspension of material during maintenance dredging, but this is considered to be minor compared with the potential problems during construction.

Changes in sedimentation are predicted to result in a reduction over current levels, but deposition rates are predicted to remain higher than those during the 1980s. This could eventually result in a reduction in the rate of mangrove encroachment over the upper flats. Mangrove encroachment is seen as a long-term threat to the continued value of Inner Deep Bay as a site of international importance for waterfowl. Because there is no evidence of the intertidal flats increasing in area, the continued expansion of mangroves over the flats must be a matter of concern – all the more so, in view of two recent Shenzhen SEZ reclamation projects which look set to destroy a significant proportion of the intertidal area of the bay (Figure 1).

THE UNKNOWNS

The Shenzhen River study was the first attempt to consider the ecology of Inner Deep Bay as a whole. Funding and other constraints meant that much of the work was of a basic nature, and clearly much remains to be determined regarding its ecology.

There are, however, more fundamental unknowns. The new river channel will end at the point where it discharges into Inner Deep Bay. At this point the new channel will be some 2.5 m lower than the existing navigation channel. There is a possibility that in future the main drainage channel through the Inner Bay will be dredged to improve navigability for vessels. This could profoundly affect hydrodynamics and sediment transport in the Inner Bay and compromise the results of the present study. Possible changes to the Inner Bay channel were omitted from the present EIA study.

Already, doubt has been cast on the validity of some of the hydrodynamics/sediment transport/water quality model results following two reclamation projects on the north shore of the bay which resulted in the loss of some 6.5 km^2 of intertidal flats (*ca* 24% of the total). These projects were not included in the model design for the study and no assessment has been made of their potential value as feeding areas for waterbirds – the loss of these sites could place more pressure on the Mai Po flats by feeding waterfowl.

Table 2. Summaries of benthic invertebrate production estimates, consumption by shorebirds and consumption efficiencies

Locality	Energy equivalent (kJ m^{-2} yr^{-1}) Consumption by birds	 Invertebrate production	Consumption efficiency Invertebrates to birds (%)
Dutch Wadden Sea (intertidal zone)*	103.6	619.2	17.0
Grevelingen estuary*	71.5	1201.4	6.0
Ythan estuary*	873.6	2448.1	36.0
Tees estuary*	367.0	851.0	44.0
Langebaan lagoon*	141.6	705.0	20.0
Mai Po, Deep Bay			41.5

*Source: Baird *et al.* (1985)

CONCLUSION

Deep Bay may be near carrying capacity for waterfowl in late winter/spring. Based on the results of model studies of hydrodynamics, sediment transport and water quality, it is not anticipated that there will be major impacts on benthic invertebrates and waterfowl during either the construction or operation phases of the Shenzhen River Regulation Project. However, the modelling of shallow estuarine systems is inherently imprecise and some uncertainties remain over the model outputs. An increase in the area of mangrove, and the resulting reduction in tidal flats and waterbird feeding area, is a possible long-term problem which may be exacerbated by increased sediment deposition during construction. In view of current and anticipated changes resulting from other construction projects in the bay, which were not modelled, the model results and subsequent ecological predictions may be open to question. The cumulative impacts of current projects have yet to be assessed.

ACKNOWLEDGEMENTS

This study was conducted on behalf of the Shenzhen River Regulation Office of the Shenzhen Municipal Government and the Environmental Protection Department of the Hong Kong Government. Peking University was the lead consultant, and the main Hong Kong subconsultants were Axis Environmental Consultants Ltd and CES (Asia) Ltd. The authors are very grateful to Dr S Y Lee, the Swire Institute of Marine Science, University of Hong Kong, for support during the study and critical comments on the work. Dr L Young also kindly commented on the draft.

REFERENCES

Anderson, C. 1994. *The production ecology of the mangrove at the Mai Po Nature Reserve, Hong Kong.* PhD thesis, University of Hong Kong.

Baird, D., Evans, P.R., Milne, H. & Pienkowski, M.W. 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. *Oceanography and Marine Biology: Annual Review*, **23**, 573–597.

Barter, M. 1992. Distribution, abundance, migration and moult of the red knot *Calidris canutus rogersi.* In: *The migration of knots*, edited by T. Piersma & N. Davidson, 64–70. (Wader Study Group Bulletin no. 64, Supplement.) Tring: Wader Study Group.

Dudgeon, D. & Corlett, R. 1994. *Hills and streams: an ecology of Hong Kong.* Hong Kong: Hong Kong University Press.

Klaassen, M., Kersten, M. & Ens, B.J. 1990. Energetic requirements for maintenance and premigratory body mass gain of waders wintering in Africa. *Ardea*, **78**, 209–220.

Lee, S.Y. 1993. Invertebrate species new to science recorded from the Mai Po marshes, Hong Kong. In: *The marine biology of the South China Sea*, edited by B. Morton, 199–209. Hong Kong: Hong Kong University Press.

McChesney, S. 1997. *The benthic invertebrate community of the intertidal mudflat at the Mai Po Marshes Nature Reserve, with special reference to resources for migratory shorebirds.* MPhil thesis, University of Hong Kong.

Meire, P.M., Schekkerman, H. and Meininger, P.L. 1994. Consumption of benthic invertebrates by waterbirds in the Oosterschelde estuary, SW Netherlands. *Hydrobiologia*, **282/283**, 525–546.

Melville, D.S. 1995. Report on bird ringing in Hong Kong in 1994. *Hong Kong Bird Report 1994*, 98–109.

Minton, C. 1995. Sightings of waders leg-flagged in Victoria, Australia – list no. 3. *Stilt*, **27**, 30–32.

Minton, C. 1996. Analysis of overseas movements of red-necked stints and curlew sandpipers. *Victorian Wader Study Group Bulletin*, **20**, 39–43.

Pearson, T.H. & Rosenberg, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: Annual Review*, **16**, 229–311.

Peking University. 1995. *Environmental impact assessment study on Shenzhen River Regulation Project. Final EIA study.* Shenzhen: Shenzhen River Regulation Office of Municipal Government.

Piersma, T., de Goeij, P. & Tulp, I. 1993. An evaluation of intertidal feeding habitats from a shorebird perspective: towards relevant comparisons between temperate and tropical mudflats. *Netherlands Journal of Sea Research*, **31**, 503–512.

Schekkerman, H., Meininger, P.L. and Meire, P.M. 1994. Changes in the waterbird populations of the Oosterschelde, SW Netherlands, as a result of large-scale coastal engineering works. *Hydrobiologia*, **282/283**, 509–524.

Treca, B. 1993. Oiseaux d'eau et besoins energetiques dans le delta du Senegal. *Alauda*, **61**, 73–82.

Tulp, I., McChesney, S. & de Goeij, P. 1994. Migratory departures of waders from north-western Australia: behaviour, timing and possible migration route. *Ardea*, **82**, 201–221.

Wiersma, P. & Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. *Condor*, **96**, 257–279.

Young, L. & Melville, D.S. 1993. Conservation of the Deep Bay environment. In: *The marine biology of the South China Sea*, edited by B. Morton, 211–231. Hong Kong: Hong Kong University Press.

Carrying capacity of seagrass beds predicted for redheads wintering in Chandeleur Sound, Louisiana, USA

T C Michot

US Geological Survey, Biological Resources Division, National Wetlands Research Center, 700 Cajundome Boulevard, Lafayette, Louisiana 70506, USA

SUMMARY

The Chandeleur Islands are a 65 km barrier island chain in the Gulf of Mexico, about 40 km off the coast of Louisiana, USA. The waters of Chandeleur Sound adjacent to the largest island in the chain are a traditional wintering area for about 15 000–20 000 redheads. Chandeleur Sound, the Laguna Madre of Texas, the Laguna Madre de Tamaulipas in Mexico, and Apalachee Bay in Florida are the four major wintering areas for redheads along the Gulf Coast, and all four areas are estuarine seagrass meadow habitat. I predicted the carrying capacity of the Chandeleur Sound study area to assess whether redheads could be limited by their winter habitat. The model was based on the availability of shoalgrass, which makes up 83% of the birds' diet. The following parameters made up the major parts of the model: average redhead stay, shoalgrass habitat, shoalgrass biomass, redhead consumption, shoalgrass standing crop, and carrying capacity. Based on population surveys conducted over a five-year period (1987–92), I estimated the average redhead stay on the wintering grounds to be 94 days. I calculated shoalgrass habitat at about 13 km^2; below-ground biomass was estimated at 119 g m^{-2}, but only 56 g m^{-2} was deemed usable by redheads. Redhead consumption was estimated from the literature at 77 g bird^{-1} d^{-1}, of which 55 g d^{-1} was estimated to be shoalgrass rhizomes. Winter consumption, based on daily consumption and average stay, was 5195 g per bird per winter. The standing crop of shoalgrass rhizomes, based on usable biomass, shoalgrass habitat, and root-to-rhizome ratio, was estimated at 118 t. Carrying capacity was then estimated at 22 831 redheads (peak population) per winter, based on standing crop and winter consumption rate. I concluded from this study that redheads at Chandeleur Sound could be limited by wintering habitat, specifically food (shoalgrass) resources. Therefore, protection of shoalgrass beds should be the highest conservation priority within the winter range of this diving duck species.

INTRODUCTION

The concept of carrying capacity was first introduced by Errington (1934) and is defined herein as the maximum number of individuals of a certain species that a given habitat will support. Inherent in this definition is the assumption that some resource in that habitat is limiting, or can be limiting under certain conditions. For ducks in North America, the dominant paradigm is that limitation occurs on the breeding grounds (Lynch 1984), but several studies have suggested that conditions on the wintering grounds can have a dominant role in the annual cycle of some species (Heitmeyer & Fredrickson 1981; Krapu 1981; Haramis *et al.* 1986; Miller 1986; Raveling & Heitmeyer 1989; Dubovsky & Kaminski 1994; Hohman, Moore & Franson 1995). The use of seagrasses as a food source for wintering waterfowl is well documented (Cottam, Lynch & Nelson 1944; Campbell 1946; Yocom & Keller 1961; Ogilvie & Matthews 1969; Phillips 1984; Mayhew 1988) and several authors have estimated that the removal of plant biomass by waterfowl can be extensive (Ranwell & Downing 1959; Stieglitz 1966; Cornelius 1977; Kiorboe 1980; Jacobs *et al.* 1981; Nienhuis & Groenendijk 1986; Madsen 1988; Baldwin & Lovvorn 1994; Mitchell, Custer & Zwank 1994).

Redheads (*Aythya americana*) breed in fresh and alkali wetlands in the interior of North America, but they winter almost exclusively in coastal seagrass ecosystems. Between 1969 and 1994, 93% of the North American continental population of redheads wintered along the coast of the Gulf of Mexico, with the remaining 7% wintering along the Atlantic

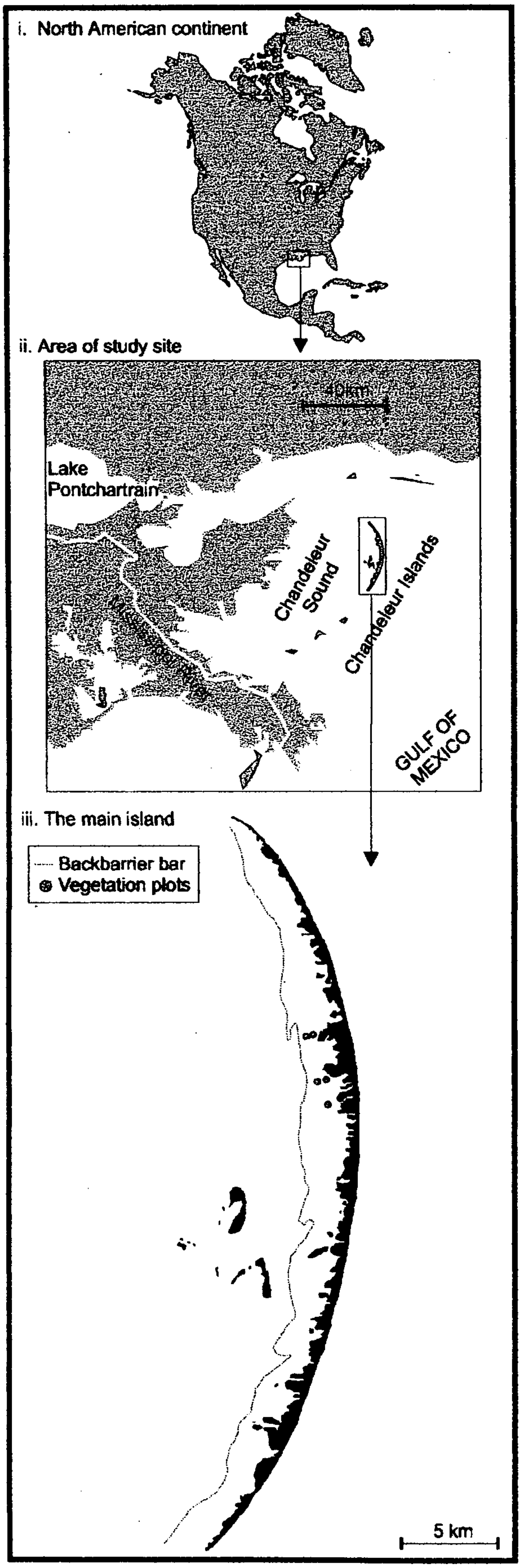

Figure 1. Map of study area showing location (i) on the North American continent and (ii) on the Louisiana coast, and (iii) detail of the main island in the chain (Chandeleur Island) with locations of backbarrier bar and vegetation plots used by Michot and Chadwick (1994) to estimate October biomass

and Pacific coasts (calculated from US Fish & Wildlife Service (USFWS) Midwinter Waterfowl Inventory and Special Redhead Survey data (USFWS, unpublished data)). The four major redhead wintering areas along the Gulf Coast in Florida (Apalachee Bay), Louisiana (Chandeleur Sound), Texas (Laguna Madre), and Mexico (Laguna Madre de Tamaulipas) are dominated by subtropical seagrass meadows. Turtlegrass (*Thalassia testudinum*), shoalgrass (*Halodule wrightii*), and manateegrass (*Syringodium filiforme*) are the predominant seagrass species in those four areas, and redheads wintering there feed almost exclusively on the rhizomes of shoalgrass (Stieglitz 1966; Cornelius 1977; Michot & Nault 1993; Michot, Woodin & Nault 1996).

Decreases in the areal coverage of seagrass meadows has been documented in most of the major beds along the Gulf Coast over recent decades (Handley 1995; Onuf 1995, 1996). Because of the dependence of wintering redheads on a single seagrass species as a food source, potential impacts of seagrass declines could be great if the bird populations are currently at or near the carrying capacity for these habitats. The goal of this study was to construct a model that would predict the number of redheads that can be supported by the seagrass meadows in Chandeleur Sound, Louisiana. The objectives were:

- to identify the various parameters that contribute to the carrying capacity, and their relationships with each other;
- to determine the effects of variation in those parameters, based on values from the published and unpublished literature, on the predicted carrying capacity; and
- to determine the most realistic carrying capacity estimate for the area.

STUDY AREA

The Chandeleur Islands (Figure 1) are a 72 km barrier island chain in the Gulf of Mexico, about 40 km off the Louisiana coast, and constitute the largest barrier island system in the Mississippi River delta plain (Suter *et al.* 1988; Ritchie *et al.* 1992). The southern tip of the chain is approximately 15 km north of the Main Pass of the Mississippi River, and the Chandeleur Lighthouse, on the northern tip (30°03'N, 88°52'W), is 42 km south of Biloxi, Mississippi (Ritchie *et al.* 1992).

Chandeleur Island, the largest island in the chain (Figure 1), is oriented generally in a north–south direction. The eastern shoreline is subject to continuous wave action from the Gulf of Mexico; consequently, the northern and southern tips are curved westward. The island's inner (western) shoreline is an irregular margin between emergent marsh (predominantly *Spartina alterniflora*) and shallow open water. Small bays, finger-like peninsulas, and small grassy islands make up the configuration of the shoreline and thus provide potential shelter from wind for the redhead flocks. Chandeleur Island is 45 km in length (Ritchie *et al.* 1992), and the width averages about 500 m, with peninsulas extending an additional 500–2000 m into the backbarrier flats of Chandeleur Sound. The aquatic seagrass beds used by redheads extend about 2000 m from the island's inner shoreline to the backbarrier bar (Figure 1), which runs parallel to the island's inner (protected) shoreline. Water depth averages about 1 m at mean low water (MLW) and ranges from 0 m at the island's western shoreline to 2.5 m MLW near the backbarrier bar. The diurnal tidal cycle had a maximum winter amplitude during the study of about 1 m. Salinities on the area during the study ranged from $20^0/_{00}$ to $36^0/_{00}$.

The Chandeleur Sound study area consisted of approximately 79 km^2 of estuarine (polyhaline) subtidal and intertidal (irregularly exposed) rooted vascular aquatic bed habitat (classified according to Cowardin *et al.* 1979). The aquatic bed habitat was in tidal pools and inlets and in open water that occurred along the main island from the shoreline to the backbarrier bar. The area was vegetated with five seagrass species. The three dominant species were turtlegrass, shoalgrass, and manateegrass; widgeongrass (*Ruppia maritima*) and stargrass (*Halophila engelmanii*) were also present on the study area.

METHODS

My carrying capacity model is based on the assumption that, if redheads are food-limited on the wintering grounds, the limitation would be from a single food source, shoalgrass. This assumption is based on my finding that shoalgrass made up 80% of the oesophageal contents of 188 redheads collected from Chandeleur Sound (Michot & Nault 1993). This finding was consistent with similar findings by other researchers for wintering redheads from Texas (Cornelius 1977; Michot *et al.* 1996) and Florida (Stieglitz 1966; T C Michot, unpublished data). Most of the remainder of the redhead diet is about 18 species of marine gastropods (Michot *et al.* 1996), and my assumption is that the diversity and abundance of gastropod fauna currently found in the seagrass beds of Chandeleur Sound would provide ample animal food for redheads as long as the seagrass beds themselves remain. A reduction in shoalgrass, however, would be most likely to have a direct impact on redhead carrying capacity for the area. Therefore, the carrying capacity in this model is based solely on the available standing crop of shoalgrass.

To model carrying capacity for the area I used existing data from my own studies at Chandeleur Sound and from the literature. These data were used to obtain values for the following parameters that made up the major parts of the model: average redhead stay, shoalgrass habitat, shoalgrass biomass, redhead consumption, shoalgrass standing crop, and carrying capacity. Each of those model components is discussed in a separate section below. The general equation used to estimate carrying capacity was:

$$K = StgCrpRhiz/WintCnsump \qquad (1)$$

where:
K = carrying capacity of the area in number of redheads per winter (peak population),
StgCrpRhiz = standing crop of shoalgrass rhizomes on the study area, and
WintCnsump= shoalgrass consumed per redhead per winter.

AVERAGE REDHEAD STAY

I conducted aerial surveys over the study area during five winters, 1987–88 through 1991–92. Surveys were conducted from a high-winged, single-engine aircraft from an altitude of approximately 50 m using the cruise method to locate flocks, and I or an experienced observer estimated the number of redheads in each flock. The number of birds per flock averaged 230 redheads (range=3–7000 birds, n=1721 flocks). I compared visual estimates of number of birds per flock to counts obtained from

Table 1. Peak populations of redheads aerially surveyed at Chandeleur Sound, Louisiana, during the winters of 1987–88 to 1991–92, and the dates and mean of those five peak populations

Year	Nos of surveys	Peak population Nos of redheads	Date
1987–88	13	19 700	Feb 02
1988–89	12	18 900	Feb 21
1989–90	5	15 200	Jan 22
1990–91	10	15 800	Feb 28
1991–92	3	15 115	Jan 02
Total	43	16 943	(5-yr mean)

photographs of the same flocks and found that the ocular estimates were accurate to within 2% (average difference between visual estimate and photo count was 18 birds, range=–218 to 89 birds, n=81 flocks).

Surveys were typically conducted approximately every two weeks from October to March of each year, although surveys were spaced up to 4–6 weeks apart in some years; every year I flew at least one survey per month during December, January, and February. During the first year, surveys were conducted from September to April in order to establish the earliest arrivals and latest departures of redheads from the study area. The earliest arrival date for redheads on the area was between 9 October and 21 October, and the latest departure date was between 16 March and 29 March. Therefore, I interpolated between those dates to establish 15 October and 22 March as the estimated beginning and end of the redhead wintering period on the study area. The total wintering period, therefore, would be 159 days. This value could not be used as the average redhead stay, however, because only a small number of birds actually stayed on the study area for the entire 159-day period. The number of birds on the area peaked each year in January or February (Table 1), with a gradual slope in early winter for arrivals and a steep slope in late winter for departures (Figure 2).

I multiplied the average number of redheads per month for each month by the number of days in that month to obtain the number of redhead use-days for each month (Table 2). The total redhead use-days (TotUseDays) for the winter, then, was 1 585 809. To calculate the average stay (AvgStay) per redhead, I divided this number (TotUseDays) by the average peak population (AvgPeakPop) for the five-year period (Table 1). Thus,

$$\begin{aligned}\text{AvgStay} &= \text{TotUseDays}/\text{AvgPeakPop} \qquad (2)\\ &= 1\ 585\ 809/16\ 943\\ &= 94 \text{ d per redhead}\end{aligned}$$

SHOALGRASS HABITAT

To estimate the total coverage of seagrasses, and of each seagrass species, in the study area, I used data from 16 transects that were surveyed in August 1989 (H A Neckles & T C Michot, US Geological Survey (USGS), unpublished data). The transects were set up in an east–west fashion, perpendicular to the island, and ran from the highest point on the beach westward to a point beyond the backbarrier bar at which several successive bottom samples (spaced at 5 m intervals) failed to yield any seagrasses on the sediment surface. The northernmost transect was located approximately 1 km south of the northern tip of the island, and the southernmost transect was about 3 km north of the southern tip; the average distance between transects was 2 km (range=1–6, n=16). Along the length of each transect we used underwater snorkelling gear to estimate seagrass cover visually at 5 m intervals for all open-water areas. At each sample point we recorded the cover class (Orth & Moore 1983) for each seagrass species present, or unvegetated bare substrate, as appropriate.

The average transect length (AvgTransLth) for the open-water portion, from the island's western shoreline to the point where a seagrass sample was last observed, was 1763

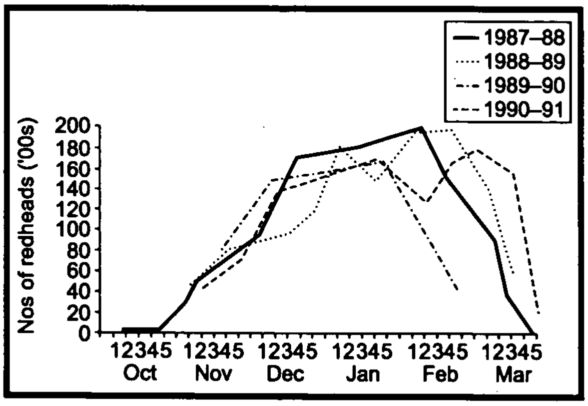

Figure 2. Population estimates of redheads aerially surveyed at Chandeleur Sound, Louisiana, during four of the five winters studied (data from the last year, 1991–92, were not included because only three surveys were flown that year). Numerals on the x axis indicate weeks for each month

m (range=800–2500). This value represents the average width of the backbarrier flat or seagrass habitat, between the island and the backbarrier bar (Figure 1). I multiplied that value by the island length (IslndLth) to obtain the total area of seagrass habitat (TotSgHab):

$$\begin{aligned} \text{TotSgHab} &= \text{AvgTransLth} \times \text{IslndLth} \\ &= 1763 \text{ m} \times 45\,000 \text{ m} \\ &= 79\,335\,000 \text{ m}^2 \end{aligned} \tag{3}$$

I determined the dominant cover species (or bare substrate) for each sample and determined that shoalgrass was the dominant species (%Hal) for 16.8% of the samples (n=5126) over the entire 16 transects. Therefore, the area of available shoalgrass habitat (HalHab) was:

$$\begin{aligned} \text{HalHab} &= \text{TotSgHab} \times \text{\%Hal} \\ &= 79\,335\,000 \text{ m}^2 \times 16.8\% \\ &= 13\,312\,413 \text{ m}^2 \end{aligned} \tag{4}$$

SHOALGRASS BIOMASS

Michot and Chadwick (1994) determined the October total below-ground biomass (including roots and rhizomes (TotBio)) in homogeneous shoalgrass plots at Chandeleur Sound to be 119.13 g dry mass (gdm) m^{-2}. I used this value to represent the average biomass for all patches in the study area where shoalgrass was the dominant species. Mitchell *et al.* (1994) found that redheads in the Laguna Madre of Texas would forage on a given shoalgrass patch until the rhizome biomass was depleted to 10 gdm m^{-2}; below that threshold level, the rhizomes became too difficult for the birds to extract from the ramet of the shoalgrass plant. That 10 gdm m^{-2} of rhizomes, then, was unusable to redheads. The same researchers also determined that the root-to-rhizome ratio in the below-ground portion of shoalgrass in ungrazed patches was consistent throughout the winter at 5.3:1 (Mitchell *et al.* 1994). Therefore, for every 10 gdm m^{-2} of unusable rhizomes there are 53 gdm m^{-2} of unusable roots, or a total of 63 gdm m^{-2} of unusable below-ground material (UnusablBio). The unusable portion, then, would be available at the beginning of the next growing season for plant recovery, even after extensive redhead grazing.
Accordingly, the model would allow for redhead consumption of 100% of the usable shoalgrass biomass without having completely wiped out the food source. Applying these numbers I determined the usable portion of shoalgrass below-ground biomass at Chandeleur Sound (UsablBio) to be:

$$\begin{aligned} \text{UsablBio} &= \text{TotBio} - \text{UnusablBio} \\ &= 119.13 \text{ gdm m}^{-2} - 63 \text{ gdm m}^{-2} \\ &= 56.13 \text{ gdm m}^{-2} \end{aligned} \tag{5}$$

Table 2. Mean numbers of redheads, days per month, and redhead use-days (nos of redheads x nos of days) for each month from Chandeleur Sound, Louisiana, over five winters (1987–88 to 1991–92); surveys with 0 redheads were not included in the calculations

Month	Nos of surveys	Nos of redheads Mean	Min	Max	Nos of days	Redhead use-days
Oct	3	33	0	50	17	567
Nov	9	4 989	2 300	7 500	30	149 667
Dec	9	11 936	8 800	16 700	31	370 002
Jan	6	15 669	13 900	17 800	31	485 744
Feb	9	13 794	2 800	19 700	28	386 229
Mar	7	8 800	0	13 500	22	193 600
Total	43				159	1 585 809

REDHEAD CONSUMPTION

The only study of redhead consumption rates on shoalgrass was by Cornelius (1975, 1977) who, in an experiment with ten pen-raised redheads in coastal Texas, found that the birds consumed an average of 77.4 gdm per day. The available diet in that study consisted of fresh shoalgrass and manateegrass and commercial gamebird ration, and the food was available *ad libitum* over a 34-week period in the winter (September–May). The monthly means (n=9) over this period were fairly consistent, ranging from 62 gdm d^{-1} to 92 gdm d^{-1} (Cornelius 1975). Cornelius (1975, 1977) did not report what percentage of the redhead consumption was commercial food *versus* shoalgrass, but he considered his calculated consumption rate to be maximal. His consideration was based on lower reported rates for the larger canvasbacks (23 gdm d^{-1}; Longcore & Cornwell 1964), on a lower consumption rate for redheads (45 gdm d^{-1}) that Cornelius (1975) calculated using mallard (*Anas platyrhynchos*) data from Moyle (1961), on reported metabolic differences between wild and captive birds (Bardwell, Glasgow & Epps 1962), and on some minor biases associated with his (Cornelius') experimental setup.

Consideration of several factors, however, lead me to conclude that Cornelius' (1975, 1977) estimate of redhead consumption is realistic, and not an overestimate. Madsen (1988) estimated that wigeon (*Anas penelope*), a smaller bird than redheads, consumed 74.5 gdm d^{-1} of above-ground and below-ground parts of the seagrass *Zostera* (calculated from his reported rate of 64.8 g d^{-1} of ash-free dry mass, his reported ash composition for above-ground and below-ground parts, and percentages of each in the diet). Perry *et al.* (1986) found that captive canvasbacks fed an experimental diet similar to a vegetation diet consumed 90 gdm d^{-1}. Based on the above, and the fact that redheads at Chandeleur Sound were larger (mean body mass=1133 g, n=273; T C Michot, unpublished data) than the captive birds used in Cornelius' experiment (900 g; Cornelius 1975), I assume that it is just as likely that the actual consumption rate be higher as lower than the 77.4 gdm d^{-1} reported by Cornelius (1975, 1977). Therefore, and because his is the only consumption study on wintering redheads at a coastal Gulf of Mexico location using shoalgrass as a food source, I assume that his estimate is the most realistic for the purposes of this model. I do, however, present in a later section (below) the effect of higher or lower consumption rates on the model.

Because Cornelius' (1975, 1977) redhead consumption rate was based on a diet of seagrasses (primarily shoalgrass) and high-protein commercial ration, I assume that it would be equivalent to the diet of Chandeleur Sound redheads, with the commercial ration being equivalent to the occurrence of molluscs in the diet. Therefore I had to adjust the total consumption rate (TotCnsump) by the percentage of shoalgrass rhizomes in the redhead diet (%HalRhiz). As shoalgrass made up 83% of the oesophageal contents of redheads from Louisiana (Michot & Nault 1993), 96% of the shoalgrass consumed was below-ground material (Michot *et al.* 1996), and 90% of the shoalgrass below-ground biomass in the diet was rhizomes (T C Michot, USGS, unpublished data), %HalRhiz was estimated at 71.7% (0.83 × 0.96 × 0.90). Therefore, the consumption rate (HalCnsump) was:

$$\begin{aligned}\text{HalCnsump} &= \text{TotCnsump} \times \%\text{HalRhiz} \qquad (6)\\ &= 77.4 \text{ gdm bird}^{-1}\text{ d}^{-1} \times 71.7\%\\ &= 55.5 \text{ gdm bird}^{-1}\text{ d}^{-1}\end{aligned}$$

The consumption rate per winter (WintCnsump) was then calculated based on the average redhead stay (AvgStay, Equation 2):

$$\begin{aligned}\text{WintCnsump} &= \text{HalCnsump} \times \text{AvgStay} \qquad (7)\\ &= 55.5 \text{ gdm bird}^{-1}\text{ d}^{-1} \times 94 \text{ d}\\ &= 5195 \text{ gdm bird}^{-1}\text{ winter}^{-1}\end{aligned}$$

SHOALGRASS STANDING CROP

I calculated the usable standing crop (UsblStgCrp) for shoalgrass as the usable biomass (UsablBio, Equation 5) times the total area of shoalgrass habitat (HalHab, Equation 4):

$$\begin{aligned}\text{UsblStgCrp} &= \text{UsablBio} \times \text{HalHab} \qquad (8)\\ &= 56.13 \text{ gdm m}^{-2} \times 13\ 312\ 413 \text{ m}^2\\ &= 747\ 225\ 700 \text{ g}\end{aligned}$$

Based on the root-to-rhizome ratio (RRRatio) of 5.3:1 (Mitchell *et al.* 1994), I calculated the standing crop for rhizomes (StgCrpRhiz) as:

$$\begin{aligned}\text{StgCrpRhiz} &= \text{UsblStgCrp}/(\text{RRRatio}+1) \qquad (9)\\ &= 747\ 225\ 700 \text{ g}/(5.3+1)\\ &= 118\ 607\ 300 \text{ g}\end{aligned}$$

CARRYING CAPACITY

Using my original carrying capacity equation (Equation 1), I calculated carrying capacity (K) from the standing crop (StgCrpRhiz, Equation 9) and shoalgrass consumption (WintCnsump, Equation 7) as follows:

$$\begin{aligned}K &= \text{StgCrpRhiz}/\text{WintCnsump} \qquad (10)\\ &= 118\ 607\ 300 \text{ g}/5195 \text{ g bird}^{-1}\text{ winter}^{-1}\\ &= 22\ 831 \text{ birds winter}^{-1}\end{aligned}$$

PARAMETER VARIATION

Approximately 40 variables were used to estimate K in the model, and some of those variables could vary over time and space. I examined the five major parameters of the model (ie average redhead stay, shoalgrass habitat, shoalgrass biomass, redhead consumption, and shoalgrass standing crop) to determine the potential effects of variation within each of those parameters on K.

I believe that the average redhead stay estimate of 94 days is a realistic estimate, and I do not expect it to fluctuate significantly from year to year. The estimate for shoalgrass habitat probably does fluctuate somewhat, and I would predict that it is steadily decreasing over time. Although there have been no calculations of shoalgrass coverage for years other than 1989, the total land area of the Chandeleur Islands has decreased from 2763 ha in 1855 to 1749 ha in 1989, or at an average rate of 7.6 ha yr^{-1} (Ritchie *et al.* 1992). Therefore, assuming that the areal coverage of seagrasses is positively correlated with island size, and that the proportion of shoalgrass to total seagrasses is relatively constant, it is likely that the coverage of shoalgrass has been decreasing as well. The shoreline of Chandeleur Island in 1951 was approximately 4.6 km longer than it was in 1989 (estimated from maps in Ritchie *et al.* 1992). If I increase IslndLth (Equation 3) to 49 600 m (45 000+4600 m), the predicted K becomes 25 149, which is only a slight (9%) increase from my original K of 22 831 (Table 3).

I found considerable variation in the published and unpublished literature for shoalgrass biomass. In my August 1989 seagrass transect study, for seagrass patches where shoalgrass was present (n=50), below-ground biomass (TotBio, Equation 5) for individual cores ranged from <1 gdm m^{-2} to 199 gdm m^{-2}, with a mean of 48 gdm m^{-2} (H A Neckles & T C Michot, USGS, unpublished data). Some of the same transects run in September of 1988 showed higher biomass values for individual cores (n=55) with a maximum value of 366 gdm m^{-2} and a mean of 70 gdm m^{-2} (H A Neckles & T C Michot, USGS, unpublished data). Means from both years (August and September samples) were considerably lower than my October value of 119 gdm m^{-2} used for the model, although both years had several individual cores that exceeded the mean October value. Winter means were >100 gdm m^{-2} for October–December, then dropped to 30–60 gdm m^{-2} in January to March (Michot & Chadwick 1994). The reason for this disparity (ie higher biomass in fall and early winter than in late summer) is unclear. It could be that the plants continued to grow until October, or at least they may have transferred more biomass to the below-ground portion in advance of the oncoming winter. The winter samples all came from three homogeneous shoalgrass patches, whereas the August–September samples were from throughout the study area, and hence included patches in which shoalgrass coverage was more sparse. If I considered only shoalgrass patches that had the highest above-ground density (71–100% above-ground canopy coverage), however, the August 1989 mean for below-ground biomass was 75.3 gdm m^{-2}, still considerably lower than my October value for similar patches. The substitution of the overall August 1989 mean (48 gdm m^{-2}) in the model (TotBio, Equation 5) resulted in a K of 0 because that value was below the threshold for redheads grazing of 63 gdm m^{-2} (Mitchell *et al.* 1994). If I used values of 70 gdm m^{-2} (September 1988 mean) or 75 gdm m^{-2} (August 1989, dense patches only) the predicted K became 3136 and 4881 redheads, respectively, still very much below the observed peak population levels (Table 3).

In Texas, Mitchell *et al.* (1994) reported a winter biomass value in the lower Laguna Madre of 189 gdm m^{-2} (31.8 g roots and 157.8 g rhizomes; no change October–March) in four shoalgrass patches from which redheads were excluded. The authors made no attempt to extrapolate this value across the entire Laguna Madre, so I assume that biomass in those patches was higher than the Laguna average (although the patches may be similar to the patches I used for my October value at Chandeleur Sound). Cornelius (1975) reported a mean shoalgrass biomass (above-ground and below-ground combined) for the Laguna Madre of Texas at 82 gdm m^{-2} (range=66–139 in six zones). The highest value for shoalgrass below-ground biomass that I could find for an entire bay or lagoon system in which redheads winter was a mean of 130 gdm m^{-2} (max=332 gdm m^{-2}) for data from transects across the upper Laguna Madre of Texas during the growing season (C P Onuf, USGS, pers. comm.). In Texas, as in Louisiana, a disparity was shown among biomass estimates. When I substituted the two highest Texas values (130 gdm m^{-2} and 189 gdm m^{-2}) in the model (TotBio, Equation 5), the predicted K for Chandeleur Sound increased to 27 252 and 56 723, respectively (Table 3).

The proportion of shoalgrass in the diet of wintering redheads is well established in the literature, and seems fairly consistent. As discussed earlier, however, values for waterfowl food consumption in the literature varied between 23 gdm d^{-1} (Longcore & Cornwell 1964) and 90 gdm d^{-1} (Perry *et al.* 1986). Substitution of these two extremes in

Table 3. Effect of variation in selected model variables on predicted carrying capacity (K) of Chandeleur Sound, Louisiana, for wintering redheads (variable names as in text)

Changed variable	Direction of change	Original value	New value	K	Source
K	–	–	–	22 831	This paper (original model estimate)
IslndLth	increase	45 000 m	49 600	25 149	Ritchie *et al.* 1992
TotBio	decrease	119 g m^{-2}	48	0	Neckles & Michot, unpublished
TotBio	decrease	119 g m^{-2}	70	3 136	Neckles & Michot, unpublished
TotBio	decrease	119 g m^{-2}	75	4 881	Neckles & Michot, unpublished
TotBio	increase	119 g m^{-2}	130	27 252	Onuf, pers. comm.
TotBio	increase	119 g m^{-2}	189	56 723	Mitchell *et al.* 1994
TotCnsump	decrease	77 g d^{-1}	23	84 633	Longcore & Cornwell 1964
TotCnsump	increase	77 g d^{-1}	90	21 628	Perry *et al.* 1986

my model (TotCnsump, Equation 6) yielded predicted K values of 84 633 and 21 628, respectively (Table 3). Interestingly, the higher consumption value only lowered K slightly, but the lower consumption value resulted in a substantial increase in K.

Standing crop of shoalgrass in the model would only vary as a function of shoalgrass biomass and shoalgrass habitat, both of which have already been considered in this section. Both the usable fraction of the shoalgrass biomass and the rhizome fraction of the usable biomass (Equations 8 & 9) were based on the work of Mitchell *et al.* (1994), and no other studies were available that presented alternative values for these parameters.

DISCUSSION

The predicted K from this study (22 831) was greater than the five-year average peak population of 16 943 (Table 1). This indicates that the redhead population at Chandeleur Sound during that period was at 74% of carrying capacity, although the highest peak during the study (19 700; Table 1) was 86% of K. The peak number of redheads censused at Chandeleur Sound in 1955–96 (42 years) averaged 14 316 and ranged from 2600 to 29 900 (USFWS, unpublished data; T C Michot, unpublished data). The peak population exceeded my predicted K during seven years over that time period, but all were prior to 1974. Because my predicted K was based on the coverage of shoalgrass in 1989, it is possible that K would have been higher in those earlier years because shoalgrass coverage was probably greater. Accordingly, K may have been higher between 1955 and 1974 than it is today, which would account for the support of higher numbers of birds during that earlier period. The increased K that I calculated using the 1951 shoreline (ie 25 149; Table 3) helped explain some of those high years, but even that revised K was exceeded during three years (1957, 1958, 1970). All other parameters being held constant, the implication is either a greater width of total seagrass habitat between the island and the backbarrier bar (AvgTransLth, Equation 3), or a greater percentage of shoalgrass coverage within the total seagrass habitat (%Hal, Equation 4) during those early years.

Shoalgrass biomass and redhead consumption were the parameters that showed the greatest degree of variation in the literature, and substitution of alternate values resulted in considerable variation in the estimated K (Table 3). The low shoalgrass biomass values from Chandeleur Sound summer data are probably unrealistic for this model because the K estimates were well below the observed population levels during this study, assuming that all other model parameters are correct. The high shoalgrass biomass values from Texas are probably unrealistic as well for Chandeleur Sound, but they do show that any management actions or natural phenomena that could alter shoalgrass biomass at Chandeleur Sound could significantly increase the area's carrying capacity for redheads. The low consumption rate for canvasbacks (Longcore & Cornwell 1964) may be unrealistic in that it is out of line with other values from the literature, but the diet used in that experiment was similar to the diet of redheads at Chandeleur Sound. The higher consumption value shown for canvasbacks by Perry *et al.* (1986) may be more realistic for that species, and is probably high for the smaller redhead.

The predicted effect of parameter variation in the model is dependent on the assumption that all other model parameters are held constant. Calculation of the usable fraction of the shoalgrass biomass and the rhizome fraction of the usable biomass had a considerable effect on the model. These estimates were based on the work of Mitchell *et al.* (1994), who also found shoalgrass biomass values that were considerably higher than mine. Although it is probable that redheads in the Laguna Madre of Texas forage in shoalgrass patches that are similar in biomass to those found in Chandeleur Sound, as suggested by Onuf (C P Onuf, USGS, pers. comm.), it is possible that biomasses in Texas are higher. If so, it could be that redheads in Louisiana would have to work a little harder to continue to extract rhizomes below the 63 gdm m^{-2} (UnusablBio, Equation 5) threshold found in Texas. If they did so, however, shoalgrass patches would likely be negatively impacted to such an extent that recovery during the next growing season would be less than adequate to support the following year's population of redheads (Mitchell *et al.* 1994). Belowground biomass at Chandeleur Sound in shoalgrass plots from which redheads were not excluded was reduced 73% from 119 gdm m^{-2} in October to 33 gdm m^{-2} in March (Michot & Chadwick 1994), but it is not known how much of that reduction was from redhead grazing and how much was from other factors. If redheads at Chandeleur Sound are able to graze patches to below the 63 gdm m^{-2} threshold found in Texas, then it is likely that the carrying capacity in Louisiana would be greater than predicted.

My finding that K was exceeded during several years in the past, and that the observed population during the five-year study period came up to 86% of predicted K, indicates that redheads wintering at Chandeleur Sound could indeed be limited by food resources, at least during some years. This limitation may come into play only during years of an ecological 'crunch' (Weins 1977). Because redheads on the wintering grounds depend almost exclusively on a single seagrass species and its associated faunal assemblage, and because the population may indeed be limited by those food resources, protection and enhancement of shoalgrass beds should be the highest conservation priority within the winter range of this diving duck species.

ACKNOWLEDGMENTS

I was assisted in redhead aerial surveys by D L Mackey, D P Rave, P C Chadwick, A J Nault, and W Norling. H A Neckles, C P Onuf, A R Brazda, and F H Roetker graciously provided me with information from unpublished data, as referenced in this study. S Lauritzen prepared Figure 1, and A J Nault prepared Figure 2.

REFERENCES

Baldwin, J. R. & Lovvorn, J. R. 1994. Expansion of seagrass habitat by the exotic *Zostera japonica*, and its use by dabbling ducks and brant in Boundary Bay, British Columbia. *Marine Ecology Progress Series*, **103**, 119–127.

Bardwell, J. L., Glasgow, L. L. & Epps, E. A., Jr. 1962. Nutritional analyses of foods eaten by pintail and teal in south Louisiana. *Proceedings of the Southeastern Association of Game and Fish Commissioners*, **16**, 217–220.

Campbell, J. W. 1946. The food of the wigeon and brent goose. *British Birds*, **39**, 194–200.

Cornelius, S. E. 1975. *Food choice of wintering redhead ducks* (Aythya americana) *and utilization of available food resources in lower Laguna Madre, Texas.* MSc thesis, Texas A&M University, College Station, Texas.

Cornelius, S. E. 1977. Food and resource utilization of wintering redheads on lower Laguna Madre. *Journal of Wildlife Management*, **41**, 374–385.

Cottam, C., Lynch, J. J. & Nelson, A. L. 1944. Food habits and management of American sea brant. *Journal of Wildlife Management*, **8**, 36–56.

Cowardin, L. M., Carter, V., Golet, F. C. & LaRoe, E. T. 1979. *Classification of wetlands and deepwater habitats of the United States.* (FWS/OBS–79/31.) Washington, DC: US Fish and Wildlife Service, Office of Biological Services.

Dubovsky, J. A. & Kaminski, R. M. 1994. Potential reproductive consequences of winter-diet restriction in mallards. *Journal of Wildlife Management*, **58**, 780–786.

Errington, P. L. 1934. Vulnerability of bob-white populations to predation. *Ecology*, **15**, 110–127.

Handley, L. R. 1995. Seagrass distribution in the northern Gulf of Mexico. In: *Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems*, edited by E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, & M. J. Mac, 273–275. Washington, DC: US Department of the Interior, National Biological Service.

Haramis, G. M., Nichols, J. D., Pollock, K. H. & Hines, J. E. 1986. The relationship between body mass and survival of wintering canvasbacks. *Auk*, **103**, 506–514.

Heitmeyer, M. E. & Fredrickson, L. H. 1981. Do wetland conditions in the Mississippi delta hardwoods influence mallard recruitment? *Transactions of the North American Wildlife and Natural Resources Conference*, **46**, 44–57.

Hohman, W. L., Moore, J. L. & Franson, J. C. 1995. Winter survival of immature canvasbacks in inland Louisiana. *Journal of Wildlife Management*, **59**, 384–392.

Jacobs, R. P. W. M., Den Hartog, C., Braster, B. F. & Carriere, F. C. 1981. Grazing of the seagrass *Zostera noltii* by birds at Terschelling (Dutch Wadden Sea). *Aquatic Botany*, **10**, 241–259.

Kiorboe, T. 1980. Distribution and reproduction of submerged macrophytes in Tipper Grund (Ringkobing Fjord, Denmark), and the impact of waterfowl grazing. *Journal of Applied Ecology*, **17**, 675–687.

Krapu, G. L. 1981. The role of nutrient reserves in mallard reproduction. *Auk*, **98**, 29–38.

Longcore, J. R. & Cornwell, G. W. 1964. The consumption of natural foods by captive canvasbacks and lesser scaups. *Journal of Wildlife Management*, **28**, 527–531.

Lynch, J. 1984. Escape from mediocrity: a new approach to American waterfowl hunting regulations. *Wildfowl*, **35**, 5–13.

Madsen, J. 1988. Autumn feeding ecology of herbivorous wildfowl in the Danish Wadden Sea, and impact of food supplies and shooting on movements. *Danish Review of Game Biology*, **13**, 1–32.

Mayhew, P. W. 1988. The daily energy intake of European wigeon in winter. *Ornis Scandinavica*, **19**, 217–223.

Michot, T. C. & Chadwick, P. C. 1994. Winter biomass and nutrient values of three seagrass species as potential foods for redheads (*Aythya americana* Eyton) in Chandeleur Sound, Louisiana. *Wetlands*, **14**, 276–283.

Michot, T. C. & Nault, A. J. 1993. Diet differences in redheads from nearshore and offshore zones in Louisiana. *Journal of Wildlife Management*, **57**, 238–244.

Michot, T. C., Woodin, M. C. & Nault, A. J. 1996. *Food habits of redheads wintering in seagrass beds of coastal Louisiana and Texas*. Submitted manuscript.

Miller, M. R. 1986. Northern pintail body condition during wet and dry winters in the Sacramento Valley, California. *Journal of Wildlife Management*, **50**, 189–198.

Mitchell, C. A., Custer, T. W. & Zwank, P. J. 1994. Herbivory on shoalgrass by wintering redheads in Texas. *Journal of Wildlife Management*, **58**, 131–141.

Moyle, J. B. 1961. *Aquatic invertebrates as related to larger water plants and waterfowl*. (Investigative Report no. 233.) St Paul, Minnesota: Department of Conservation, Division of Game and Fish.

Nienhuis, P. H. & Groenendijk, A. M. 1986. Consumption of eelgrass, *Zostera marina*, by birds and invertebrates: an annual budget. *Netherlands Journal of Sea Research*, **12**, 180–194.

Ogilvie, M. A. & Matthews, G. V. T. 1969. Brent geese, mudflats and man. *Wildfowl*, **20**, 119–125.

Onuf, C. P. 1995. Seagrass meadows of the Laguna Madre of Texas. In: *Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems*, edited by E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, & M. J. Mac, 275–277. Washington, DC: U.S Department of the Interior, National Biological Service.

Onuf, C. P. 1996. Seagrass responses to long-term light reduction by brown tide in upper Laguna Madre, Texas: distribution and biomass patterns. *Marine Ecology Progress Series*, **138**, 219–231.

Orth, R. J. & Moore, K. A. 1983. Submersed vascular plants: techniques for analyzing their distribution and abundance. *Marine Technology Society Journal*, **17**, 38–52.

Perry, M. C., Kuenzel, W. J., Williams, B. K. & Serafin, J. A. 1986. Influence of nutrients on feed intake and condition of captive canvasbacks in winter. *Journal of Wildlife Management*, **50**, 427–434.

Phillips, R. C. 1984. *The ecology of eelgrass meadows in the Pacific Northwest: a community profile*. (FWS/OBS-84/24.) Washington, DC: US Fish and Wildlife Service.

Ranwell, D. S. & Downing, B. M. 1959. Brent goose (*Branta bernicla* (L.)) winter feeding pattern and *Zostera* resources at Scolt Head Island, Norfolk. *Animal Behavior*, **7**, 42–56.

Raveling, D.G. & Heitmeyer, M.E. 1989. Relationship of population size and recruitment of pintails to habitat conditions and harvest. *Journal of Wildlife Management*, **53**, 1088–1103.

Ritchie, W., Westphal, K. A., McBride, R. A. & Penland, S. 1992. *Coastal sand dunes of Louisiana: the Chandeleur Islands barrier system*. (Coastal Geology Technical Report no. 7.) Baton Rouge, Louisiana: Louisiana Geological Survey; Aberdeen, Scotland: Department of Geography, University of Aberdeen.

Stieglitz, W. O. 1966. Utilization of available foods by diving ducks on Apalachee Bay, Florida. *Proceedings of the Southeastern Association of Game and Fish Commissioners*, **20**, 42–50.

Suter, J. R., Penland, S., Williams, S. J. & Kindinger, J. L. 1988. Transgressive evolution of the Chandeleur Islands, Louisiana. *Transactions of the Gulf Coast Association of Geological Societies*, **38**, 315–322.

Weins, J. A. 1977. On competition and variable environments. *American Scientist*, **65**, 590–597.

Yocum, C. F. & Keller, M. 1961. Correlation of food habits and abundance of waterfowl, Humboldt Bay, California. *California Fish and Game*, **47**, 41–53.

Population behaviour in response to anthropogenic change in wetland habitats: the use of long-term datasets as tools in conservation

R A Pettifor
The Wildfowl & Wetlands Trust, Slimbridge, Gloucestershire GL2 7BT, UK

SUMMARY
Conservation biology is becoming an increasingly exact science, whilst at the same time the demands made upon it are more urgent, more frequent, and often of increasing complexity. In particular, the ability of applied ecology to predict the likely outcome of some perturbation to an ecosystem is an essential tool in effective conservation. In this paper I review the insights that the correct statistical and mathematical modelling of population estimates and time series of count data can potentially provide to conservation biologists, using as examples some current work into wetland ecology and conservation being undertaken by the Wildfowl and Wetlands Trust. Much of this research makes use of the extensive long-term datasets that we hold, which, with the exception of some of the data discussed at the end of this paper, are no more complex than simple counts of total numbers carried out over time, supplemented by estimates of productivity obtained in the field through direct observation. I highlight problems associated with the analyses of these data, suggest alternative ways of examining them, and then go on to show how simple, stochastic matrix models of population behaviour can lead to insights useful to conservation management. My starting point is partly based on the ancient Simian proverb that what one fool can do, another can too. I trust also that readers will discern various examples by which C J Krebs' (1991, p3) assertion that 'Two reasons for *not* doing long-term studies are to assess density-dependence and to monitor ecosystem health' can be strongly refuted.

INTRODUCTION

Outside of the breeding season, the United Kingdom hosts in excess of 3 million waterfowl that either stage or overwinter on the country's wetlands, be these estuaries and along the coastline, or inland waterbodies such as lakes, rivers, and their associated floodplains, and, more recently, those of human origin (eg reservoirs and gravel pits). These wetlands are habitats of outstanding international importance for waterfowl and support around 17% of the estimated 17.5 million wildfowl which overwinter in north-west Europe and around 40% of the wintering waders of the east Atlantic flyway. Table 1 lists the proportion of the international populations of various wildfowl species which overwinter in the United Kingdom. These wetlands and their associated habitats are thus critical as overwintering grounds for the total complement of some subpopulations – Svalbard barnacle goose (*Branta leucopsis*), Icelandic whooper swan (*C. cygnus*) and greylag goose (*A. anser*) – and a high proportion of the population of some other species, including various ducks.

The United Kingdom, along with the other signatories of various international conventions and European Community legislation, has specific obligations towards the conservation of the natural environment and its associated species. Consequently, knowledge of the distribution and abundance of species on their associated habitats is an essential first step towards their effective conservation and management. Thirty years ago, writing in the foreword of a book dedicated to the conservation of waterfowl, E M Nicholson noted that 'Before undertaking the conservation of animals and plants it is necessary scientifically to learn at least something of their numbers and distribution ...' (E M Nicholson in Atkinson-Willes 1963).

Table 1. The total number of birds overwintering in the UK for a selection of wildfowl species, relative to their respective flyway population estimates. The UK winter totals were taken from Stone *et al.* (1997), whilst the flyway populations are from Scott and Rose (1996)

Species/population	Scientific name	UK winter total	Flyway total	UK total as % of flyway
Mute swan	*Cygnus olor*	25750	25750	100
Bewick's swan	*Cygnus columbianus bewickii*	7590	16000	47
Icelandic whooper swan	*Cygnus cygnus*	16000b	16000	100
Bean goose	*Anser fabalis*	450	80000	1
Icelandic/greenlandic pink-footed goose	*Anser brachyrhynchus*	225000	225000	100
European white-fronted goose	*Anser a. albifrons*	6100	600000	1
Greenland white-fronted goose	*Anser albifrons flavirostris*	13860	30000	46
Icelandic greylag goose	*Anser anser*	100000	100000	100
Greylag goose (NW Scotland)	*Anser anser*	5250	5250	100
Greenland barnacle goose	*Branta leucopsis*	26950	32000	84
Svalbard barnacle goose	*Branta leucopsis*	12000	12000	100
Dark-bellied brent goose	*Branta bernicla bernicla*	103300	300000	34
Greenland light-bellied brent goose	*Branta bernicla hrota*	14600	20000	73
Svalbard light-bellied brent goose	*Branta bernicla hrota*	2430	5000	49
Shelduck	*Tadorna tadorna*	76400	300000	25
Wigeon	*Anas penelope*	291000	1250000	23
Gadwall	*Anas strepera*	8400	30000	28
Teal	*Anas crecca*	141000	400000	35
Pintail	*Anas acuta*	28100	60000	47
Shoveler	*Anas clypeata*	10300	40000	26
Pochard	*Aythya ferina*	81200	350000	23
Tufted duck	*Aythya fuligula*	90100	1000000	9

THE ABUNDANCE OF WATERFOWL POPULATIONS

In order to 'learn at least something of the distribution and abundance' of waterfowl, the International Wildfowl Inquiry Committee instigated the first national counts of wildfowl in the United Kingdom in 1947, using both professional staff and volunteer counters. The Wildfowl Trust (now the Wildfowl & Wetlands Trust (WWT)) took responsibility for the National Wildfowl Counts in 1954, with the aim of obtaining as broad a coverage of UK wetlands as possible. This scheme, plus the Birds of Estuaries Enquiry (BoEE) begun in 1969 by the British Trust for Ornithology (BTO) and others, was combined in 1993 with the launch of a single monitoring scheme, the Wetland Bird Survey (WeBS), jointly funded by the BTO, WWT, the Royal Society for the Protection of Birds and the Joint Nature Conservation Committee (see Cranswick *et al.* 1996a). The mission of WeBS is *to monitor all non-breeding waterfowl in the UK to provide the principal data on which the conservation of their populations and wetland habitats is based* (Cranswick *et al.* 1996b). To this end WeBS has four primary objectives:

- to assess the size of non-breeding waterfowl populations in the UK;
- to assess trends in their numbers and distributions;
- to assess the importance of individual sites for waterfowl; and
- to contribute to the understanding of waterfowl ecology, including the effects of habitat change and anthropogenic impacts.

The first objective relates directly to the designation of a site as being of 'international importance', such designation being determined by the site regularly supporting 20 000 waterfowl, or regularly supporting 1% of the total population of a species or subspecies of any waterfowl (Ramsar Convention Bureau 1988). These criteria therefore require knowledge of the number of waterfowl using a site, and accurate estimates of the total size of the differing waterfowl populations. I will not consider this objective further, but refer the reader to Underhill and Prŷs-Jones (1994), Kirby *et al.* (1995), and Kirby (1995).

Trends in count data at different scales – methods of analysis

The second and third objectives will be discussed in more detail, as these address both the issue of scale and the detection of

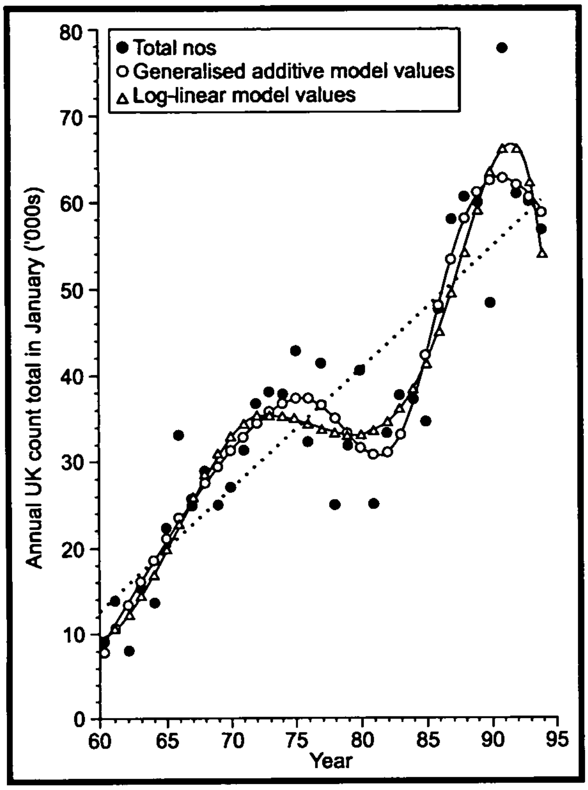

Figure 1. The total number of pochard recorded in January each year in the UK (•). The broken line is the linear best fit to the data, whilst the open triangles are the fitted values from a log-linear model and the open circles are the fitted values from a generalised additive model

trends in the data, whether at international, national, regional or local site levels, and require the application of suitable statistical techniques. A number of problems in the statistical analysis of these data are inherent, and include the following.

- ***Non-linearity***
  Many of the trends in the count data, both within season (ie seasonal phenology) and between years, are non-linear, and therefore traditional polynomial expansions and/or transformations may be inadequate to model the observed data.

- ***Heterogeneity in the variance distributions***
  Classical models with appropriate error structures do not adequately fit the data: most models are highly overdispersed.

- ***Missing data***
  Very few sites have complete coverage (ie sites tend not to have been counted on all possible dates, resulting in extensive 'missing values'). Current methods for imputing missing values do not allow the subsequent statistical testing of trends, etc, where these imputed values are included.

- ***Variable length of data from individual sites***
  In addition to missing counts, many sites 'drop in' and 'fall out' of the database over time as sites (and counters) change.

- ***Non-stratified samples***
  Virtually all the WeBS sites are counted by volunteers, who identify which sites they wish to count. The assumptions are that they will tend to count the 'better' sites, and therefore the majority of birds are counted (for most species), and that 'important' changes in site, regional or national trends will be detected. However, no stratified sampling is undertaken.

- ***Explanatory variables***
  Whilst trends or other patterns of interest can be described with some degree of statistical confidence, linking these observed patterns to causal factors tends not to be currently feasible.

I will consider the first two problems in some detail, as they both appear to occur in the analyses of many datasets based on sample counts, and the possible techniques that may be used to overcome them are common to both. Figure 1 illustrates a

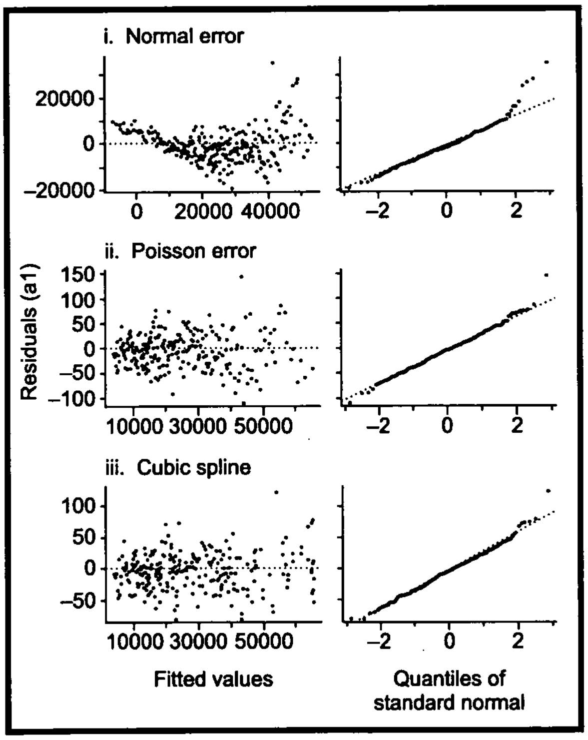

Figure 2. Plots of the standardised residuals against the fitted values (left-hand column) or as quantile plots (right-hand column) for three models: (i) a GLM with Normal error structure; (ii) a GLM with Poisson error structure; and (iii) a GAM using the cubic spline as the smoothing algorithm

typical series of count data collected over time: in this instance, the total number of pochard (*Aythya ferina*) recorded in the UK in January of each year since 1960. Whilst a statistically significant linear line can be fitted to these data (broken line in Figure 1), there is clearly considerable scatter around this line, and visual inspection suggests some brief stabilisation or possible decline in numbers in the 1970s. A number of different statistical models were fitted to these data, and various checks on their suitability were carried out. The fitted values of the two most parsimonious are superimposed on the observed data in Figure 1, whilst Figure 2 examines the statistical suitability of the three fits shown in Figure 1 by plotting their relevant (standardised) residuals against the fitted values, and as normal probability plots. The Generalised Linear Model (GLM) with normal or Gaussian errors provides a poor fit to the data, with a clear pattern present in the standardised residuals when plotted against the fitted values, and considerable divergence amongst the larger observed data when the standardised residuals are ordered and plotted against the standard normal cumulative distribution function. Clearly, the assumption of a Gaussian error distribution is incorrect. A log-linear GLM with a Poisson error distribution provides a much better fit, with no apparent pattern when the deviance residuals are plotted against the fitted values, and a better-behaved pattern in the residuals in the quantile plot. In fact, there appears little to choose between the behaviour of the Poisson GLM and the non-parametric Generalised Additive Model (GAM) using a cubic spline as the smoothing function (Figure 2).

In the above specific instance, graphical inspection of both Figures 1 and 2 indicates that both the parametric Poisson GLM and the smoothing GAM adequately fit the data, although the log-linear model is considerably overdispersed. However, once we examine these count data stratified by region and habitat, it is clear that not only do our assumptions about the error structure need to be re-examined, but many of the trends are non-linear (*cf* Figure 3). In addition, the inclusion of higher-order polynomial terms to GLMs (eg year, year^2, year^3, ..., year^5) results in aliasing owing to the colinearity between these variables, and to model instability. The choice of correct error structure is essential in the fitting of any GLM, and most of our analyses to date indicate that not only are Gaussian errors wholly inappropriate, but that Poisson errors (considered to be typical of count data – see Crawley 1993) result in massive overdispersion in the final model. Frequently, this overdispersion parameter (scaled deviance of final model divided by residual df) is in excess of 100, instead of being nearer the expected scale parameter value of unity (ie where the mean is equal to the variance). The use of alternative error structures may be more appropriate (eg negative binomial or gamma errors), although in our experience these also tend not to fit the relatively aggregated data common to counts of wildfowl (the aggregation parameter, k, is generally >>1.0). One way round this problem of overdispersion is to rescale the Poisson model, such that the (refitted) ratio of the final deviance to residual degrees of freedom approximates unity. An alternative approach is to transform the response variable: we have found that either taking the natural logs of the count data, or their square roots, when coupled with Poisson errors, often provides well-behaved models. The problem with this latter approach comes

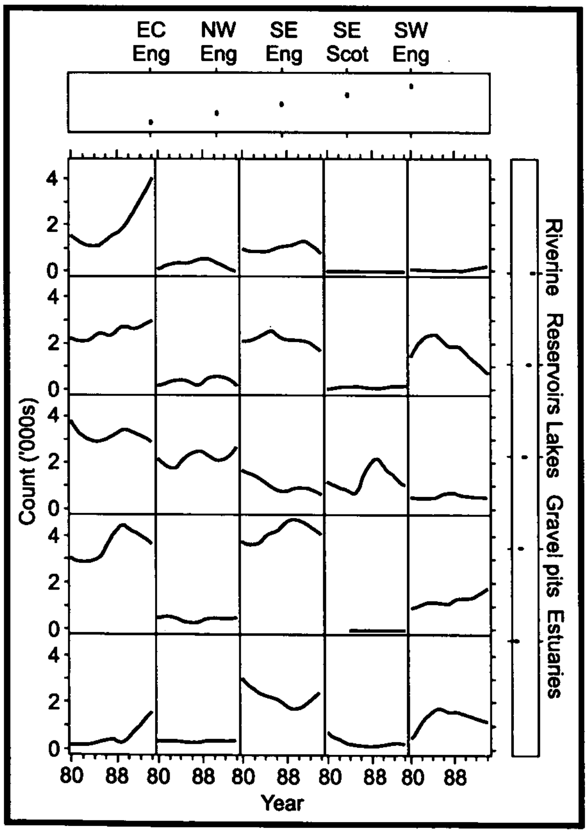

Figure 3. The fits from a local regression model of pochard numbers in relation to different habitats and regions of the UK

Table 2. Generalised linear models fitted to the count data of pochard overwintering in Britain between 1980 and 1993. The GLMs were fitted with either a normal or Poisson error structure, whilst the response variable (y-var) was either the raw summed count data or log- or square root-transformed. The changes in deviance given for the first two models are after rescaling following the fit of the complete model, whilst the final two models have a scale parameter set at unity

	Df	Normal error	Normal error	Poisson error	Poisson error	Poisson error	Poisson error	Poisson error	Poisson error
Y-var		Count	Count	Count	Count	ln count	ln count	√ count	√ count
Variable		Δ deviance	P	Δ deviance	P	Δ deviance	P	Δ deviance	P
Year	1	0.02	NS	2.00	NS	0.08	NS	1.69	NS
Month	1	130.80	<0.001	4799.00	<0.001	258.10	<0.001	4828.00	<0.001
Year^2	1	0.03	NS	1.52	NS	0.07	NS	1.42	NS
Month^2	1	127.70	<0.001	4699.00	<0.001	218.70	<0.001	4461.00	<0.001
Year^3	1	0.04	NS	1.12	NS	0.05	NS	1.18	NS
Region	10	879.10	<0.001	25855.00	<0.001	3193.00	<0.001	34263.00	<0.001
Habitat	4	128.60	<0.001	4933.00	<0.001	1319.00	<0.001	6991.00	<0.001
RegionxYear	10	18.64	<0.001	94.13	<0.001	23.20	<0.05	210.60	<0.001
RegionxMonth	10	294.50	<0.001	143.0	<0.001	22.43	<0.05	182.70	<0.001
RegionxYear^2	10	16.81	<0.001	88.76	<0.001	21.87	<0.05	199.10	<0.001
RegionxMonth^2	10	304.00	<0.001	240.70	<0.001	18.62	<0.05	253.80	<0.001
RegionxYear^3	10	15.15	<0.001	83.74	<0.001	20.63	<0.05	188.40	<0.001
HabitatxYear	4	1.94	NS	12.16	<0.001	2.25	NS	18.05	<0.010
HabitatxMonth	4	37.95	<0.001	196.10	<0.001	93.22	<0.001	18.02	<0.010
HabitatxYear^2	4	2.02	NS	12.48	<0.001	2.22	NS	18.02	<0.010
HabitatxMonth^2	4	37.85	<0.001	91.56	<0.001	66.43	<0.001	434.00	<0.001
HabitatxYear^3	4	2.10	NS	12.83	<0.001	2.12	NS	241.10	<0.001
RegionxHabitat	37	2170.00	<0.001	18177.00	<0.001	3615.00	<0.001	29496.00	<0.001
RegionxHabitatxYear	32	6.30	NS	46.50	<0.050	8.02	NS	113.30	<0.001
RegionxHabitatxMonth	36	660.10	<0.001	119.80	<0.001	173.60	<0.001	476.70	<0.001
RegionxHabitatxYear^2	32	6.79	NS	46.34	<0.050	7.94	NS	112.10	<0.001
RegionxHabitatxMonth^2	36	697.20	<0.001	105.20	<0.001	144.60	<0.001	413.90	<0.001
RegionxHabitatxYear^3	32	7.34	NS	46.18	NS	7.87	NS	110.90	<0.001
%R^2			75.40		93.40	84.90		92.00	
Initial deviance		191551x10^6	4687.00*	8759725	65382.00*	10931.00		90638.00	
Final deviance		3765x10^6	1152.00*	577329	4309.00*	1645.00		7275.00	
Residual df			4400.00		4400.00	4400.00		4400.00	

* Rescaled values

in the interpretation of any curvilinearity present in the raw data. An example of these differing ways of examining count data is given in Table 2, where the significance of various explanatory variables is explored in four GLMs fitted to the most recent 15 years (1980–94) of count data for the pochard in Great Britain. The basic model structure was the same in each case, with the models including a squared term for month to account for seasonal phenology, and a squared and cubic term for year to account for curvilinearity between years. All first-order interactions were included, plus within- and between-season interactions with region and habitat together. Whilst each of the GLMs seems very powerful in explaining the amount of variance in the data (r^2 values in excess of 75%), the degree of overdispersion in the model with the normal error distribution and in the unscaled Poisson model is unacceptably high (their respective overdispersion indices (Pearson's χ^2/residual df) being 855 682 and 131). The graphical checks of the models (Figure 4) also indicate the inappropriateness of these two models, whilst the model where the count data were first square root-transformed would seem the better behaved of the four. However, all three Poisson models (raw count data, model rescaled; and count data either square root- or log-transformed) confirm the statistical importance of differences between regions and habitats, and in their specific patterns both within and between years, as originally determined from visual inspection of Figure 3.

Readers may feel much of the above is simply one of statistical semantics, especially with respect to the theme of these Proceedings. It is not! As conservation biologists, one of the fundamental questions that we ask is whether a population is stable, declining or increasing.

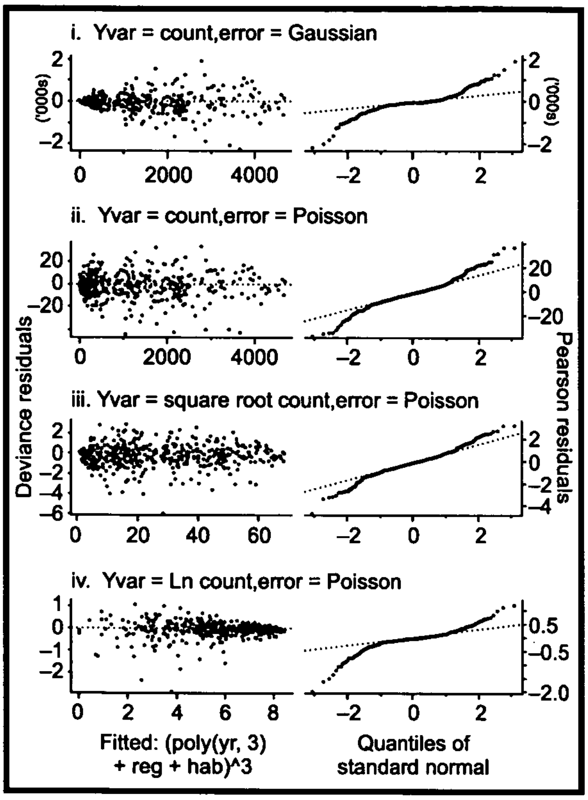

Figure 4. Plots of the standardised residuals against the fitted values (left-hand column) or as quantile plots (right-hand column) for four models: (i) a GLM with Normal error structure where the response variable is the untransformed count data; (ii) a GLM with Poisson error structure where the response variable is the untransformed count data; (iii) a GLM with Poisson error structure where the response variable is the square root of the count data; and (iv) a GLM with Poisson error structure where the response variable is the natural log of the count data

If we use the wrong statistical techniques in the analysis of the data, then we are very likely to obtain an incorrect assessment of the behaviour of the population. Thus, inappropriate error structure leads to conflated upper and lower confidence intervals around the mean, such that the standard errors associated with each of the parameter estimates are too narrowly defined: the net result may be the detection of spuriously significant trends, as well as the underestimation of the natural variance present in the trends. In order to investigate the effects and potential threats of anthropogenic change on waterfowl populations, we need to know what is happening at a range of scales to the species or population under consideration, ensuring the use of appropriate statistical models. In addition, correct statistical models are essential in order to extract parameter estimates for subsequent modelling exercises (see below) – in population viability analyses, it is not only the means of these parameters that need to be accurately estimated, but also the errors surrounding them. Possibly, the most important lesson from these examples is the absolute necessity of careful model checking (see Aitken *et al.* 1989 for detailed statistical descriptions, and Crawley 1993 for a field biologist's guide). The most sensible approach is to use GAMs to provide graphical output by which the data may be interpreted (eg as in Figure 3), and to transform data as required to allow precise statistical confidence limits to be calculated.

Trends in count data at different scales – uses in conservation biology

How can the correct statistical analyses of trends in count data aid in waterfowl conservation? First, they can provide an indication as to the behaviour of the population at various scales, allowing reactive, and occasionally proactive, action. Thus, national (or international) trends can be put into the context of 'national alert limits', and remedial action taken as and when deemed necessary (see Kirby & Bell 1997). However, the national population in winter is scattered across various natural water catchment areas and differing habitats within each area, as highlighted in Figure 3. The next logical step for wetland ecologists is the development of 'site alert limits'. Under the Ramsar Convention and EC Birds Directive, the UK Government has specific responsibility to designate internationally important wetlands and sites important for bird species as Ramsar sites and Special Protection Areas (SPA), based in part on the 1% criterion. Three approaches may be taken in order to examine patterns in population size over time at individual sites, thereby allowing proactive conservation action to be taken in some instances:

- site-specific annual rates of growth;
- change in population size at a site relative to the total population size;
- detecting density dependence.

Below, I use a recent analysis of trends in shelduck (*Tadorna tadorna*) numbers on estuaries in Great Britain (Pettifor & Kershaw 1997) to examine these approaches.

Site-specific annual rates of growth

In order to quantify trends in the number of wintering shelduck on individual estuaries over time, we used ln-transformed counts as the response variable and a normal error structure, with month and the square of month to control for seasonal phenology:

$$\ln(\text{count}) = \text{month} + \text{month}^2 + \text{estuary} + \text{estuary} \times \text{year} \quad (1)$$

The parameter estimates from the interaction between estuary and year were used to derive mean percentage annual rates of change for each individual estuary, r:

$$r = (e^b - 1) \times 100 \quad (2)$$

where b is the slope of the regression of ln-transformed counts on years (ie b is the parameter estimate from the GLM for each site × year interaction).

Change in population size at a site relative to the total population size

In addition to looking at rates of change over time, trends on individual estuaries with respect to the total British overwintering population were also examined in order to determine whether some estuaries have reached their 'carrying capacity' for wintering shelduck, using ln–ln plots. Rates of change at individual sites relative to change in total population size may be assessed by fitting:

$$N_{site} = a \times (N_{total})^b \quad (3)$$

where N_{site} is the site total and N_{total} is the total number of shelduck in Britain in that year and month. This is equivalent to:

$$\ln(N_{site}) = \ln(a) + b \times \ln(N_{total}) \quad (4)$$

where, in this latter form, *a* represents the intercept and b the slope of the straight-line regression. The value of b thus indicates varying strengths of any potential density-dependent relationship between the number of birds at a site and the global population size, such that when b is significantly ≥1, then there is no evidence of density dependence; slopes where 1>b>0 suggest density dependence and the possible existence of some carrying capacity, whilst b<0 indicates that the local population is significantly declining relative to the global population.

Detecting density-dependent limitation in numbers

Pollard, Lakhani and Rothery (1987) developed a procedure for testing for density dependence in a series of annual censuses of a population. We refer to this in the following as the 'Pollard test'. The procedure involves calculating a series, d_i, from the census data, $x_1, x_2, x_3, \ldots, x_n$, such that:

$$d_1=\ln(x_2)-\ln(x_1),\ d_2=\ln(x_3)-\ln(x_2),\ \ldots, d_{n-1}= \ln(x_n)-\ln(x_{n-1}).$$

The regression coefficient of the observed d_i against $\ln(x_i)$ is then compared to a large number of coefficients generated through the random re-ordering of d_i and reconstruction of the $x_{i\text{–}n}$ series.

We have recently used combinations of these three approaches to detect site-specific trends in a range of wildfowl populations both throughout Europe and in the UK (Kershaw, Pettifor & Quinn 1996; Kershaw *et al.* 1995; Pettifor & Kershaw 1997). For example, examining the numbers of shelduck overwintering on British estuaries between 1960 and 1993 indicated an annual rate of growth of 6.1%, this rate falling to 4.8% over the last ten-year period. Examining data from 74 of the 127 estuaries within Britain that held 'good' series of count data, we found that shelduck numbers had increased significantly on 19 of these estuaries, and declined on nine sites. Over the period 1974–93, the numbers of shelduck on 35% of these estuaries showed no evidence of density-dependent limitation (ie b>1 in equation (4) above), whilst over the most recent ten-year period this proportion had declined to 11%. The statistically more robust and conservative method of Pollard *et al.* (1987) indicated that 28 (38%) of the sites were showing evidence of density-dependent limitation in numbers, of which ten were nationally or internationally important. Non-hierarchical cluster analyses of the extent of density dependence as determined above indicated that those estuaries showing the strongest evidence of limitation tended to be smaller in total area and with shorter linear dimensions in shore length, channel length, tidal range and shape index than those estuaries showing no density-dependent limitation of numbers. Analyses of this type potentially allow sites to be ranked in order of conservation concern, and, if nothing else, would allow conservation managers to be more vigilant in detecting potential

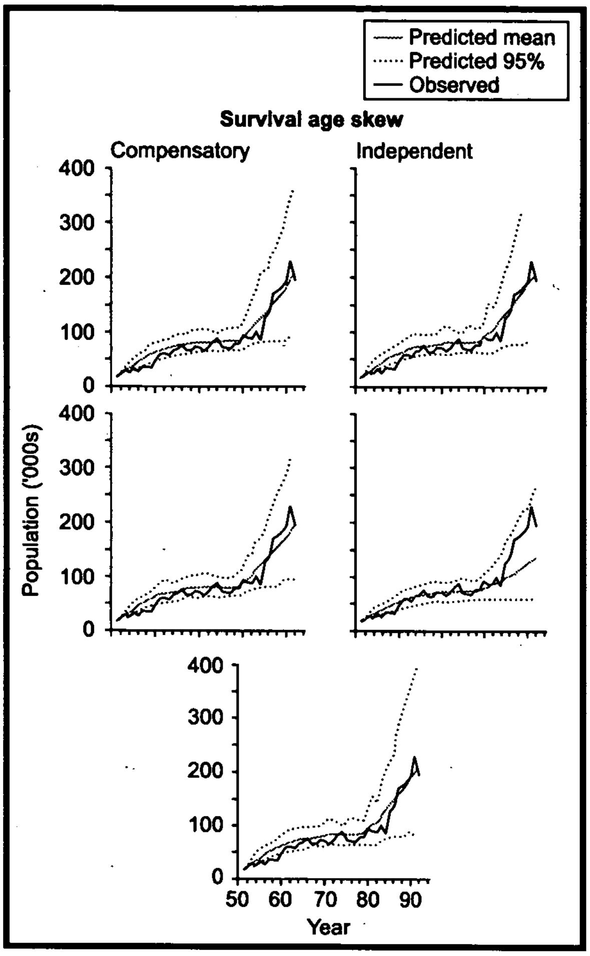

Figure 5. Comparison of predicted (thin line=mean, dashed lines=95% confidence interval) and observed (thick line) Icelandic/Greenlandic pink-footed goose population trends between 1950 and 1992; predictions are from the model assuming observed levels of density dependence up to 1979 and density independence thereafter. The results of different assumptions regarding juvenile survival relative to adult, and methods of modelling this age skew, are also shown. In the top two graphs, survival varied – before 1980, juvenile = 0.9 adult, but from 1980 onwards juvenile = adult. In the middle two graphs, survival is constant and juvenile = 0.9 adult. In the bottom graph, survival is constant and juvenile = adult

threats to sites of high conservation concern, as well as the more efficient targeting of resources. However, it is hoped that further development of these techniques will provide sufficient information for long-term strategic conservation action plans to be drawn up for all of the UK wetland resource.

Clearly, long-term count data are of value to conservation biologists, especially when used to determine potentially serious declines in waterfowl populations outside of the stochastic variation in total population size brought about by annual variations in productivity and mortality schedules. Thus, 'site alert limits' are a powerful tool in the conservation of important overwintering areas for wildfowl. However, equally important to a conservation biologist is the ability to make predictions about likely future trends in overall population size.

Waterfowl population dynamics

The above statistical approaches allow us to describe the trends in a population at various scales, but provide little or no insight into the demography of the population, or any understanding of the actual processes determining population growth. The mathematical modelling of populations can give us some information about the latter. The size of any closed population (N) in any given year (t) is simply:

$$N_t = S(N_{t-1}) + P(N_{t-1}) \qquad (5)$$

where S is the annual rate of survival and P is the annual rate of productivity. However, for this relationship to be of any value to us, we need in the first instance to determine how the productivity and survival rates may be changing over time, especially with respect to the total number of conspecifics (ie we need to determine the existence or otherwise of density dependence in these two vital rates). Through the foresight of the late Sir Peter Scott and his scientific staff at WWT, we are fortunate in having estimates of total population size (N_t) and both mean brood size (BS) and the proportion of juveniles (P_{JUV}) for many populations of geese dating back to at least the 1950s. From these three basic annual measures, it is possible to calculate both annual productivity and crude annual survival rates. The number of juveniles each year (NJ_t) is:

$$NJ = N_t \times P_{JUV}, \qquad (6)$$

allowing the number of potential breeding females to be calculated as:

$$A_{pt} = (N_t - NJ_t) \qquad (7)$$

The annual productivity can then be estimated as:

$$P_t = NJ_t / A_{pt} \qquad (8)$$

and the survival rate S_t as:

$$S = (N_{t+1} - NJ_{t+1})/N_t. \qquad (9)$$

Owen (1982) provides further details.

We have used these above basic estimates of vital rates to develop models of various goose populations (Pettifor & Rowcliffe 1995; Rowcliffe *et al.* 1995; Pettifor, Fox & Rowcliffe 1996; Pettifor, Percival & Rowcliffe 1996). For example, we used the basic census data and the derived demographic rates to model the observed and predicted future trends in the Icelandic/Greenlandic pink-footed goose (*Anser brachyrhynchus*) population (Figure 5). Plotting the estimated annual survival rate (ie S_t) against the lagged population size (ie N_{t-1}) for this population provided no evidence for any density-dependent function, whilst annual productivity declined significantly with increasing population size between 1950 and 1975, but levelled off thereafter. Using these parameter estimates in a simple population projection matrix incorporating partial age structure into both productivity and survival rates, and introducing stochasticity through the variance associated with the respective parameter estimates provides various model projections as illustrated in Figure 5.

Table 3. The relative slope estimates in the logistic regression relating the quasi-extinction risk (thresholds 200 000 and 150 000) over 100 years to variations in parameter estimates for the Icelandic/Greenlandic pink-footed goose population. The parameters tested are derived from the relationships between survival/productivity and population size, with intercept values representing variation in absolute levels and slope representing variation in the strengths of density dependence. Sensitivities to variations in central values and standard deviations of each parameter are shown, giving a total of eight sensitivity values for each of the two quasi-extinction thresholds. Quasi-extinction risks were derived from 5000 iterations. The central value of survival slope was varied between 0 and $2e^{-6}$, and its standard deviation between 0 and $2e^{-7}$. Other parameter estimates were varied by 25% either side of central values

Quasi-extinction threshold	Central value 200 000	Central value 150 000	Standard deviations 200 000	Standard deviations 150 000
Survival				
Intercept	–39.0	–37.8	5.8	5.8
Slope	–5.4	–4.4	0.1	0.1
Productivity				
Intercept	–4.8	–3.6	0.5	0.5
Slope	–18.5	–14.5	0.9	0.9

In themselves, these stochastic matrix models do little more than indicate whether the models reveal any resemblance to reality (eg Figure 5), and inform us as to the likely future behaviour of the population assuming that the circumstances under which the model parameters were derived *do not change in the future*. However, a major reason for modelling population behaviour is to be able to explore various 'what if' scenarios. Population viability analysis is the generic name given to this approach, whereby a change in parameter value or some perturbation is introduced into the model system, and the behaviour of this new model compared to the earlier one. Initially, this modelling approach was developed in order to assess times to, and probabilities of, extinction for small, endangered populations, where stochastic events could easily lead to their demise (see Soulé 1987 for an overview). However, using 'quasi-extinction rates' – the probability of a population falling below some threshold value – a similar approach can be adopted for any population. Sensitivity analyses are one such example, allowing one to examine how sensitive the population is to a given change in a parameter value, and thus answer a basic question of the type: is the population more susceptible to a 5% decline in productivity or a 5% increase in mortality? Table 3 gives the results of such an exercise in the Icelandic/Greenlandic pink-footed goose population. The conclusion from this approach is that this population is most sensitive to changes in the absolute levels of mortality experienced (ie the survival intercept), and, to a lesser extent, to the strength of the density dependence affecting productivity (ie the slope of productivity), but not to the associated variances. A similar conclusion was reached in our analyses of the Greenland barnacle goose (*Branta leucopsis*) population (Pettifor, Percival & Rowcliffe 1996), where sensitivity analyses indicated the population to be far more susceptible to quasi-extinction when mean survival rates were changed relative to change in mean productivity, whilst the population was relatively insensitive to changes in the variance around both of these parameters (Figure 6).

The robustness of a population in surviving catastrophic events can also be examined, as illustrated in Figure 7, where the Icelandic/Greenlandic pink-footed goose population was modelled with productivity being either density-dependent or density-independent, and the probability of the population declining to 'quasi-extinction thresholds' of either 100 000 or 10 000 was examined. It can be seen that the density-dependent

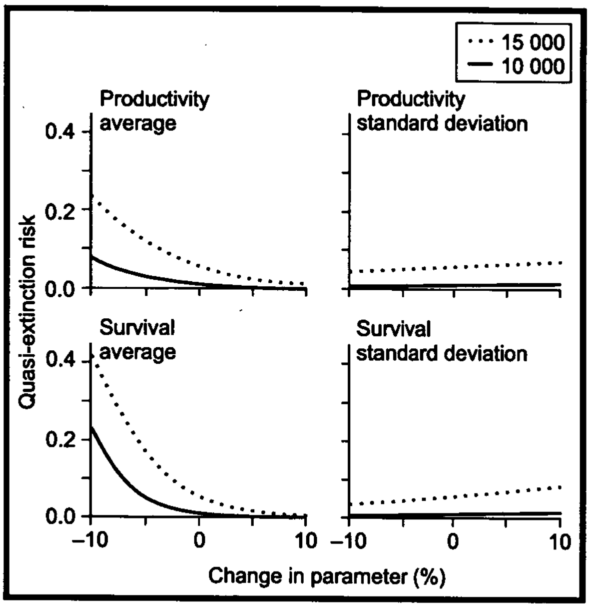

Figure 6. A graphical representation of the sensitivity analyses for the Greenland barnacle goose Scottish population, showing the relationships between the risk of quasi-extinction (reduction below 10 000 (solid lines) or 15 000 (broken lines) within 100 years) in relation to changes in parameter values. Relatively small changes in average survival rate cause large changes in quasi-extinction risk, indicating the greater sensitivity of the model to this parameter than to any of the others

populations exhibit a different pattern to the density-independent ones, with the latter reflecting a slower recovery rate in the absence of density dependence, which in turn compounds the effects of consecutive catastrophic events. However, in the case of this particular population, the risks of quasi-extinction are relatively low; for example, for the population to fall below the 100 000 threshold, a 50% mortality rate would need to occur more often than once every 100 years. This should not lead to complacency though: the catastrophic events modelled here are isolated events, whereas many anthropogenic effects can be frequent and continuous. For example, despite 'licensed' shooting in the USA, high kill rates coupled with a run of poor breeding seasons resulted in a 50% crash in the light-bellied brent goose (*Branta bernicla hrota*) population overwintering in North America (Rogers 1979), from which level recovery has been poor. In the case of the Icelandic/Greenlandic pink-footed goose modelled above, there was a proposal in the late 1960s to flood an area of Iceland as part of a hydro-electric scheme: a survey in 1970 located 10 700 nests in this area (75% of the population's total), of which over 85% would have been directly impacted had the scheme gone ahead, whilst the remaining vegetation would have been severely affected (Kirbes, Ogilvie & Boyd 1971).

Quantifying anthropogenic change

The above models are useful in providing insights into the current behaviour of any given population, and in answering certain 'what if' questions, providing that the basic environmental circumstances under which the original parameter estimates were derived do not change. These 'what if' scenarios may be useful in themselves to conservation biologists, ground management officers, policy officers and others, including the more 'academically inclined' population ecologists. For example, there is a long-running debate as to whether mortality due to hunting in gamebirds is additive or compensatory (*cf* Potts & Aebischer 1991). Simple modelling exercises provided useful insights into this question, including the conclusion that when populations are below their equilibrium level, then hunting mortality is likely to be entirely additive (Rees & Rowcliffe 1996).

Population viability analyses, therefore, provide a powerful tool to conservation biologists in aiding the formulation of

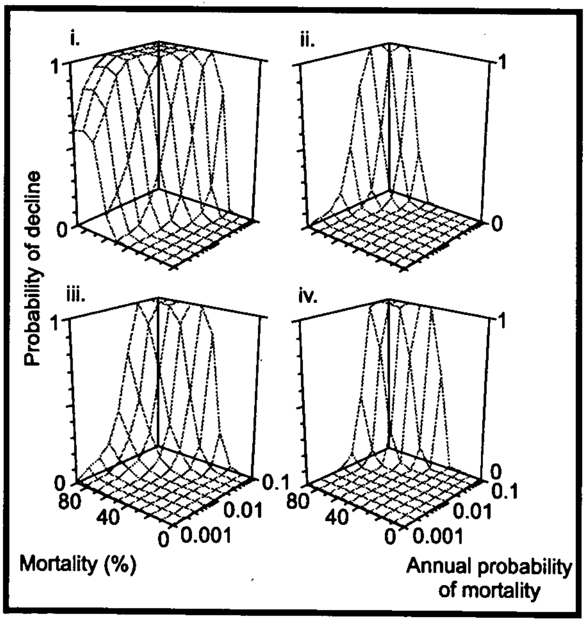

Figure 7. Quasi-extinction risk within 100 years for the Icelandic/Greenlandic pink-footed goose population in relation to variations in annual risk and severity of catastrophes. Model incorporating density dependence in productivity: (i) risk of reduction to 100 000; (ii) risk of reduction to 10 000. Density-independent model: (iii) risk of reduction to 100 000; (iv) risk of reduction to 10 000. Note that the vertical axis represents the probability of decline to the set levels, whilst the two horizontal axes represent the amount of mortality occurring at each event (% mortality) and the annual probability of the mortality event

management plans. However, there are three shortfalls in this approach:

- emigration and immigration may need to be incorporated into the models;
- variation between individuals is frequently ignored (other than as the variance around the mean of the parameter estimates); and
- the specific effects of removing or changing a certain amount of habitat cannot be quantified.

The first two of these shortfalls can easily be incorporated into the model structure: the first as subpopulations within the larger model, and the second through stage-structured models, whereby, for example, different productivity or mortality rates can be allocated to different age classes of birds (see McDonald & Caswell 1993). Relative rates of emigration and immigration can have large effects on population viability and on equilibrium population size; for example, the productivity and mortality rates of differing subpopulations may be subject to varying strengths of any density dependence in these relationships. Similarly, variation in vital rates with different age classes can be readily incorporated into the basic matrix structure of these models. Our long-term study of individually recognisable Svalbard barnacle geese, spanning the past 25 years, has revealed marked age-related differences in productivity (Black & Owen 1995). These differences were incorporated in a stochastic matrix model by Rowcliffe *et al.* 1995. The importance of this parameter in both population growth rate and equilibrium population size is illustrated in Figure 8 (R A Pettifor & J M Rowcliffe, unpublished). The random exclusion of birds from the breeding population with respect to age results in an 18% lower equilibrium population size (λ^*) compared with the targeted exclusion of 1st- through to 4th-year birds (Figure 8i), whilst λ^* can be as much as 50% higher if the maturation period is extended to six years (Figure 8ii). The third aspect of required output (quantifying the effects of habitat loss) can be crudely incorporated into these matrix models if the total number of habitat 'patches' is known and their carrying capacity can be determined. We are currently using such an approach to advise on the consequences of various management options for the management of Greenland barnacle geese on Islay.

An entirely different approach to understanding the consequences of anthropogenic change on populations has been the adoption of a game-theoretic approach to the distribution of individuals in response to depletion of resources, interference, and the availability of resources. This approach is fully reviewed by Sutherland (1996). Fully individual-based, game-theoretic models have recently been employed by Goss-Custard *et al.* (1996) in relation to oystercatchers (*Haematopus ostralegus*) feeding on a series of mussel beds within a single estuary. Jointly with Goss-Custard, we are expanding this approach in order to model the year-round behaviour of whole populations. It is an exciting development, and one which will allow very precise modelling of the response of

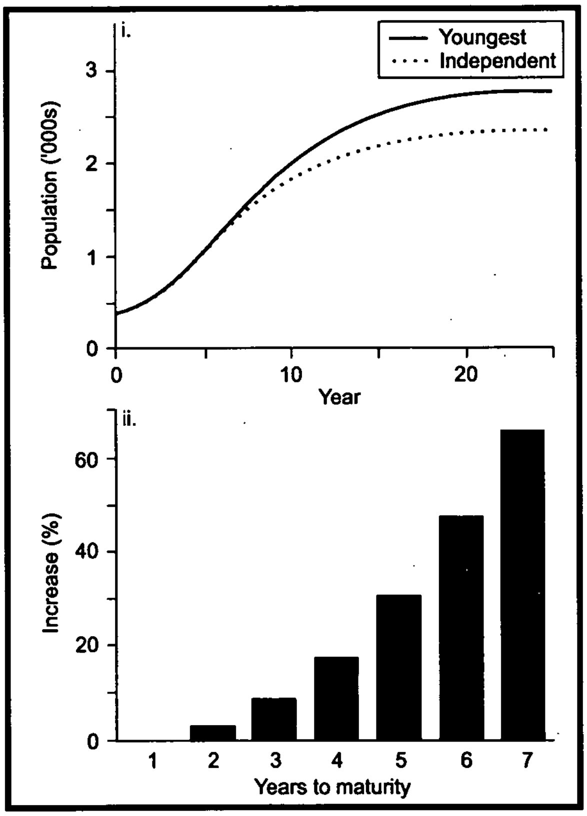

Figure 8. Modification of an age-structured model of the Svalbard barnacle goose, illustrating the importance of individual-based differences (in this instance, differences in age of maturity). Productivity increases linearly with age, and an upper ceiling is placed on the number of breeding females (1000). Exclusion from breeding is either youngest first or independent of age. The top graph illustrates the situation when breeding maturity is reached at age four, resulting in the population size being 18% higher than when exclusion from breeding is non age-dependent. The bottom Figure generalises the relative differences in equilibrium population size for maturation periods of up to seven years

individuals (and hence the population) to specified changes in habitat availability, whilst also allowing more generalised theoretical understanding of the response of animals to anthropogenic change.

CONCLUSIONS

Count data of wildfowl, collected over long periods of time from a representative number of sites, are of considerable value to conservation biologists and others, not least in providing:

- estimates of total population size at various scales;
- estimates of trends in these data, allowing for 'alert limits' to be developed for individual species and at different scales; and
- when linked to annual estimates of productivity and survival, parameters that may be estimated for use in population viability analyses, which are a powerful tool for informing management decisions and targeted conservation action.

However, the utility of the above rely on careful statistical analyses: the choice of which model structure to use is not straightforward, and it is suggested that generalised additive models with suitable smoothing parameters are used in the first instance to determine subsequent statistical testing procedures. The development of site-based 'alert limits' is also recommended as a way forward in allowing more proactive conservation action to be undertaken, as well as being a useful first step in maintaining a watch on the health of individual wetlands, especially if linked to SPA and other designation. Population viability analyses allow for a demographic understanding of populations, and, if sufficient data exist and the models are suitably structured, allow various 'what if' scenarios, including anthropogenic change (eg habitat loss, hunting, etc), to be quantified. Recent, so-called depletion and interference models, based on the Ideal Free Distribution in relation to the behaviour of birds in response to anthropogenic change, are also a powerful way forward in aiding conservation biologists to understand the effects of human activities on wildfowl populations.

ACKNOWLEDGEMENTS

Much of the above work was undertaken with the financial support of outside agencies, especially the WeBS partners (BTO, WWT, RSPB & JNCC), and the country agencies (in particular, Scottish Natural Heritage). Core funding by WWT also ensured the collection and curation of many of the long-term data on specific species. The manuscript was much improved by comments from Peter Cranswick, Melanie Kershaw, Jeff Kirby and Marcus Rowcliffe.

REFERENCES

Aitken, M., Anderson, D., Francis, B. & Hinde, J. 1989. *Statistical modelling in GLIM.* Oxford: Clarendon Press.

Atkinson-Willes, G.L., ed. 1963. *Wildfowl in Great Britain.* London: HMSO.

Black, J.M. & Owen, M. 1995. Reproductive performance and assortative pairing in relation to age in barnacle geese. *Journal of Animal Ecology,* **64,** 234–244.

Cranswick, P.A., Kirby, J.S., Salmon, D.G., Atkinson-Willes, G.L., Pollitt, M.S. & Owen, M. 1996a. A history of wildfowl counts by the Wildfowl & Wetlands Trust. *Wildfowl,* **47,** 217–229.

Cranswick, P.A., Pettifor, R.A., Rehfisch, M.M., Stroud, D.A., Craddock, D.M., Waters, R.J. & Norris, K. 1996b. *The Wetland Bird Survey: forward strategy 1996–97 to 2000–01.* (WeBS Report to the WeBS Partners.) Slimbridge: Wildfowl and Wetlands Trust.

Crawley, M. J. 1993. *GLIM for ecologists.* Oxford: Blackwell Scientific.

Goss-Custard, J.D., West, A.D., Clarke, R.T., Caldow, R.W.G. & Durell, S.E.A. le V. dit 1996. The carrying capacity of coastal habitats for oystercatchers. In: *The oystercatcher: from individuals to populations,* edited by J.D. Goss-Custard, 327–351. Oxford: Oxford University Press.

Kershaw, M., Bell, M.C. & Pettifor, R.A. 1995. *Detecting site-specific changes in waterfowl populations: an analysis of wintering pochard trends on European wetland sites.* (WWT Report to the International Waterfowl and Wetlands Bureau and the Royal Society for the Protection of Birds.) Slimbridge: Wildfowl and Wetlands Trust.

Kershaw, M., Pettifor, R.A. & Quinn, J.L. 1996. *Site-specific changes in waterfowl populations on European wetland sites, with particular reference to important bird areas.* (WWT Report to the International Waterfowl and Wetlands Bureau and the Royal Society for the Protection of Birds.) Slimbridge: Wildfowl and Wetlands Trust.

Kershaw, M., Pettifor, R.A., Bell, M.C. & Kirby, J.S. 1995. *Trends in the number of wintering pochard (*Aythya ferina *L.) in Britain, 1966/67–1993/94, at a regional, habitat and site level.* (WWT Report to Joint Nature Conservation Committee.) Slimbridge: Wildfowl and Wetlands Trust

Kirbes, R.H., Ogilvie, M.A. & Boyd, H. 1971. Pink-footed geese on Iceland and Greenland: a population review based on an aerial survey of Bjórsárver in June 1970. *Wildfowl,* **22,** 5–17.

Kirby, J.S. 1995. Winter population estimates for selected waterfowl species in Britain. *Biological Conservation,* **73,** 189–198.

Kirby, J.S. & Bell, M.C. 1997. Surveillance of non-breeding waterfowl populations: methods to trigger conservation action. Proceedings of the Anatidae 2000 Conference, Strasbourg, France. *Gibier Faune Sauvage - Game and Wildlife,* **12.**

Kirby, J.S., Slamon, D.G., Atkinson-Willes, G.L. & Cranswick, P.A. 1995. Index numbers for waterbird populations, III: Long-term trends in the abundance of wintering wildfowl in Great Britain, 1996/67–1991/92. *Journal of Applied Ecology,* **32,** 536–551.

Krebs, C.J. 1991. The experimental paradigm and long-term population studies. *Ibis,* **133,** supplement 10, 3–8.

McDonald, D.B. & Caswell, H. 1993. Matrix methods for avian demography. In: *Current ornithology,* edited by D.M. Power, vol. 10, 139–185. New York: Plenum Press.

Owen, M. 1982. Population dynamics of Svalbard barnacle geese 1979–1980. *Aquila,* **89,** 229–247.

Owen, M., Atkinson-Willes, G.L. & Salmon, D.G. 1986. *Wildfowl in Great Britain.* 2nd ed. Cambridge: Cambridge University Press.

Pettifor, R.A. & Kershaw, M. 1997. *Shelduck numbers on British estuaries: carrying capacity and estuary characteristics.* (WWT Report to the Wetland Bird Survey Steering Group (BTO, WWT, RSPB & JNCC).) Slimbridge: Wildfowl & Wetlands Trust.

Pettifor, R.A. & Rowcliffe, J.M. 1995. *Population viability analysis of Icelandic/Greenlandic pink-footed geese.* (WWT Report to Scottish Natural Heritage.) Slimbridge: Wildfowl & Wetlands Trust.

Pettifor, R.A., Fox, A.D. & Rowcliffe, J.M. 1996. *Greenland white-fronted geese: collation and statistical analysis of data and population viability analyses phase I.* (WWT Report to Scottish Natural Heritage.) Slimbridge: Wildfowl & Wetlands Trust.

Pettifor, R.A., Percival, S. & Rowcliffe, J.M. 1996. *Greenland barnacle geese: collation and statistical analysis of data and population viability analyses phase I.* (WWT Report to Scottish Natural Heritage.) Slimbridge: Wildfowl & Wetlands Trust.

Pollard, E., Lakhani, K.L. & Rothery, P. 1987. The detection of density dependence from a series of annual censuses. *Ecology,* **68,** 2046–2055.

Potts, G.R. & Aebischer, N.J. 1991. Modelling the population dynamics of the grey partridge: conservation and management. In: *Bird population studies – relevance to conservation and management,* edited by C.M. Perrins, J-D. Lebreton & G.J.M. Hirons, 373–390. Oxford: Oxford University Press.

Ramsar Convention Bureau. 1988. *Convention on wetlands of international importance especially as waterfowl habitat.* Gland, Switzerland.

Rees, E.C. & Rowcliffe, J.M. 1996. *Comparative analysis of the extent to which shooting mortality is compensatory or additive in different populations and circumstances.* (WWT Report to the Joint Nature Conservation Committee.) Slimbridge: Wildfowl & Wetlands Trust.

Rogers, J.P. 1979. *Branta bernicla hrota* in the USA – a management review. *1st technical meeting on western Palearctic migratory bird management. Compte rendu proceedings,* 198–207. Slimbridge: IWRB.

Rowcliffe, J.M., Pettifor, R.A., Black, J.M. & Owen, M. 1995. *A population viability analysis of the Svalbard barnacle goose using census and ringing data.* (WWT Report to Scottish Natural Heritage.) Slimbridge: Wildfowl & Wetlands Trust.

Scott, D.A. & Rose, P.M. 1996. *Atlas of Anatidae populations in Africa and western Eurasia.* (WI Publication #41.) Wageningen: Wetlands International.

Soulé, M.E. 1987. *Viable populations for conservation.* Cambridge: Cambridge University Press.

Stone, B.H., Sears, J., Cranswick, P.A., Gregory, R.D., Gibbons, D.W., Rehfisch, M.M., Aebischer, N.J. & Reid, J.B. 1997. Population estimates of birds in Britain and in the United Kingdom. *British Birds,* **90,** 1–22.

Sutherland, W.J. 1996. *From individual behaviour to population ecology.* Oxford: Oxford University Press.

Underhill, L.G. & Prýs-Jones, R.P. 1994. Index numbers for waterbird populations. I. Review and methodology. *Journal of Applied Ecology,* **31,** 463–480.

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

M M Rehfisch[1], S J Holloway[1], M G Yates[2], R T Clarke[3], G Austin[1], N A Clark[1], S E A le V dit Durell[3], J A Eastwood[2], J D Goss-Custard[3], R Swetnam[2] & J R West[4]

[1]*British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK*
[2]*Institute of Terrestrial Ecology, Monks Wood, Abbots Ripton, Huntingdon, Cambs PE17 2LS, UK*
[3]*Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset BH20 5AS, UK*
[4]*School of Civil Engineering, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK*

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.

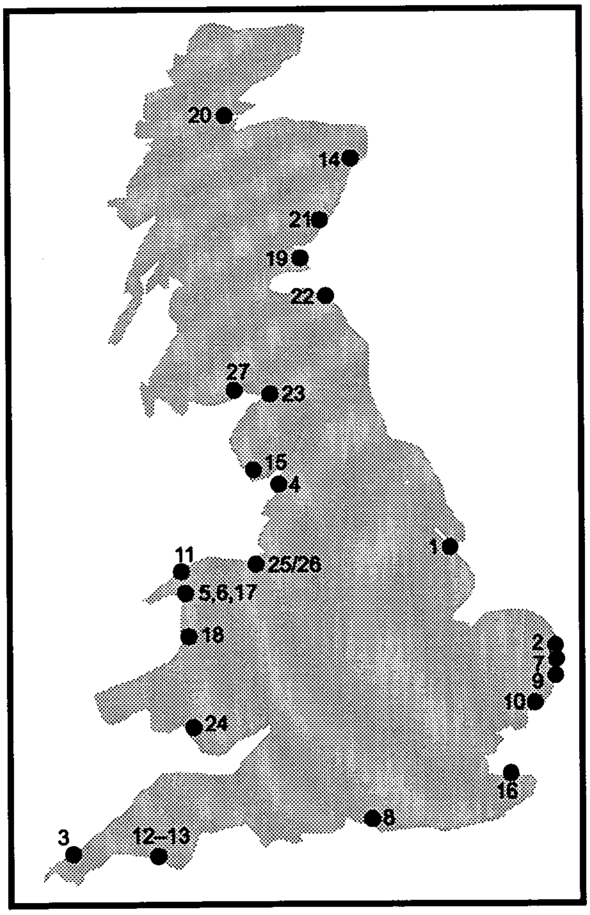

Figure 1. The 27 sites surveyed at low tide during the 1993–94 and 1994–95 winters. 1 Humber, 2 Breydon Water, 3 Hayle, 4 Eden, 5 Glaslyn/Dwyryd, 6 Artro, 7 Blyth, 8 Pagham, 9 Alde, 10 Deben, 11 Foryd Bay, 12/13 Plym/Tamar, 14 Ythan, 15 Duddon, 16 Swale, 17 Mawddach, 18 Dyfi, 19 Eden, 20 Cromarty Firth,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

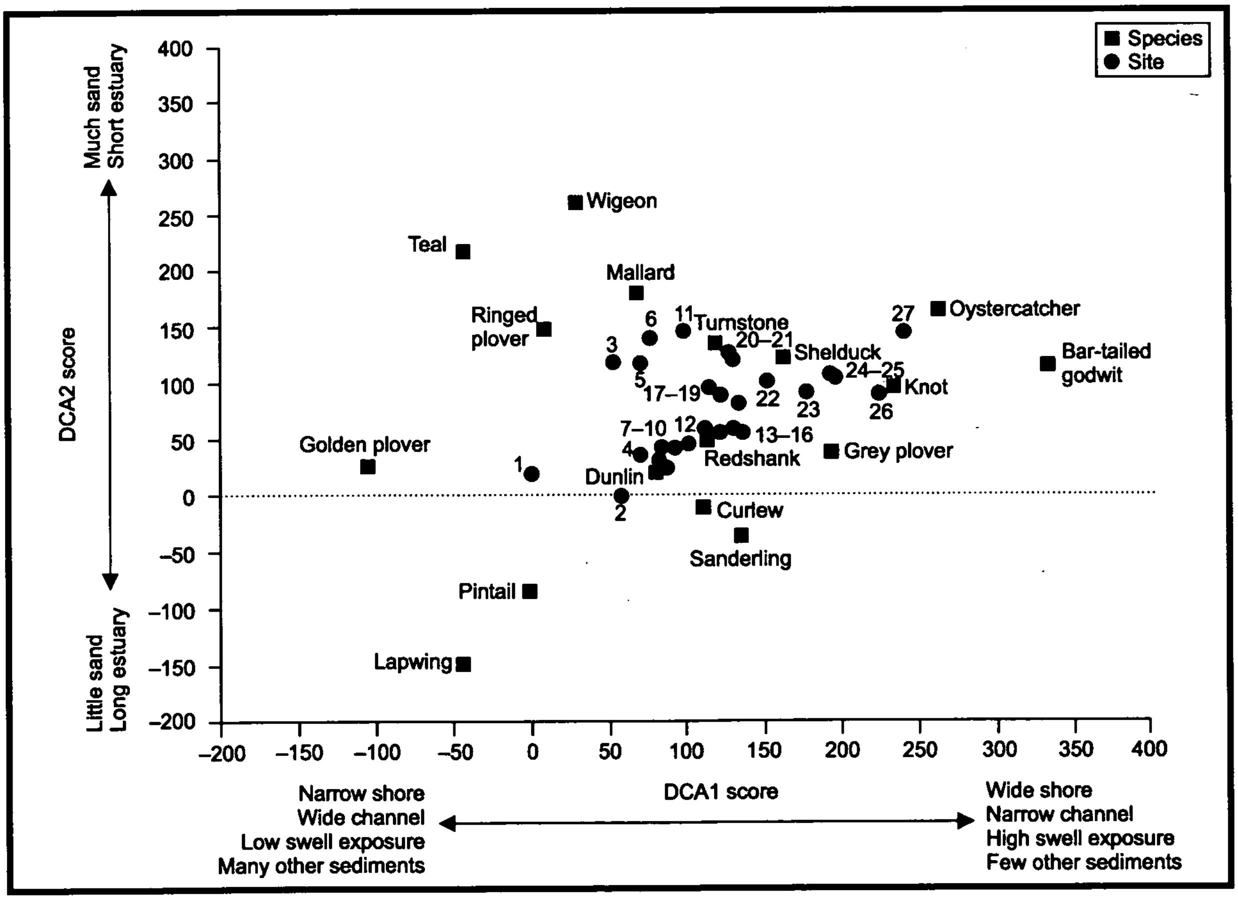

Figure 2. DCA ordination of the waterfowl data from the 27 sites, numbered as in Figure 1. The variables by the axes help explain the site waterfowl communities

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≥0.05 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

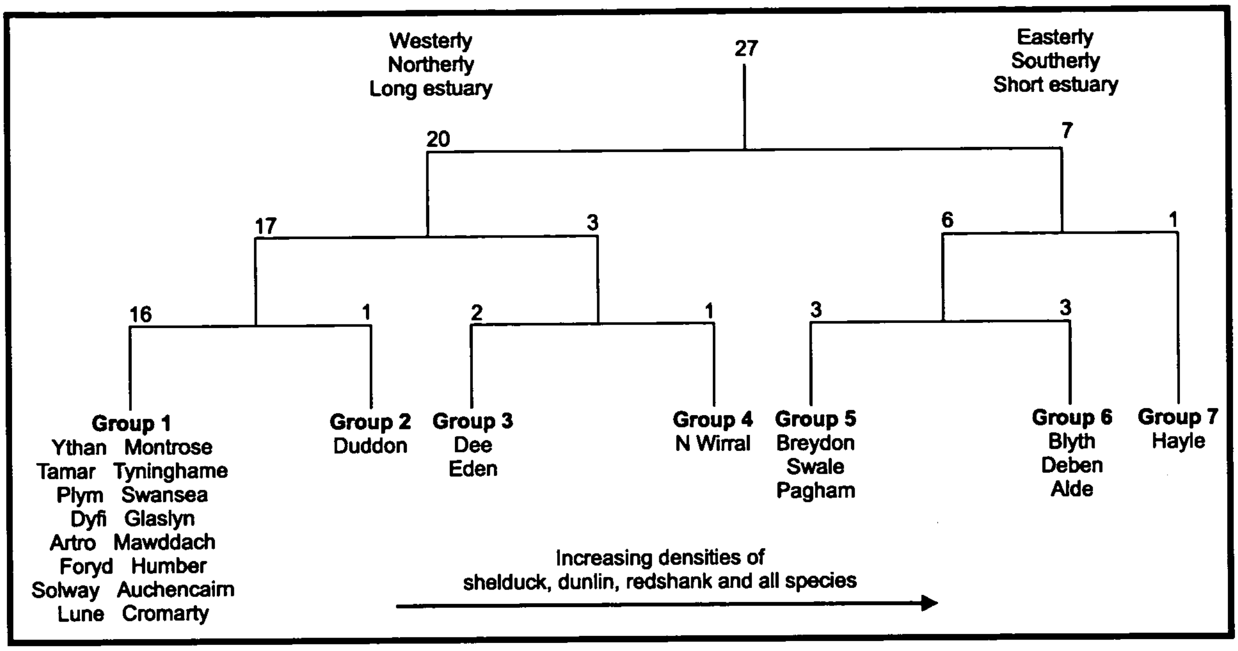

Figure 3. TWINSPAN dendrogram showing the site hierarchical classification on the basis of their wader communities. The variables at the top of the Figure help explain the first division. The arrow at the base of the dendrogram indicates the direction of the species' gradients across the final seven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

ACKNOWLEDGEMENTS

This research was funded by the Department of Trade and Industry, under contract to the Energy Technology Support Unit (ETSU Project T/04/00206, BTO Project ETSU08) and completed under Agreement no. T/04/

00206/00/00 between UKAEA (ETSU) and the British Trust for Ornithology. Nick Cutts, Dr Malcolm Joslin and British Petroleum (Saltend) kindly made some low-tide waterfowl counts and maps available to us for part of the Humber estuary. The project would not have been possible without the dedication of the many BTO volunteer low-tide count organisers and counters who carried out the mapping and counting of waterfowl on their estuaries over two winters. Rui Rufino and Rob Fuller commented usefully on the manuscript.

REFERENCES

Austin, G., Rehfisch, M.M., Holloway, S.J., Clark, N.A., Balmer, D.E., Yates, M.G., Clarke, R.T., Swetnam, R.D., Eastwood, J.A., Durell, S.E.A. le V. dit, West, J.R. & Goss-Custard, J.D. 1996. *Estuary, sediments and shorebirds III. Predicting waterfowl densities on intertidal areas.* (BTO Research Report no. 160.) Thetford: British Trust for Ornithology.

Cayford, J. & Waters, R. 1996. Population estimates for waders (Charadrii) wintering in Great Britain, 1987/88 – 1991/92. *Biological Conservation*, **77**, 7–17.

Cresswell, W. 1994. Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology*, **63**, 589–600.

Davidson, N.C. & Evans, P.R. 1986. The role of man-made and man-modified wetlands in the enhancement of the survival of overwintering shorebirds. *Colonial Waterbirds*, **9**, 176–188.

Davidson, N.C. & Rothwell, P.I. 1993. Disturbance to waterfowl on estuaries. *Wader Study Group Bulletin*, **68**, Special Issue.

Davidson, N.C., Laffoley, D. d'A., Doody, J.P., Way, L.S., Key, R., Drake, C.M., Pienkowski, M.W., Mitchell, R. & Duff, K.L. 1991. *Nature conservation and estuaries in Great Britain.* Peterborough: Nature Conservancy Council.

Fretwell, S.D. & Lucas, H.L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16–36.

Goss-Custard, J. 1977. The ecology of the Wash 3. Density related behaviour and the possible effects of the loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology*, **14**, 721–739.

Goss-Custard, J.D. & Yates, M.G. 1992. Towards predicting the effect of salt-marsh reclamation on feeding bird numbers on the Wash. *Journal of Applied Ecology*, **29**, 330–340.

Goss-Custard, J.D., Jones, R.E. & Newberry, P.E. 1977. The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology*, **14**, 681–700.

Goss-Custard, J.D., Warwick, R.M., Kirby, R., McGrorty, S., Clarke, R.T., Pearson, B., Rispin, W.E., Durell, S.E.A. le V. dit & Rose, R.J. 1991. Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn Estuary. *Journal of Applied Ecology*, **28**, 1004–1026.

Goss-Custard, J.D., Clarke, R.T., Briggs, K.B., Ens, B.J., Exo, K-M., Smit, C., Beintema, A.J., Caldow, R.W.G., Catt, D.C., Clark, N.A., Durell, S.E.A. le V. dit, Harris, M.P., Hulscher, J.B., Meininger, P.L., Picozzi, N., Prŷs-Jones, R., Safriel, U.N. & West, A.D. 1995a. Population consequences of winter habitat loss in a migratory shorebird. I. Estimating model parameters. *Journal of Applied Ecology*, **32**, 320–336.

Goss-Custard, J.D., Clarke, R.T., Caldow, R.W.G., Durell, S.E.A. le V. dit & Ens, B.J. 1995b. Population consequences of winter habitat loss in a migratory shorebird. II. Model predictions. *Journal of Applied Ecology*, **32**, 337–351.

Hill, D., Rushton, S.P., Clark, N., Green, P. & Prŷs-Jones, R.P. 1993. Shorebird communities on British estuaries: factors affecting community composition. *Journal of Applied Ecology*, **30**, 220–234.

Hill, M.O. 1979a. *DECORANA. A Fortran program for detrended correspondence analysis and reciprocal averaging.* New York: Cornell University, Ithaca.

Hill, M.O. 1979b. *TWINSPAN. A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* New York: Cornell University, Ithaca.

Holloway, S.J., Rehfisch, M.M., Clark, N.A., Balmer, D.E., Austin, G., Yates, M.G., Clarke, R.T., Swetnam, R.D., Eastwood, J.A., Durell, S.E.A. le V. dit, Goss-Custard, J.D. & West, J.R. 1996. *Estuary, sediments and shorebirds II. Shorebird usage of intertidal areas.* (BTO Research Report no. 156.) Thetford: British Trust for Ornithology.

James, M. 1985. *Classification algorithms.* London: Collins.

Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. 1995. *Data analysis in community and landscape ecology.* Cambridge: Cambridge University Press.

Kirby, J. 1995. Winter population estimates for selected waterfowl species in Great Britain. *Biological Conservation*, **73**, 189–198.

McCulloch, M.N. & Clark, N.A. 1991. *Habitat utilisation by dunlin on British estuaries.* (BTO Research Report no. 86.) Thetford: British Trust for Ornithology.

Myers, J.P., Williams, S.L. & Pitelka, F.A. 1980. An experimental analysis of prey availability for sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. *Canadian Journal of Zoology*, **58**, 1564–1574.

Newton, I. & Dale, L. 1996. Relationship between migration and latitude among west European birds. *Journal of Animal Ecology*, **65**, 137–146.

Piersma, T. 1994. *Close to the edge: energetic bottlenecks and the evolution of migratory pathways in knots.* PhD thesis, Rijksuniversiteit Groningen.

Prater, A.J. 1981. *Estuary birds of Britain and Ireland.* Calton: Poyser.

Quammen, M.L. 1982. Influence of subtle substrate differences on feeding by shorebirds on intertidal mudflats. *Marine Biology,* **71**, 339–343.

Rehfisch, M.M. 1994. Man-made lagoons and how their attractiveness to waders might be increased by manipulating the biomass of an insect benthos. *Journal of Applied Ecology,* **31**, 383–401.

Rehfisch, M.M., Clark, N.A., Langston, R.H.W. & Greenwood, J.J.D. 1996. A guide to the provision of refuges for waders: an analysis of thirty years of ringing data from the Wash, England. *Journal of Applied Ecology,* **33**, 673–687.

SAS Institute Inc. 1989. *SAS/STAT user's guide, version 6, fourth edition, vols 1–2.* Cary, NC: SAS Institute Inc.

Thompson, P.S. & Hale, W.G. 1993. Adult breeding survival and numbers in a coastal breeding population of redshank *Tringa totanus* in northwest England. *Ibis,* **135**, 61–69.

United Kingdom Climate Change Impacts Review Group. 1996. *Review of the potential effects of climate change in the United Kingdom.* (Second report to the Department of the Environment.) London: HMSO.

Watkinson, A.R. & Sutherland, W.J. 1995. Sources, sinks and pseudo-sinks. *Journal of Animal Ecology,* **64**, 126–130.

Yates, M.G., Goss-Custard, J.D., McGrorty, S., Lakhani, K.H., Durell, S.E.A. le V. dit, Clarke, R.T., Rispin, W.E., Moy, I., Yates, T., Plant, R.A. & Frost, A.E. 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *Journal of Applied Ecology,* **30**, 599–614.

Yates, M.G., Clarke, R.T., Swetnam, R.D., Eastwood, J.A., Durell, S.E.A. le V. dit, West, J.R., Goss-Custard, J.D., Clark, N.A., Holloway, S.J. & Rehfisch, M.M. 1996. *Estuary, sediments and shorebirds I. Determinants of the intertidal sediments of estuaries.* (Natural Environment Research Council contract report to the Energy Technology Support Unit.) Huntingdon: Institute of Terrestrial Ecology.

Loss and change of habitat and possible effects on mallard populations of Mondego and Vouga river basins

D Rodrigues & A Fabião

Departamento de Engenharia Florestal, Instituto Superior de Agronomia, Tapada da Ajuda, P-1399 Lisboa Codex, Portugal

SUMMARY

The present mallard habitat loss and change in Mondego and Vouga river basins are mainly the result of modern agriculture and intensive fish rearing. As a result of a loss of refuge areas, that were also important for moulting and breeding, we have recorded a decline in the local mallard population numbers from 1000 to 50 individuals, as well as significant decreases in the weight and body condition indices of adult birds, with an average weight loss of more than 100 g being observed. The modernisation of agricultural practices in the Mondego lowland rice fields induced the concentration of mallard populations in old rice fields, leading in an extreme situation to there being more than 1600 birds in a 20 ha rice field. The change in habitat caused by the modernisation of rice fields caused a decline of approximately 75% in the number of birds shot by hunters.

INTRODUCTION

The mallard (*Anas platyrhynchos*) is the most abundant resident duck in Portugal (Rufino 1989b). The species shows high adaptability to different types of wetlands, including those created by or related to human activities, and is also tolerant of human disturbance. The mallard is also very much appreciated as a quarry species.

Recent research in the Mondego and Vouga river basins concluded that there is only one mallard population in the area; although two different subpopulations may be associated with each river basin, there are very frequent movements between them. This interchange may be linked to the different proportions of suitable habitats in each river basin; the Vouga has more than 20 000 ha of estuary, saltmarsh and fish ponds, but only about 300 ha of rice fields, whereas the Mondego lowlands have only 400 ha of estuary, freshwater marsh and fish ponds but approximately 6800 ha of rice fields.

The mallard population of Vouga and Mondego lowlands is resident, but a small immigration of migrants may occur, especially during winter. The number of immigrants is estimated at less than 10% of the total winter population (D Rodrigues, unpublished).

The habitat requirements of mallard change through the year. During the shooting season (15 August–31 January), distinct feeding grounds and refuge areas can usually be recognised. Feeding occurs mostly in rice fields and saltmarshes. The refuge areas are mainly man-made habitats, such as abandoned rice fields which have turned into marshes (eg Arzila, Taipal and Madriz marshes, in Mondego lowlands) and small lakes especially created as waterfowl refuges (eg the duck pond in S Jacinto Natural Reserve and Braças Lagoon). Ponds that were used for extensive fish culture and left abandoned are preferred by mallards during breeding and moulting.

THE EFFECT OF THE LOSS OF REFUGE AREAS ON THE MALLARD POPULATION

The mallard population was monitored in a national hunting reserve in the Mondego lowlands, consisting of a feeding area with irrigated crops, mainly rice (Quinta do Canal, 276.5 ha), and a refuge area with abandoned salt-pans and fish ponds, used by wildfowl for resting, nesting and moulting (Ínsua, 50 ha). The Ínsua was destroyed by drainage in the winter 1991–92.

A census conducted two days before the first hunt in 1991 estimated the mallard population to be 1000 birds. Shooting

Table 1. Mallard biometrics in 1991, 1992 and 1994. The values represent the mean ± standard deviation. The values of the same parameter followed by different characters were significantly different from each other ($\alpha<0.05$). The values in brackets correspond to a single observation and were not compared

Parameter	Males Juvenile	Adult	Females Juvenile	Adult
1991				
Number of observations	68	38	67	29
Weight (g)	1105±72a	1242±56b	975±68c	1070±64d
Wing length (mm)	268±12a	275±8b	255±11c	259±11d
Body condition (g mm^{-1})	4.13±0.32a	4.52±0.23b	3.83±0.29c	4.14±0.23d
1992				
Number of observations	40	23	46	21
Weight (g)	1020±14e	1092±8f	908±9g	954±10h
Wing length (mm)	270±1e	277±9b	254±12c	256±1d
Body condition (g mm^{-1})	3.77±0.42e	3.95±0.30f	3.57±0.34g	3.72±0.38h
1994				
Number of observations	34	5	34	1
Weight (g)	1025±9e	1118±4f	926±8g	(980)
Wing length (mm)	276±1i	284±0.4b	260±1k	(270)
Body condition (g mm^{-1})	3.71±0.27e	3.94±0.18f	3.56±0.29g	(3.63)

occurred in the rice fields twice during late August, from 0600 to 1200 hours, in 1991, 1992, and 1994. The shot birds were sexed and aged, following Office National de la Chasse (1989) and Gatti (1983), weighed to the nearest 2 g, and the flattened wing measured, according to the methodology described by Svensson (1975). The body condition – the fitness of a bird to cope with its present and future needs (Owen & Cook 1977) – was assessed by the ratio between body weight and wing length. One- and two-way ANOVA were used to compare biometric parameters within sex and age classes, and also between years.

The results from biometric measurements of birds shot in 1991, 1992 and 1994 are summarised in Table 1. The decreases in weight and body condition index from 1991 to 1992 were very significant ($P<0.01$) for all sexes and age classes, but those from 1992 to 1994 were not ($P>0.05$). The significant decrease seems to have been associated with the destruction of the Ínsua refuge area; because the new refuge areas are located 13 km further from the feeding grounds, the higher energy costs of travelling may have caused the loss in body mass.

THE EFFECT OF HABITAT CHANGES ON THE MALLARD POPULATION

There are approximately 6800 ha of rice fields in the Mondego lowlands and three main refuge areas – Madriz, Taipal and Arzila marshes, with a total area of about 200 ha. These consist of old abandoned rice fields that have turned into freshwater marshes, with dense areas of plant cover dominated by common reed (*Phragmites australis*) and common bull-rush (*Scirpus lacustris*), and small areas of free water without submerged vegetation apart from milfoil (*Myriophyllum aquaticum*). The number of mallards shot in 1993–96 on all hunting days from 15 August to 15 September – during which time most of the mallard deaths from shooting occur – was counted. We consider this to provide good estimates of the total number of mallards shot during these periods. In early August 1995, before the shooting season began, the total number of mallards in all the Mondego rice fields was estimated from direct counts.

In the most important shooting area, the Foja farm, the number of birds shot within the study period decreased from 316 in 1993 to 87 in 1996. In other areas, similar decreases were observed: from 61 to 6 in Vila Nova de Anços, 95 to 23 in Samuel, and 30 to 2 in Abrunheira. The latter was particularly interesting, because the decrease from 1993 to 1994, following the levelling of all old rice fields (60 ha), was from 30 to 7 shot birds. A similar trend was observed at Foja from 1995 to 1996, following the levelling of the last 20 ha of old rice fields: the number of birds shot within the observation period decreased from 179 to 87. Moreover, in the early August morning counts of all Mondego rice fields in 1995, 1600 of the 1800 birds counted stayed in the last 20 ha of rice fields in the Foja shooting club area that had not yet been levelled.

These findings suggest that the modernisation of rice fields impoverishes the areas as mallard habitats. This impoverishment could be related to the loss of heterogeneity within the rice areas. Old rice fields are more variable in water depth and also vegetation cover because they have more weeds and variable plant density and there is free water in the middle. This results in more diversified food items (including temporal availability) and better shelter. The results obtained through the regular January counts (Rufino 1988, 1989a, 1990, 1991, 1992; Costa & Serra Guedes 1994) and our own counts starting in January 1993 also suggest a relatively regular decrease in mallard numbers after 1991. However, modernisation of rice fields with LASER levelling reached its peak during 1994. It is not clear if the regulation and channelling of the Mondego main course had some influence on mallard numbers at the beginning of the decade, but the decrease in the total area of rice fields (8000 ha in 1991, 7400 in 1994, and 6800 in 1995) could be responsible for part of the decline in mallard numbers.

DISCUSSION AND MANAGEMENT IMPLICATIONS

The values obtained for mallard body condition before the destruction of the Ínsua refuge area were high (Folk, Hudec & Toufar 1966; Street 1975; Owen & Cook 1977; D Rodrigues, unpublished). Body weight and body condition may be related to the nature and quantity of food consumed, which is abundant in mature rice fields. Nevertheless, the roosting area in Ínsua, which was situated very close to the fields (less than 100 m), was very important during the moulting and breeding seasons as it provided an undisturbed place for nesting and resting and a high diversity of food items, specially invertebrates. The availability of animal food items provided access to the high-protein foods that are needed during breeding and moulting, but these disappeared after the destruction of Ínsua by drainage. As a consequence, adult birds showed a larger decrease in body weight and body condition than juveniles, indicating the importance of the refuge area during moulting (Table 1). This was particularly important as the other Mondego refuge areas had poor limnological conditions, being hypereutrophic and having high turbidity levels, with no submerged vegetation besides *Myriophyllum aquaticum* (a ditch rice field weed), and thus provided only small amounts of animal foods.

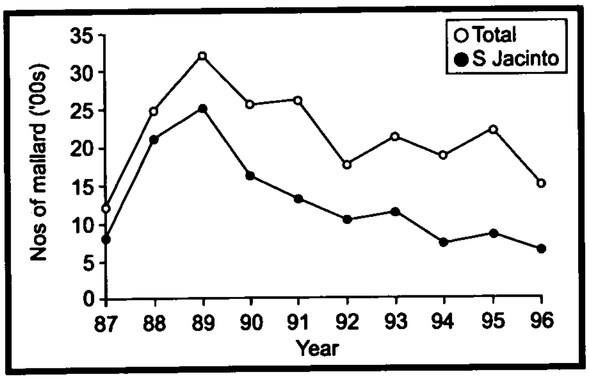

Figure 1. Results obtained in the January count of the total mallard population within the study area (S Jacinto, Braças Lagoon, Canal Farm, Taipal Marsh, Madriz Marsh and Arzila Marsh). The data for S Jacinto (Vouga basin) are also shown separately

The decrease in weight and body condition also probably reduced the survival rates and breeding success of the population (Heitmeyer & Frederickson 1990; Hepp *et al.* 1986; Street 1975; Whyte, Baldassarre & Bolen 1986). This is probably one of the reasons why the mallard counts from 1993–96 never reached the values of the 1988–91 counts (Figure 1). Local summer counts decreased from 1000 in 1991 to 50 in 1996, revealing a drastic reduction in the use of these rice fields as a summer feeding ground.

The counts of birds shot early in the hunting season, before the rice harvest and the arrival of the non-resident birds, clearly suggest a strong effect of the levelling of rice fields on the number of birds shot. The numbers in Figure 1 probably do not reveal all the effect of the modernisation of rice fields upon the mallard population. The January counts do not show the abundance of birds at the beginning of the shooting season because it is affected by shooting mortality; for example, a decrease in the number of birds shot early in the season increases the January counts, when the population is mainly resident.

Rice fields provide a very special aquatic environment, half-way between natural and full agro-ecosystems. They are shallow in depth, have small areas of open water, provide excellent shelter, where abundant vegetal and animal food may provide nutritionally as well as energetically favourable diets for mallards (Delnicki & Reinecke 1986; Pirot, Chessel & Tamisier 1984; Rodrigues & Ferreira 1993). However, a variety of areas of different characteristics may prove to be indispensable to provide the necessary diversity of diet and shelter conditions for breeding, moulting and resting. For the best management of mallard populations, both for shooting and conservation, a good balance between the availability of managed refuge and feeding areas is of the utmost importance.

ACKNOWLEDGEMENTS

The research work was funded by Junta Nacional de Investigação Científica e Tecnológica (JNICT), through a doctoral scholarship to David Rodrigues (Programs CIENCIA and PRAXIS XXI), by Project STRD/AGR/0038 (JNICT) and by the research line 7 (Freshwater Resources and Wetland Management) of Centro de Estudos Florestais. The authors also wish to acknowledge the co-operation of the Instituto da Conservação da Natureza (ICN) through the Coimbra co-ordination and through the Centro de Estudos de Protecção e Migração de Aves (CEMPA), as well as of the Instituto Florestal, through the Direcção de Serviços de Caça and the Delegação Florestal da Beira Litoral.

REFERENCES

Costa, L.T. & Serra Guedes, R. 1994. *Contagens de Anatídeos Invernantes em Portugal 1992/93.* (Estudos de Biologia e Conservação da Natureza 14.) Lisbon: ICN.

Delnicki, D. & Reinecke, K. 1986. Mid-winter food use and body weights of mallards and wood ducks in Mississippi. *Journal of Wildlife Management,* **50,** 43–51.

Folk, G., Hudec, K. & Toufar, J. 1966. The weight of the mallard, *Anas platyrhynchos* and its changes in the course of the year. *Zoologické Listy,* **15,** 249–260

Gatti, R.C. 1983. Spring and summer age separation techniques for the mallard. *Journal of Wildlife Management,* **47,** 1054–1062.

Heitmeyer, M.E. & Fredrickson, L.H. 1990. Fatty acid composition of wintering female mallards in relation to nutrient use. *Journal of Wildlife Management,* **54,** 54–61.

Hepp, G.R., Blohm, R.J., Reynolds, R.E., Hynes, J.E. & Nichols, J.D. 1986. Physiological condition of autumn-banded mallards and its relationship to hunting vulnerability. *Journal of Wildlife Management,* **50,** 177–183.

Office National de la Chasse. 1989. Le canard Colvert. *Bulhetin Mensuel de l'Office National de la Chasse,* **140,** *Notes Techniques, Fiche,* **60.**

Owen, M. & Cook, W.A. 1977. Variations in body weight, wing length and condition of mallard *Anas platyrhynchos platyrhynchos* and their relationship to environmental changes. *Journal of Zoology, London,* **183,** 377–395.

Pirot, J.Y., Chessel, D. & Tamisier, A. 1984. Exploitation alimentaire des zones humides de Camargue par cinq especes de canards de surface en hivernage et en transit: modelation spacio-temporelle. *Terre et Vie,* **39,** 167–192.

Rodrigues, D. & Ferreira, M.T. 1993. Summer food and body condition of mallards (*Anas platyrhynchos* L.) in River Mondego lowlands. *Doñana, Acta Vertebrata,* **20,** 87-94.

Rufino, R., compiler. 1988. *Contagens de aves aquáticas – Jan/Fev 1988.* Lisbon: CEMPA.

Rufino, R., compiler. 1989a. *Contagens de aves aquáticas – Jan/Fev 1989.* Lisbon: CEMPA.

Rufino, R., compiler. 1989b. *Atlas das aves que nidificam em Portugal continental.* Lisbon: SNPRCN.

Rufino, R., compiler. 1990. *Contagens de aves aquáticas –inverno 1987 e 1990.* Lisbon: CEMPA.

Rufino, R., compiler. 1991. *Contagens de aves aquáticas invernantes – Janeiro 1991.* (Estudos de Biologia e Conservação da Natureza 4.) Lisbon: SNPRCN.

Rufino, R., compiler. 1992. *Contagens de aves aquáticas invernantes – Janeiro 1992.* (Estudos de Biologia e Conservação da Natureza 12.) Lisbon: SNPRCN.

Street, M. 1975. Seasonal changes in the diet, body weight and condition of fledged mallard (*Anas plathyrhynchos plathyrhynchos* L.) in eastern England. *Proceedings of the XII Congress of the International Union of Game Biologists,* 339–347.

Svensson, L. 1975. *Identification guide to European passerines.* Stockholm: Svensson.

Whyte, R.J. & Bolen, E.G. 1985. Variation in mallard digestive organs during winter. *Journal of Wildlife Management,* **49,** 1037–1040.

Whyte, R.J., Baldassarre, B.A. & Bolen, E.G. 1986. Winter condition of mallards on the southern high plains of Texas. *Journal of Wildlife Management,* **50,** 52–57.

Were the effects of Nile perch introduction on Lake Victoria's birds predictable?

J H Wanink

Institute of Evolutionary and Ecological Sciences, Section Dynamic Morphology, University of Leiden, PO Box 9516, 2300 RA Leiden, The Netherlands

SUMMARY

Feeding habitats of Lake Victoria's birds changed after the introduction of Nile perch. Ecological research in the lake and in a comparable ecosystem could predict the main trends. Unforeseen life history tactics of prey fish and adaptive foraging behaviour of birds prohibited precise predictions of the changes and their effects on bird populations.

INTRODUCTION

The population level of any species is ultimately determined by the available resources within its habitat. Because food is a key resource, knowledge of the food supply is essential for predicting effects of habitat change. The food stocks of piscivorous birds have been studied relatively well, although mostly not by ornithologists. Fishery biologists commonly assess the impact of human perturbation, eg introducing alien species or overfishing local stocks.

Traditionally, fish were considered more as isolated natural renewable resources than as integral components of the aquatic ecosystem (Lévêque 1995). However, over the past decade, food web interactions were addressed in the application of trophic cascade theory to lakes (Carpenter & Kitchell 1993). According to this theory, changes at the top of the food web cascade downwards, acting by selective predation, through all trophic levels, to affect ecosystem processes. Although the theory was developed to analyse changes in lake productivity, it may also be used as a feedback model to predict the effects of the changes on top predators.

In this paper I summarise the changes in east African Lake Victoria after the introduction of the large predatory Nile perch (*Lates niloticus*). This perturbation at the top of the food web caused dramatic changes in the fish fauna and the extinction of many species (eg Ogutu-Ohwayo 1990b; Witte *et al.* 1992a, b). It affected the diet and foraging behaviour of otters (Kruuk & Goudswaard 1990) and fish-eating birds (Goudswaard & Wanink 1993; Wanink, Berger & Witte 1993; Wanink & Goudswaard 1994b; Wanink 1996a). I compare predicted habitat changes and their effects on birds with observations of what really happened, and I discuss the predictive power of the trophic cascade theory in this situation.

EFFECTS OF NILE PERCH INTRODUCTION ON THE FISH COMMUNITY

Predicted effects

Two ideas dominated the discussion which preceded the introduction of Nile perch. Supporters of the introduction assumed that the perch would exploit the species flock of small haplochromine cichlids (Anderson 1961), which comprised more than 80% of the lake's demersal fish biomass (Kudhongania & Cordone 1974). The opponents thought that haplochromines would be unprofitable prey and feared that Nile perch would select the larger, economically important, tilapiine cichlids (Fryer 1960). In contrast, the supporters predicted a positive effect on the tilapias, as a new fishery on the more offshore-living Nile perch would remove the pressure from the overfished populations (Anderson 1961). Both sides agreed in their view that the perch would deplete its prey stock.

About 25 years after its introduction, Nile perch had invaded most parts of the vast lake (69 000 km^2) and the population started to increase explosively. By then it was known that haplochromines were the principal prey

(Gee 1969; Okemwa 1981). An almost complete eradication of the stock, followed by a collapse of the Nile perch population, was predicted (Barel *et al.* 1985). Only zooplanktivorous haplochromines were expected to survive relatively well, because they spend part or all of their time away from the bottom, the habitat of Nile perch (Witte & Goudswaard 1985). The same was predicted for the small zooplanktivorous cyprinid dagaa (*Rastrineobola argentea*), which was supposed to be a permanent surface-dweller.

Observed effects

In the southern waters the explosive increase in Nile perch occurred between 1983 and 1985, while at the same time the haplochromines virtually disappeared from the sublittoral and offshore waters. Although most species from the shallow inshore waters survived, their numbers decreased (Barel *et al.* 1991; Witte *et al.* 1992a, b). As predicted, the zooplanktivores were the best-surviving haplochromines but also reduced to very low numbers (Wanink 1991; Seehausen & Witte 1995; Witte, Goldschmidt & Wanink 1995).

The predicted survival of dagaa was confirmed but considerable changes occurred in this species. Mean body size decreased by 18% while the population increased six-fold during the upsurge of Nile perch (Wanink 1991, 1997; Witte *et al.* 1992a). Some years later, when most fishermen targeted Nile perch, increased catches of Nile tilapia (*Oreochromis niloticus*) confirmed Anderson's (1961) prediction of released fishing pressure on the tilapias (Ligtvoet *et al.* 1995). Nile tilapia was introduced shortly before the Nile perch and eliminated three other introduced and two indigenous tilapias through competition and hybridisation (Ogutu-Ohwayo 1990b; Ligtvoet *et al.* 1995).

In addition to the rise of dagaa, an unforeseen increase of the prawn *Caridina nilotica* occurred after the disappearance of the haplochromines (Goldschmidt, Witte & Wanink 1993). Nile perch switched to *Caridina*, dagaa and their own juveniles, and the availability of these alternative prey prevented the predicted collapse of the predator (Mkumbo & Ligtvoet 1992).

WERE THE CHANGES IN THE FISH COMMUNITY PREDICTABLE?

Investigating a comparable ecosystem

Pilot introductions of Nile perch were done in the Ugandan lakes Nabugabo and Kyoga, which had a comparable fish fauna to the much larger Lake Victoria, although less speciose (Ogutu-Ohwayo 1995). Research in these lakes should have provided the base for a sound decision on the proposed introduction in Lake Victoria, but the validity of this comparative method was debated (Fryer 1960; Anderson 1961). Unfortunately, Nile perch found its way into Lake Victoria before the pilot studies showed results, and additional stocking was done after its presence was determined.

Data from lakes Nabugabo and Kyoga reveal that the comparative method would have adequately predicted the main changes in Lake Victoria's fish community. In both lakes haplochromines were reduced by Nile perch, while dagaa and Nile tilapia managed to coexist with the predator (Ogutu-Ohwayo 1990a, 1995).

Research in Lake Victoria

Relative survival of prey species may be estimated from their habitat overlap with predators. However, the knowledge that the habitat of relatively offshore-living Nile perch overlapped more with most haplochromines than with the tilapias was not used in the debate on the proposed introduction (Anderson 1961). In later years stomach analysis confirmed that Nile perch rarely take Nile tilapia at Lake Victoria (Mkumbo & Ligtvoet 1992). A positive relationship exists between tilapia size and distance from shore. The large tilapias which occupy Nile perch habitat can only be ingested by the less abundant large individuals.

A relatively high survival of zooplanktivorous cichlids and dagaa was predicted from their vertical distribution, which differed from that of Nile perch. Although this prediction was confirmed, its assumptions could not explain the difference between the eventually disappearing cichlids and thriving dagaa. Dagaa was not such a strict surface-dweller as supposed, so its habitat overlapped more with Nile perch than expected (Wanink

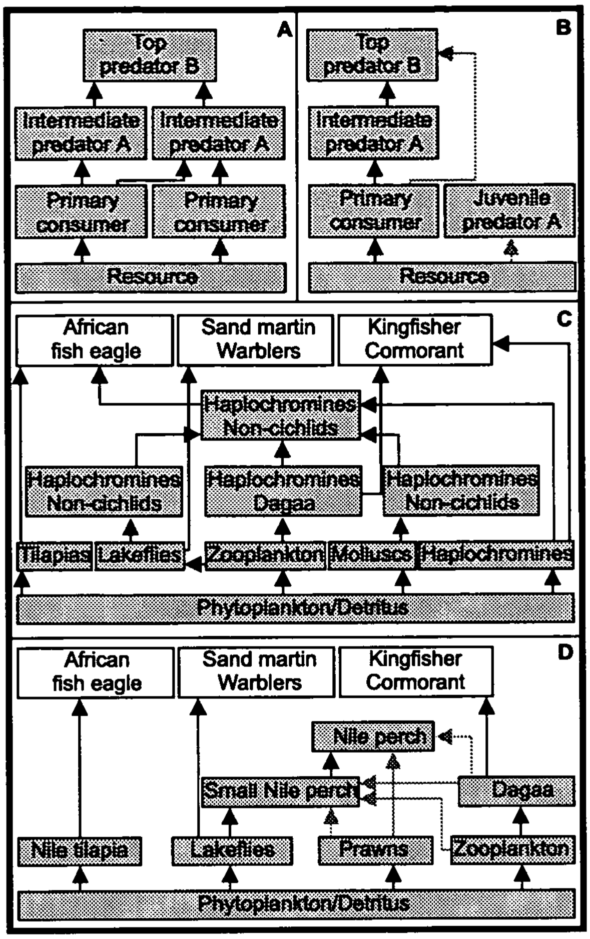

Figure 1. Two hypothetical food webs without (A) and with (B) intraguild predation (IGP) and two simplified food webs of Lake Victoria, showing the key taxa before (C) and after (D) the Nile perch boom. IGP links are indicated by grey arrows. A and B modified after Polis and Holt (1992); C and D modified after Ligtvoet and Witte (1991)

1992). There are indications, however, that dagaa started to use the bottom area after the decline of the cichlids. This habitat shift supports the hypothesis that dagaa benefited from reduced competition with cichlids (Wanink 1991).

Another explanation for the different survival of cichlids and dagaa was found in their reproductive strategies (Wanink 1991). The cichlids were K-selected mouth-breeders, producing far less eggs than r-selected dagaa, so theoretically dagaa should survive better. Some cichlid zooplanktivores showed a small increase in egg numbers, which was probably limited by the size of their buccal cavity. In contrast, the average fecundity of dagaa decreased by 50% as a result of their size reduction and an unchanged positive relationship between body length and egg number. Nevertheless, the average egg number in dagaa (1100) remained much higher than that in the cichlids (40–60). Reduced predation on juvenile dagaa after the Nile perch boom enabled more fish to reach maturity (Wanink *et al.* 1993; Wanink, Goudswaard & Berger 1997). As predicted by life history theory, dagaa reacted to the shift from juvenile to adult mortality by maturing at a smaller size. Combined with an increased growth rate, this strongly reduced the generation time and was probably the most important cause of the population increase in dagaa (Wanink 1996b).

EFFECTS OF CHANGES IN THE FISH COMMUNITY ON PISCIVOROUS BIRDS

Predicted effects

Diet changes were predicted for some common avian piscivores (Goudswaard & Wanink 1993). Great cormorant (*Phalacrocorax carbo lucidus*) and pied kingfisher (*Ceryle rudis*), which took mainly haplochromines, were expected to switch to dagaa. A less-pronounced increase of dagaa was expected in the diet of long-tailed cormorant (*P. africanus*), as it hunted in the least-affected inshore areas. The African fish eagle (*Haliaeetus vocifer*) was expected to switch to Nile tilapia, because its traditional prey – the indigenous tilapias, catfishes (mainly *Clarias gariepinus*) and the lungfish (*Protopterus aethiopicus*) – was reduced to very low numbers.

Switching to energetically poor dagaa would force great cormorant and pied kingfisher to increase their daily catches considerably (Goudswaard & Wanink 1993; Wanink & Goudswaard 1994b). The strongest effect was expected in pied kingfisher, which exploits the surface layer where mainly juvenile dagaa and parasitised adults occur during day-time (Wanink 1992). Only a small effect was expected for long-tailed cormorant, while the abundance and size of Nile tilapia might even have improved the feeding conditions for the fish eagle (Goudswaard & Wanink 1993). Consequently, negative effects of Nile perch introduction on bird populations were expected only in great cormorant and pied kingfisher.

Observed effects

Dagaa increased according to the predictions in the diet of cormorants and kingfishers (Goudswaard & Wanink 1993; Wanink & Goudswaard 1994b). A few observations on foraging fish eagles support the idea that they switched to Nile tilapia. They were only seen taking dead Nile perch floating at the surface.

There are not enough data to compare the daily catches of cormorants and kingfishers before and after the Nile perch boom. However, the birds adapted to the reduced food supply by changing their foraging behaviour and becoming very size-selective. Great cormorant used to take surface-dwelling cichlids at 2–3 km from shore but hunted dagaa near the bottom at about 500 m from shore after the Nile perch boom. The inshore movement was probably a trade-off between the birds' diving limits and the size of dagaa (Goudswaard & Wanink 1993; Wanink 1996a). They selected the largest size classes from the available range (Wanink & Goudswaard 1994a). Pied kingfisher fed as far as 3 km offshore after the Nile perch boom, while they stayed within 750 m before (Wanink *et al.* 1993). Concentrating their efforts in the hours before sunset, when large dagaa move towards the surface, kingfishers took larger sizes than expected (Wanink & Goudswaard 1994a; Wanink *et al.* 1997).

Population levels of great cormorant and pied kingfisher around Mwanza remained stable between 1982 and 1990 (Goudswaard & Wanink 1993). The value of 3600 great cormorants estimated for this period is close to the 3300 birds counted in 1995 (Dodman & Taylor 1995). No data are available for population trends in long-tailed cormorant and African fish eagle, although the number of more than 1000 eagles counted around the lake in 1995 was regarded as high (Dodman & Taylor 1995).

WERE THE EFFECTS ON THE BIRDS PREDICTABLE?

The trophic cascade theory

Trophic cascade theory predicts that an increase in piscivores causes a decrease in zooplanktivores, followed by an increase in zooplankton and a decrease in phytoplankton (Carpenter & Kitchell 1993). According to this prediction, not only zooplanktivores but also phytoplankton should have decreased. The increased visibility would enhance the hunting success of cormorants and kingfishers. In reality, however; a strong increase in phytoplankton reduced the water transparency significantly (Witte *et al.* 1992a).

Looking at the complex food web in Lake Victoria, it is not surprising that the changes did not agree with trophic cascade theory, which applies to simply structured systems (Figure 1 – A). Polis and Holt (1992) showed how intraguild predation (IGP) – the killing and eating of species that use similar resources and are thus potential competitors – may change the prediction. If a top predator takes primary consumers (herbivores) in addition to intermediate predators, the relative strengths of both links determine whether the resource (phytoplankton) will increase or decrease (Figure 1 – B). Before the Nile perch boom, no strong IGP links existed in Lake Victoria (Figure 1 – C). The appearance of Nile perch changed the situation completely. Nile perch originally fed on most trophic groups from the haplochromine of the food web shown in Figure 1 – C, thus creating many IGP links. Because of their abundance and habitat overlap with Nile perch, the haplochromine detriti-/phytoplanktivores probably supported the strongest IGP link (Witte *et al.* 1992b). This would explain the increase in detritus and phytoplankton. After the collapse of the haplochromines the food web was simplified, although the existence of new IGP links makes predictions of future changes complicated (Figure 1 – D).

The term 'lakefly' is used for chaoborid and chironomid midges. Before the Nile perch boom, zooplanktivorous chaoborids dominated (Figure 1 – C) while afterwards detritivorous chironomids were most abundant (Figure 1 – D). Lakeflies increased massively after the disappearance of the insectivorous fish (Witte *et al.* 1995). This increase is supposed to have caused a strong increase in wintering Palearctic sand martins (*Riparia riparia*) (A P Møller in Sutherland 1992). However, the availability of swarming lakeflies is unpredictable and lasts for a few days per month, while in former years only a small fraction of the massive clouds could be exploited before the flies decayed. Although it seems unlikely that lakeflies can support Palearctic migrants throughout their stay, the occurrence of swarms may trigger their spring departure. Warblers rapidly reach the necessary weight for long-distance flights during lakefly swarming.

A multidisciplinary approach

The trophic cascade approach is only useful when multidisciplinary research is conducted at all levels of the food web. Life history theory was needed in addition to data on spatial distribution to explain the different survival of cichlids and dagaa. Studying foraging behaviour was necessary to account for adaptive strategies of birds to cope with the reduction in food supply. The comparative method could have predicted offshore feeding in pied kingfisher after the rise of dagaa, as kingfishers started to hunt offshore at Lake Kariba (Zimbabwe) after the successful introduction of a pelagic clupeid which resembles dagaa (Junor 1972). Reduced transparency has probably caused lower hunting success of the birds. It might even lead to a shift from solitary to more rewarding social fishing in cormorants, as was recently observed in the European cormorant (*Phalacrocorax carbo sinensis*) under deteriorating visibility conditions (Van Eerden & Voslamber 1995). Although for simplicity human fishers are not shown in the food web diagram, their impact should be estimated. The developing fisheries for Nile perch and dagaa had a positive effect on the feeding, scavenging and roosting opportunities for several bird species (Goudswaard & Wanink 1993).

Although only few were predicted, most Nile perch effects on individual birds could be explained afterwards by research on the prey species. This research did not make it clear, however, whether or not the adaptive foraging behaviour of great cormorant and pied kingfisher could account for their unchanged population levels. It has been suggested that nesting opportunities for these species may be more limiting than food (Goudswaard & Wanink 1993). Changes in the breeding behaviour of pied kingfisher can also not be ruled out, as this species can increase the number of helpers at the nest under difficult circumstances (Reyer 1980).

CONCLUSIONS

Comparative studies of prey can to some extent predict habitat changes after human perturbation and their effects on individual wetland birds. Multidisciplinary research is needed for predicting population dynamics. To date, most effects of habitat change can only be explained afterwards.

ACKNOWLEDGEMENTS

The work was financed by The Netherlands Foundation for the Advancement of Tropical Research (WOTRO; grant W 87–189) and the section for Research and Technology of The Netherlands Minister of Development Cooperation for funding. The Mwanza Centre of the Tanzania Fisheries Research Institute (TAFIRI) is thanked for help and hospitality during the field work. Comments by Frans Witte improved the manuscript.

REFERENCES

Anderson, A.M. 1961. Further observations concerning the proposed introduction of Nile perch into Lake Victoria. *East African Journal of Agriculture,* **26,** 195–201.

Barel, C.D.N., Dorit, R., Greenwood, P.H., Fryer, G., Hughes, N., Jackson, P.B.N., Kawanabe, H., Lowe-McConnel, R.H., Witte, F. & Yamaoka, K. 1985. Destruction of fisheries in Africa's lakes. *Nature,* **315,** 19–20.

Barel, C.D.N., Ligtvoet, W., Goldschmidt, T., Witte, F. & Goudswaard, P.C. 1991. The haplochromine cichlids of Lake Victoria: an assessment of biological and fisheries interest. In: *Cichlid fishes, behaviour, ecology and evolution,* edited by M.H.A. Keenleyside, 258–279. London: Chapman & Hall.

Carpenter, S.R. & Kitchell, J.F., eds. 1993. *The trophic cascade in lakes.* Cambridge: Cambridge University Press.

Dodman, T. & Taylor, V. 1995. *African waterfowl census 1995. Les dénombrements internationaux d'oiseaux d'eau en Afrique, 1995.* Slimbridge: International Waterfowl Research Bureau.

Fryer, G. 1960. Concerning the proposed introduction of Nile perch into Lake Victoria. *East African Journal of Agriculture,* **25,** 267–270.

Gee, J.M. 1969. A comparison of certain aspects of the biology of *Lates niloticus* (Linne) in some East African lakes. *Review of the Zoology and Botany of Africa,* **80,** 244–262.

Goldschmidt, T., Witte, F. & Wanink, J. 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology,* **7,** 686–700.

Goudswaard, P.C. & Wanink, J.H. 1993. Anthropogenic perturbation in Lake Victoria: effects of fish introductions and fisheries on fish eating birds. *Annales Musée Royal de l'Afrique Centrale (Zoologie),* **268,** 312–318.

Junor, F.J.R. 1972. Offshore fishing by the pied kingfisher *Ceryle rudis* at Lake Kariba. *Ostrich*, **43**, 185.

Kruuk, H. & Goudswaard, P.C. 1990. Effects of changes in fish populations in Lake Victoria on the food of otters (*Lutra maculicollis* Schinz and *Aonyx capensis* Lichtenstein). *African Journal of Ecology*, **28**, 322–329.

Kudhongania, A.W. & Cordone, A.J. 1974. Batho-spatial distribution patterns and biomass estimates of the major demersal fishes in Lake Victoria. *African Journal for Tropical Hydrobiology and Fisheries*, **3**, 15–31.

Lévêque, C. 1995. Role and consequences of fish diversity in the functioning of African freshwater ecosystems: a review. *Aquatic Living Resources*, **8**, 59–78.

Ligtvoet, W. & Witte, F. 1991. Perturbation through predator introduction: effects on the food web and fish yields in Lake Victoria (East Africa). In: *Terrestrial and aquatic ecosystems: perturbation and recovery*, edited by O. Ravera, 263–268. Chichester: Ellis Horwood.

Ligtvoet, W., Mous, P.J., Mkumbo, O.C., Budeba, Y.L., Goudswaard, P.C., Katunzi, E.F.B., Temu, M.M., Wanink, J.H. & Witte, F. 1995. The Lake Victoria fish stocks and fisheries. In: *Fish stocks and fisheries of Lake Victoria: a handbook for field observations*, edited by F. Witte & W.L.T. van Densen, 11–53. Cardigan: Samara Publishing Limited.

Mkumbo, O.C. & Ligtvoet, W. 1992. Changes in the diet of Nile perch, *Lates niloticus* (L.), in the Mwanza Gulf, Lake Victoria. *Hydrobiologia*, **232**, 79–83.

Ogutu-Ohwayo, R. 1990a. Changes in the prey ingested and the variations in the Nile perch and other fish stocks of Lake Kyoga and the northern waters of Lake Victoria (Uganda). *Journal of Fish Biology*, **37**, 55–63.

Ogutu-Ohwayo, R. 1990b. The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus* and the Nile tilapia, *Oreochromis niloticus*. *Environmental Biology of Fishes*, **27**, 81–96.

Ogutu-Ohwayo, R. 1995. Diversity and stability of fish stocks in Lakes Victoria, Kyoga and Nabugabo after establishment of introduced species. In: *The impact of species changes in African lakes*, edited by T.J. Pitcher & P.J.B. Hart, 59–81. London: Chapman & Hall.

Okemwa, E.N. 1981. Changes in fish species composition of Nyanza Gulf of Lake Victoria. In: *Proceedings of the workshop of the Kenya Marine and Fisheries Research Institute on aquatic resources of Kenya*, 138–156. Mombasa: Kenya Marine and Fisheries Research Institute and Kenya National Academy for Advancement of Arts and Sciences.

Polis, G.A. & Holt, R.D. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution*, **7**, 151–154.

Reyer, H.-U. 1980. Flexible helper structure as an ecological adaptation in the pied kingfisher (*Ceryle rudis* L.). *Behavioral Ecology and Sociobiology*, **6**, 219–227.

Seehausen, O. & Witte, F. 1995. Extinction of many, survival of some. The current situation of the endemic cichlids in southern Lake Victoria. *Tropical Fish Hobbyist*, **43**, 96–105.

Sutherland, W.J. 1992. Genes map the migratory route. *Nature*, **360**, 625–626.

Van Eerden, M.R. & Voslamber, B. 1995. Mass fishing by cormorants *Phalacrocorax carbo sinensis* at lake IJsselmeer, The Netherlands: a recent and successful adaptation to a turbid environment. *Ardea*, **83**, 199–212.

Wanink, J.H. 1991. Survival in a perturbed environment: the effects of Nile perch introduction on the zooplanktivorous fish community of Lake Victoria. In: *Terrestrial and aquatic ecosystems: perturbation and recovery*, edited by O. Ravera, 269–275. Chichester: Ellis Horwood Limited.

Wanink, J.H. 1992. The pied kingfisher *Ceryle rudis* and dagaa *Rastrineobola argentea*: estimating the food-intake of a prudent predator. In: *Proceedings of the Seventh Pan-African Ornithological Congress*, edited by L. Bennun, 403–411. Nairobi: PAOCC.

Wanink, J.H. 1996a. Foraging locations of kingfishers and cormorants at Lake Victoria depend on the distribution of harvestable prey. *African Journal of Ecology*, **34**, 90–93.

Wanink, J.H. 1996b. The small pelagic *Rastrineobola argentea*: successful survivor in Lake Victoria. *Naga, the ICLARM Quarterly*, **19** (1), 48.

Wanink, J.H. 1997. Prospects for the fishery on the small pelagic *Rastrineobola argentea* in Lake Victoria. *Hydrobiologia*. In press.

Wanink, J.H. & Goudswaard, K. 1994a. Kingfishers, cormorants and man select different sizes of Lake Victoria sardine *Rastrineobola argentea*. *Journal für Ornithologie*, **135** (Supplement), 248.

Wanink, J.H. & Goudswaard, P.C. 1994b. Effects of Nile perch (*Lates niloticus*) introduction into Lake Victoria, East Africa, on the diet of pied kingfishers (*Ceryle rudis*). *Hydrobiologia*, **279/280**, 367–376.

Wanink, J.H., Berger, M.R. & Witte, F. 1993. Kingfishers at Fishburger Queens: eating Victorian fast food on the wing. *Annales Musée Royal de l'Afrique Centrale (Zoologie)*, **268**, 319–326.

Wanink, J.H., Goudswaard, P.C. & Berger, M.R. 1997. The sustainable role of the small pelagic cyprinid *Rastrineobola argentea* as a major resource in the ecosystem and the fishery of Lake Victoria. In: *Lacustrine fish communities in SE-Asia and Africa: ecology and exploitation*, edited by W.L.T. van Densen, R.H. Lowe-McConnell & M.J. Burgis. Cardigan: Samara Publishing. In press.

Witte, F. & Goudswaard, P.C. 1985. Aspects of the haplochromine fishery in southern Lake Victoria. *FAO Fishery Reports*, **335**, 81–88.

Witte, F., Goldschmidt, T. & Wanink, J.H. 1995. Dynamics of the haplochromine cichlid fauna and other ecological changes in the Mwanza Gulf of Lake Victoria. In: *The impact of species changes in African lakes,* edited by T.J. Pitcher & P.J.B. Hart, 83–110. London: Chapman & Hall.

Witte, F., Goldschmidt, T., Goudswaard, P.C., Ligtvoet, W., Van Oijen, M.J.P. & Wanink, J.H. 1992a. Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands Journal of Zoology,* **42,** 214–232.

Witte, F., Goldschmidt, T., Wanink, J., Van Oijen, M., Goudswaard, K., Witte-Maas, E. & Bouton, N. 1992b. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes,* **34,** 1–28.

The development of a correlative approach relating bird distribution and remotely sensed sediment distribution to predict the consequences to shorebirds of habitat change and loss

M G Yates[1] & J D Goss-Custard[2]
[1]*Institute of Terrestrial Ecology, Monks Wood, Abbots Ripton, Huntingdon PE17 2LS, UK*
[2]*Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset BH20 5AS, UK*

SUMMARY
The development of a model to predict the consequences to shorebirds (Charadrii) of habitat change and loss is described and discussed. The approach was based on two correlative relationships. The first related the distribution of shorebirds on their intertidal feeding areas to that of the sediments. The second related sediment distribution to those physical features of the estuary, such as shore width, which are directly influenced by natural or man-made change. In both relationships, the sediment distribution was determined by classifying remotely sensed images of the intertidal area.

INTRODUCTION

Each autumn, winter and spring, internationally important numbers of shorebirds (Charadrii) are dependent for their survival on the intertidal areas of Britain's estuaries where they feed on the benthic invertebrates. This paper describes and discusses the development of a methodology for predicting the numbers of shorebirds that would be affected by the change or loss of those intertidal feeding areas.

The study described here tested whether, in principle, it is possible to predict changes in bird numbers from physical features of intertidal areas, any change in which is usually predictable after habitat is lost or changed. First, the constancy of the bird's intertidal feeding areas between seasons and years was established, because it would be more difficult to devise a predictive methodology without some degree of constancy. Next, having tested the efficacy of using satellite images to map and quantify the distribution of intertidal surface sediments, the study then established that bird distribution in an area was related to the intertidal sediments. In turn, the sediments themselves could be related to physical features of the intertidal area so any change in those features had predictable consequences for the bird through their influence on the sediments.

THE FORM AND BIOLOGICAL BASIS OF THE METHODOLOGY

In the initial stages of its development, the aim of our work was to predict the consequence of change in a single physical variable, the shore width of intertidal areas of the Wash, east England, brought about by saltmarsh reclamation (Goss-Custard & Yates 1992). Ideally, this prediction would have been done using a dynamic approach in which the functional relationship for each of the links in the following causal chain would have been determined:

Shore width → sediment characteristics (particle size distribution and shore profile) → invertebrate densities → bird densities

The quantitative relationships between sediment characteristics, invertebrate densities and bird densities can be determined by field studies (Bryant 1979; Yates *et al.* 1993a). However, their use in predicting to the post-reclamation situation is problematical because the effects of shore

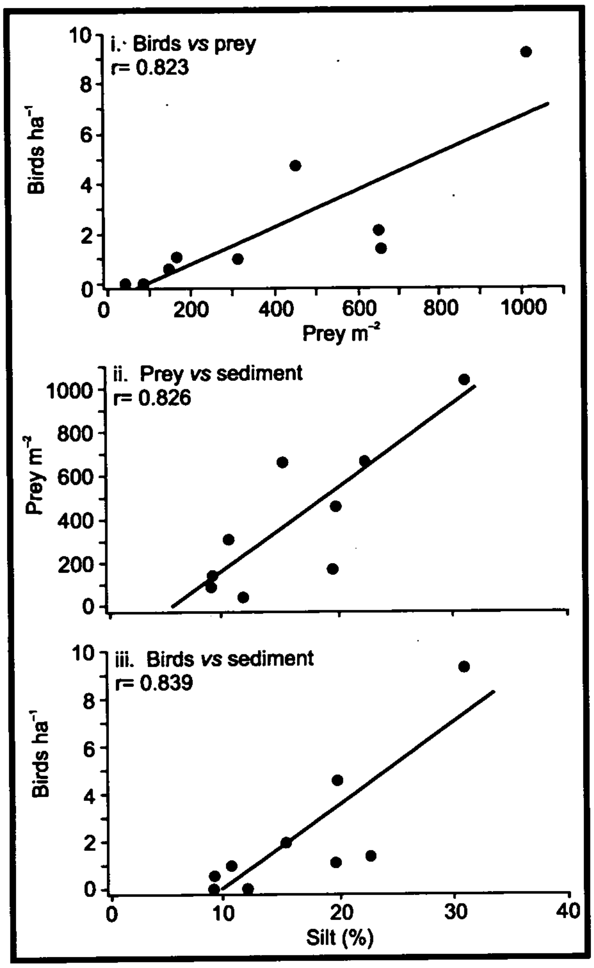

Figure 1. Relationships between (i) knot (*Calidris canutus*) density and that of its prey *Macoma balthica*, (ii) *Macoma* density and the proportion of silt in the sediment, and (iii) knot density and the proportion of silt in the south-east shore of the Wash (source: Yates *et al.* 1993a)

width on the sediments' particle size distribution and on the shore profile are difficult to predict in sufficient detail for them to be used in predicting invertebrate densities. Instead, the approach we developed used a correlative model that simply relates bird distribution directly to sediments:

Shore width → broad sediment characteristics (mud, sand) → bird numbers

The biological basis for this model had been established in the Wash for a number of shorebird species (Yates *et al.* 1993a) and elsewhere for dunlin (*Calidris alpina*) (Clark *et al.* 1993). It arises because the distribution of birds on their intertidal feeding areas is related to that of their invertebrate prey, which, in turn, is related to the particle size distribution of the sediments. It follows, then, that bird distribution will also be related to the sediment type in which their prey occurs. Figure 1 illustrates these relationships for knot (*Calidris canutus*), feeding on the Baltic tellin (*Macoma balthica*) on the south-east shore of the Wash.

CONSTANCY IN BIRD DISTRIBUTION

Clearly, it would be difficult to devise a predictive methodology without there being some degree of constancy in the distribution of feeding birds, both between season and year. To assess constancy of distribution, comparisons were made of the numbers of birds feeding in 59 one km broad transects between three seasons – autumn, winter and spring – and over four years. These showed that, in both timescales, bird distribution remained similar. Curlew (*Numenius arquata*), bar-tailed godwit (*Limosa lapponica*), oystercatcher (*Haematopus ostralegus*) and shelduck (*Tadorna tadorna*) showed the highest seasonal similarity in distribution (Goss-Custard & Yates 1992), while grey plover (*Pluvialis squartarola*) and curlew the highest similarity between years (Yates *et al.* 1996b). The distribution of knot was the least constant.

USING REMOTE SENSING TO MAP INTERTIDAL SEDIMENTS

The basic data requirement for the modelling approach was a measure of the distribution of the broad sediment categories, sand and mud, over the entire intertidal area. Mapping sediments by conventional methods needs extensive sampling programmes that are costly in time and labour and can pose problems of access and safety because of the nature and size of many intertidal areas. Furthermore, even with extensive sampling, there is always a source of error involved in extrapolating from sample sites to the whole area. Remote sensing from either aircraft or satellite provides synoptic coverage of large areas, alleviating the problems of safety and access. Image analysis techniques also allow accurate extrapolation from a few carefully selected ground observations to the whole area, provided the surface types to be mapped are spectrally separable. Muddy and sandy sediments are separable because of their surface features. Typically, the large, sandy mid-shore areas retain a film of surface water, some 1–2 cm deep, at low tide, while muddy sediments, though less

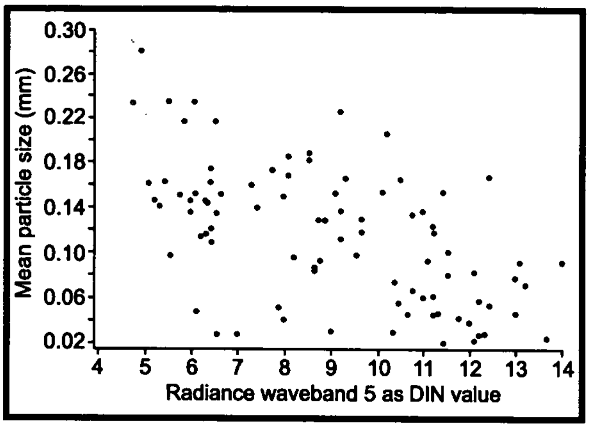

Figure 2. The relationship between the mean particle size of sediments in 192 samples sites in the Wash and the radiance, expressed as a DIN value, of middle-infra-red (Landsat thematic mapper band 5) from the sediment's surface (correlation coefficient, r=–0.552, P<0.0001). Decreasing radiance indicates increasing particle size, ie sandier sediments

permeable to water, tend to be uneven or elevated and less likely to retain water on their surface. This factor allows the two to be separated because the remote sensing instruments detect (i) visible and near- and (ii) middle-infra-red parts of the spectrum. Infra-red is absorbed by water so the presence of surface water on sandy sediments, and its absence from muddy sediments, means the two are separable by their difference in infra-red reflectance (Figure 2) (Yates *et al.* 1993b). In addition, muddy sediments tend to have higher densities of diatoms and algae on their surface than do sandy sediments. During photosynthesis, these organisms absorb visible red light. Consequently, muddy sediments are also separable from sandy ones on the basis of their greater absorption of red light (Figure 3).

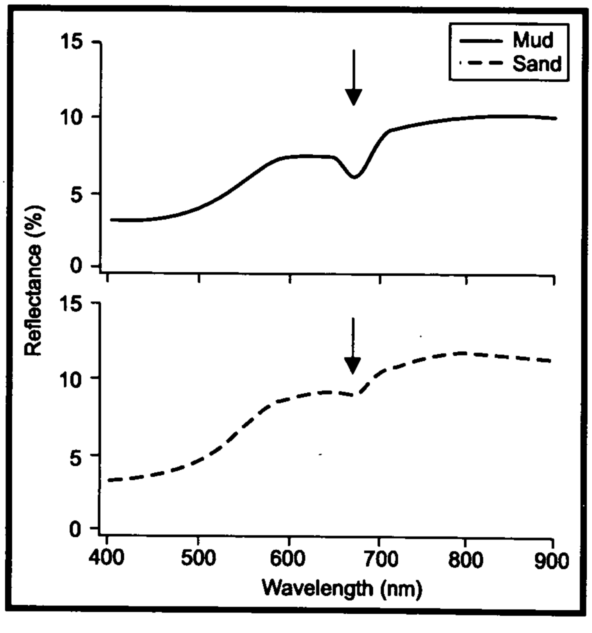

Figure 3. The spectral reflectance from muddy and sandy sediments. Note the reduced reflectance of red light at 670 nm (arrowed) that is due to the presence of higher densities of algae and diatoms on the surface of muddy sediment

Sediment distribution of the Wash was mapped by analysing a Landsat 5 remotely sensed image, taken at low tide when the whole intertidal area was exposed. The accuracy of the map was verified by comparison with ground observation data from 192 sample sites: 83% of muddy and 70% of sandy sites were correctly mapped (Yates *et al.* 1993b). This accuracy was considered to be very good compared with any other source of sediment distribution data. However, for further verification, the biological efficacy of the image-derived sediment data was also explored by testing whether the derived data could be substituted for ground-based observations to predict the density of the birds' invertebrate prey.

We had already determined equations that related ground-based sediment data, in addition to other environmental variables such as tidal inundation time, to prey density in 192 sample sites. So we were able to compare equations using sediment values obtained by ground observations with those using image-derived sediment values. This comparison showed that equations in which image-derived sediment values had been used explained the variation in invertebrate density almost as well as those using ground observations (Figure 4). In fact, in some instances, image-derived values improved the explanatory power of the equation (Yates *et al.* 1993c).

THE 'SHORE WIDTH AND SEDIMENT' MODEL

Having established the accuracy of image-derived measures of sediment distribution, the relationships between bird numbers feeding in an area and the sediments in that area, and between the sediments and the width of the shore were formulated by regression analysis. In the 'shore width' model developed for the Wash, the unit areas were contiguous, one km broad transects aligned perpendicular to the high water mark. The length of these transects was, of course, determined by the width of the shore.

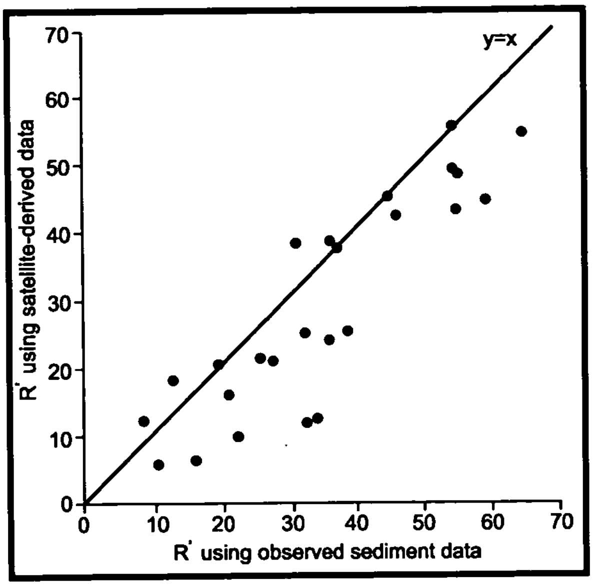

Figure 4. The percentage of the variation (R^2) in macrobenthos density explained by models in which the sediment data were derived from satellite image analysis plotted against the R^2 of models using ground-based observations of sediment. Each point represents a species of macrobenthos (source: Yates *et al.* 1993c)

Between 37% and 58% of the variation in the numbers of the eight shorebird species counted in the 59 transects was accounted for by the area of mud or sandy sediment in a transect. The numbers of four species – knot, bar-tailed godwit, oystercatcher and curlew – were linearly related to the area of mud or sand. The remaining species all showed a quadratic relationship with either mud or sand (Figure 5).

Analysis of the relationship between sediment type and shore width revealed three shore types in the Wash (Figure 6). All shores less than 2 km in width were muddy. Those greater than 2 km were either predominantly muddy or predominantly sandy. On the muddy shores, the area of mud was linearly related to shore width, while on sandy shores the area of mud remained constant so that the area of sand increased linearly with increasing shore width.

We considered the explanatory power of these functional relationships to be sufficiently good for them to be used to predict the consequence of changes in shore width. Predictions of the areas of mud and sand on a shore of a given width were made by solving the equations for the relationships illustrated in Figure 4. In turn, solving the equations illustrated in Figure 3 using the predicted sediment values enabled the number of each bird species to be determined in each transect.

TEST OF THE MODEL

The model's predictions were validated both within the Wash and on the Essex coast of east England, 150 km distant. Validation within the Wash involved using the model based on three years' bird data to predict the numbers of birds occurring in the transects in the fourth year. The precision of the model's predictions, expressed as a percentage of the variation in observed bird numbers that was explained by the model (P^2), increased as the size of the area for which the predictions were made increased (Figure 7). For example, predictions of redshank numbers increased from a P^2 value

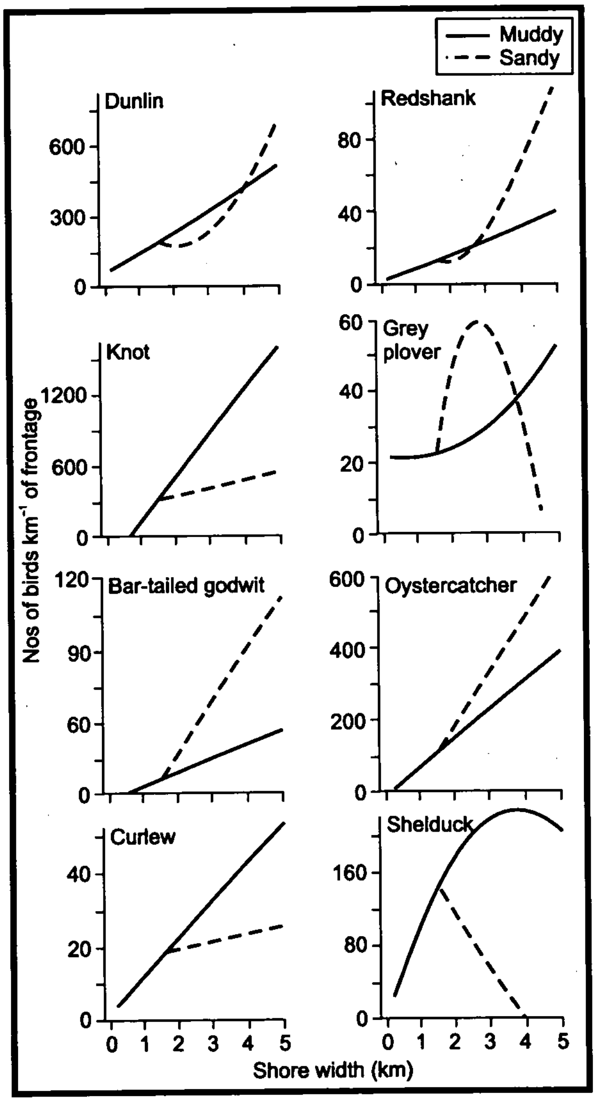

Figure 5. The predictions of the Wash 'shore width' model for the numbers of birds in one km transects in shores of various widths. The solid lines refer to shores that are predominantly muddy, the dashed lines to those that are sandy. Note that all shores less than 1.5 km wide were muddy

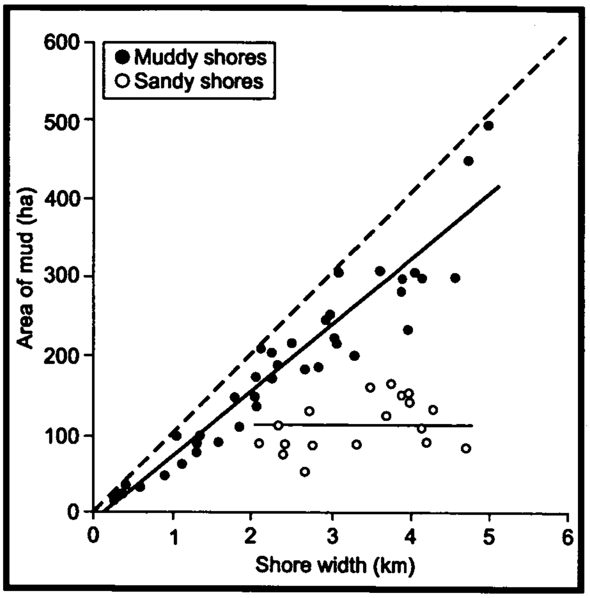

Figure 6. The area of muddy sediments in one km transects in relation to shore width on predominantly muddy shores (•) and predominantly sandy shores (o) of the Wash. The dashed line shows the expected relationship if the shores were completely muddy. The diagonal solid line shows the fitted regression for muddy shores and the horizontal line the mean area of muddy sediments on sandy shores (source: Yates *et al.* 1996b)

of 13% for areas of shore with a one km broad frontage to a value of 70% for an area of shore with a frontage of 7–11 km. In most species, P^2 values reached a maximum for areas with a 7 km broad frontage, though for grey plover and bar-tailed godwit numbers were best predicted for areas with a 3 km frontage. These findings suggested that there may be an optimal scale for the size of area for which predictions are made.

Whereas tests of the model within the Wash served as 'internal' validation of the model, those made using areas on the Essex coast provided a stringent test of the model's utility for other estuarine areas. As in the Wash, analysis of a satellite image taken at low water was used to determine the parameters of the shore width to sediment relationship for an area of the Essex coast that included Canvey Island, Maplin Sands, Dengie Flats and the River Blackwater estuary (Yates *et al.* 1996b). The model, based on bird to sediment relationships determined in the Wash, was then used to predict bird number for that area of the Essex coast. A comparison of the model's predictions with the number of birds observed at roost sites adjacent to that area during Birds of Estuaries Enquiry (BoEE) censuses indicated there was good agreement between predicted and observed numbers (Figure 8). The satisfactory outcome of this test was considered particularly important because it demonstrated the model's ability to predict bird numbers on intertidal areas other than those used to develop the model. Clearly, this suggests that the approach is applicable to other intertidal areas.

FURTHER DEVELOPMENTS TO THE METHODOLOGY

Relating within- and between-estuary variation in sediment to physical features

From dealing with changes in a single physical feature, shore width on the east coast of England, the modelling approach was subsequently developed further to include changes in a number of physical features across a range of British estuaries (Yates *et al.* 1996a). The relationship

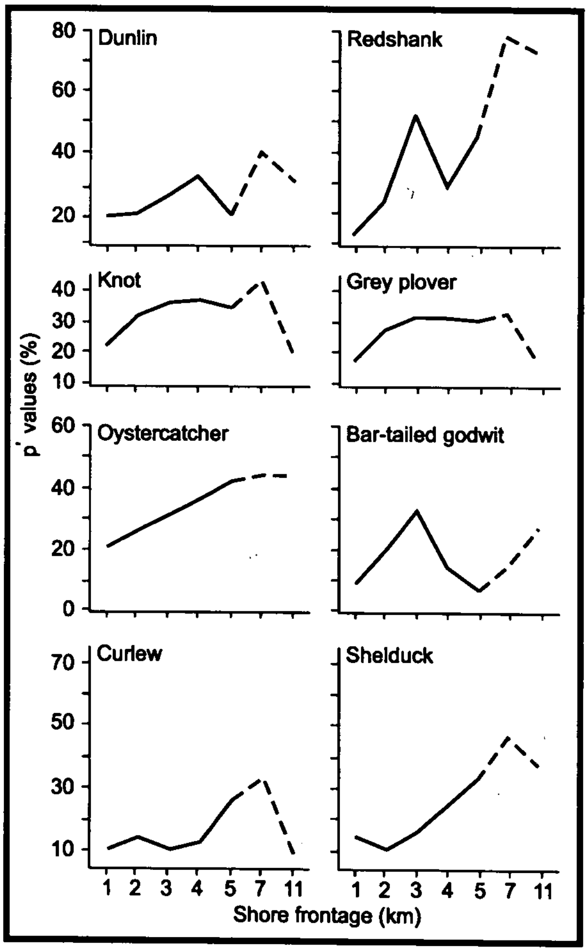

Figure 7. The percentage of variation in observed bird numbers explained by the Wash 'shore width' model's prediction (P^2) plotted against the frontage of the shore to which the predictions apply (source: Yates *et al.* 1996b). In all species the model's predictions improve as the frontage, and thus the area, of the shore increases

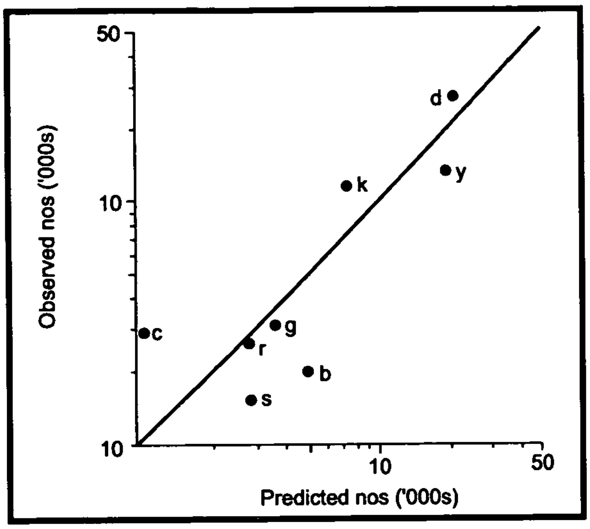

Figure 8. Comparison between the numbers of shorebirds observed on the Essex coast and those predicted by the Wash 'shore width' model. The letter by each point indicates the bird species: b=bar-tailed godwit, c=curlew, d=dunlin, g=grey plover, k=knot, r=redshank, s=shelduck and o=oystercatcher (source: Yates *et al.* 1996b)

between intertidal sediment distribution and environmental characteristics has been determined from a sample of 25 estuaries (see Figure 1 in Rehfisch *et al.*, p117). These variables were selected with two major considerations in mind. First, they were considered likely to influence either:

- within-estuary sediment distribution, eg the distance up the shore; or
- between-estuary differences in sediments, eg estuary size, shape and tidal range.

Second, the effect of natural or man-made environmental changes on these variables is readily predictable; for example, construction of a tidal barrage across an estuary would change the tidal range by a predictable amount.

As before, sediment distribution was determined from remotely sensed images (Yates *et al.* 1996a). The coarser resolution of satellite imagery was sufficient for sediment mapping in larger estuaries or embayments like the Wash, that have vast intertidal areas. For estuaries with smaller intertidal areas, typically with shores less than 2 km wide, it was more appropriate to use sensors mounted in aircraft to acquire the imagery because the spatial resolution is improved, thus allowing differences in sediments over a smaller spatial scale to be resolved.

Seventy-one per cent of the variation in the area of muddy sediments between estuaries was explained by two physical variables of the estuaries. One was the shape, defined as the estuary length divided by its maximum width. The other was the tidal range (Yates *et al.* 1996a). The proportion of the variation these two variables explained was increased to 91% if estuary location, on the east or west coast of Britain, was also taken into account.

Within an estuary, sediment distribution within a selected area of the shore was related to:

- the distance of the area along the estuary's longitudinal axis;
- its distance from the low-water mark; and
- its exposure to wave action measured as the maximum fetch (Yates *et al.* 1996).

Sediments were muddier farther up an estuary, on the upper parts of the shore and on shores with less exposure to wave action. Together, these variables explained 34% of the variation in the within-estuary distribution of muddy sediments.

Relating within- and between-estuary variation in bird numbers to sediments and physical features

Having established that within- and between-estuary variation in sediments could be predicted from environmental variables, the relationships between shorebird distribution and the sediments, and the environmental variables that explained sediment distribution were determined in the same sample of British estuaries. This study was done by the British Trust for Ornithology in conjunction with ourselves (Austen *et al.* 1996) and part of that study is described by Rehfisch *et al.* (pp116–126). It established that the proportion of the intertidal area covered by a particular sediment was indeed an important predictor of whole-estuary bird density. The predictive power of the relationship was further increased by the inclusion of estuary morphology variables. In particular, whole-estuary densities of oystercatcher, dunlin and redshank were predicted well, with 75%, 84% and 86% of the variation explained, respectively (Austen *et al.* 1996). As an example, the densities of redshank predicted by the relationship between birds and estuary morphology are compared with the actual densities observed in the sample estuaries in Figure 9.

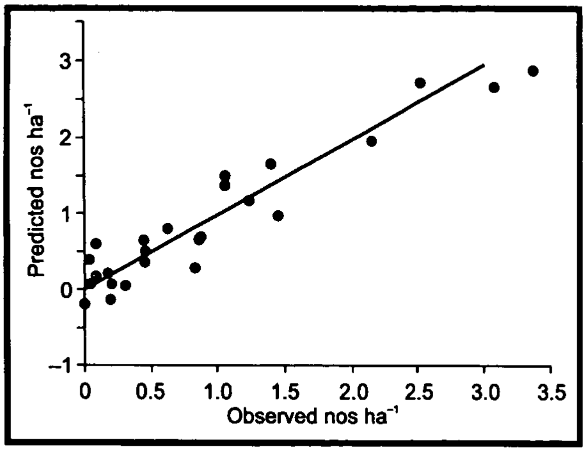

Figure 9. The densities of redshank in 25 British estuaries predicted by the relationship between the birds and the shape, tidal range and longitude of the estuary, plotted against the observed bird density. The diagonal line indicates exact correspondence between predicted and observed densities (source: Austen *et al.* 1996)

Though a full analysis of the data from this study is yet to be completed, the results emphasise further the value of a modelling approach that predicts bird numbers from estuary sediments and other physical variables influencing sediments, particularly on a whole-estuary scale.

CONCLUSIONS

The development of this modelling approach has demonstrated the value of using intertidal sediment distribution as a predictor of shorebird numbers on an intertidal area. Combined with studies on the influence of environmental and physical variables on sediments, the relationships provide a means of predicting the effect of habitat change or loss on shorebird numbers. However, the equations derived this way may only be reliable more generally if all intertidal areas are at carrying capacity in terms of the numbers of birds they can support. Birds may, however, be able to feed at higher densities than at present, in which case the predictions derived from the approach must be considered to be pessimistic; if birds can feed at densities higher than those yet observed, fewer would be influenced than the predictions suggest. Nevertheless, models developed using this approach provide an extremely useful, though perhaps conservative, tool for predicting shorebird densities on estuaries and how they might be expected to respond to man-made or natural changes to the physical features of estuaries.

REFERENCES

Austin, G., Rehfisch, M.M., Holloway, S.J., Clark, N.A., Balmer, D.E., Yates, M.G., Clarke, R.T., Swetnam, R.D., Eastwood, J.A., Durell, S.E.A. le V. dit, West, J.R. & Goss-Custard, J.D. 1996. *Estuaries, sediments and shorebirds III: Predicting waterfowl densities on intertidal areas.* (BTO Research Report no. 160.) Thetford: British Trust for Ornithology.

Bryant, D.M. 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). *Estuary, Coastal and Marine Science,* **9**, 369–384.

Clark, N.A., Evans, J., Rehfisch, M.M. & Shepherd, M. 1993. *Variability in waterfowl distribution within hypertidal estuaries in relation to sediments.* (BTO Research Report no. 109.) Thetford: British Trust for Ornithology.

Goss-Custard, J.D. & Yates, M.G. 1992. Towards predicting the effect of salt-marsh reclamation on feeding bird numbers on the Wash. *Journal of Applied Ecology,* **29**, 330–340.

Yates, M.G., Goss-Custard, J.D., McGrorty, S., Lakhani, K.H., Durell, S.E.A. le V. dit, Clarke, R.T., Rispin, W.E., Moy, I., Yates, T.J., Plant, R.A. & Frost, A.J. 1993a. Sediments characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *Journal of Applied Ecology,* **30**, 599–614.

Yates, M.G., Jones, A.R., McGrorty, S. & Goss-Custard, J.D. 1993b. The use of satellite imagery to determine the distribution of intertidal surface sediments of the Wash, England. *Estuarine, Coastal and Shelf Science,* **36**, 333–344.

Yates, M.G., Jones, A.R., McGrorty, S. & Goss-Custard, J.D. 1993c. Satellite imagery to monitor ecological change in estuarine systems: example of the Wash, England. In: *Waterfowl and wetland conservation in the 1990's – a global perspective,* edited by M.Moser, R.C. Prentice & J. Van Vessem. (IWRB Special Publication no. 26.) Slimbridge: International Waterfowl Research Bureau.

Yates, M.G., Clarke, R.T., Swetnam, R.D., Eastwood, J.A., Durell, S.E.A. le V. dit, West, J.R., Goss-Custard, J.D., Clark, N.A., Holloway, S.J. & Rehfisch, M.M. 1996a. *Estuaries, sediments and shorebirds 1: Determinants of the intertidal sediments of estuaries.* (Natural Environment Research Council contract report to the Energy Technology Support Unit.) Huntingdon: Institute of Terrestrial Ecology.

Yates, M.G., Goss-Custard, J.D. & Rispin, W.E. 1996b. Towards predicting the effect of loss of intertidal feeding areas on overwintering shorebirds (Charadrii) and shelduck (*Tadorna tadorna*); refinements and tests of a model developed for the Wash, east England. *Journal of Applied Ecology,* **33**, 944–954.

Printed in the United Kingdom for The Stationery Office
ISBN 011 702171 7 C6 8/97

These are the Proceedings of the 10th International Waterfowl Ecology Symposium, which was held at the university of Aveiro, Portugal, 18 - 21 September 1995. The Symposium covered many aspects of the ecology of waterbirds, but the papers in these proceedings address the plenary theme of the Symposium: approaches to predicting the effects of habitat loss and change on populations of waterbirds and to detecting when populations have been affected.

The Stationery Office

Published by The Stationery Office and available from:

The Publications Centre
(mail, telephone and fax orders only)
PO Box 276, London SW8 5DT
General enquiries 0171 873 0011
Telephone orders 0171 873 9090
Fax orders 0171 873 8200

The Stationery Office Bookshops
49 High Holborn, London WC1V 6HB
(counter service and fax orders only)
Fax 0171 831 1326
68–69 Bull Street, Birmingham B4 6AD
0121 236 9696 Fax 0121 236 9699
33 Wine Street, Bristol BS1 2BQ
0117 9264306 Fax 0117 9294515
9–21 Princess Street, Manchester M60 8AS
0161 834 7201 Fax 0161 833 0634
16 Arthur Street, Belfast BT1 4GD
01232 238451 Fax 01232 235401
The Stationery Office Oriel Bookshop
The Friary, Cardiff CF1 4AA
01222 395548 Fax 01222 384347
71 Lothian Road, Edinburgh EH3 9AZ
(counter service only)

Customers in Scotland may
mail, telephone or fax their orders to:
Scottish Publications Sales
South Gyle Crescent, Edinburgh EH12 9EB
0131 479 3141 Fax 0131 479 3142

Accredited Agents
(see Yellow Pages)

and through good booksellers

£28

ISBN 0-11-702171-7

9 780117 021716