UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING, SCIENCE AND MATHEMATICS
SCHOOL OF CIVIL ENGINEERING AND THE ENVIRONMENT

HUMAN IMPACTS ON COASTAL BIRD POPULATIONS IN THE SOLENT

by

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ABSTRACT
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European and UK legislation arising from The Convention on Biological Diversity 1993 aims to reduce biodiversity loss and to set guidelines for sustainable impacts of human activities. With predictions of increased biodiversity loss under climate change, it is paramount that present and future anthropogenic impacts on biodiversity are assessed, monitored and predicted. This thesis applies techniques of assessment, monitoring and prediction to cases of potential losses of ornithological diversity within the Solent, UK, through overexploitation of resources, disturbance and habitat loss.

An annual commercial harvest of the eggs of Black-headed Gulls was studied to assess impacts on their breeding success and distribution within the Solent. From *in-situ* measurements of breeding success indicators, including egg volume, hatching success and chick survival, we were able to show that harvesting of eggs reduced the breeding success of gulls, over and above effects of colony size and nest position within the colony. *Ex-situ* measurements on the yolk-to-albumen ratio and eggshell thickness showed that harvesting reduced these components, over and above effects of laying date. Harvested sites also had a higher proportion of abnormally formed eggs, particularly taking the form of small yolkless eggs and unpigmented eggs. These impacts are all consistent with known effects of depletion of the female's endogenous reserves.

Data from long-term monitoring of seabirds breeding along the south coast of England indicated that egg harvesting and the associated disturbance may be directly and negatively influencing the breeding distribution of Black-headed Gulls and also the protected Mediterranean Gull that breeds in its colonies. Data suggests that egg harvesting has prevented the colonisation of Mediterranean Gulls on these sites, whereas un-harvested sites have seen rapid colonisation in the last 10 years. On this basis, both EU and UK legislation may be being violated, through infringement of the regulations surrounding the Mediterranean Gull as an Annex 1 (EC Birds Directive 1979) and Schedule 1 (Wildlife and Countryside Act 1981) species; and through the breeding habitat within the Solent being SACs and SPAs. Protected tern species that associate with Black-headed gull colonies start laying after the harvesting season, but are nevertheless susceptible to the collapse of harvested colonies.

As well as its gull colonies, the Solent sustains important populations of wintering shorebirds that rely on the food resource supplied by estuaries and tidal flats. The quantity and composition of macrobenthic invertebrate prey in the Southampton Water SPA was sampled with a stratified-random design for ANOVA. The split-plot ANOVA revealed a higher level of heterogeneity within the estuary than could be resolved from the multiple regression techniques that are normally applied to grid-based designs. Bootstrap resampling indicated that the ANOVA design predicted invertebrate assemblages with adequate precision to produce an individual-based predictive model of site quality for shorebirds over-wintering on Southampton Water. This model accurately predicted the observed shorebird distribution, on the assumption that non-starving birds moved within restricted sections of the site, consuming any prey that yielded a threshold energy assimilation rate. Dunlin and curlew were the species predicted to be most sensitive to loss of prey biomass or overall habitat area, with losses of 5-10% provoking significant impacts on survival. When the area for the proposed development of a port terminal at Dibden Bay was modelled as habitat loss, the impacts on shorebird survival were eliminated by the proposed mitigation. However, our model did not account for the years of habitat removal and construction of the mitigation sites. Despite these limitations the model indicated the potential for evaluating ornithological losses within the Solent from a small loss of intertidal habitat.

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CHAPTER 1. GENERAL INTRODUCTION

Global biodiversity is being lost at an alarming rate; as many as 150 species are estimated to go extinct every day (Lamont, 1995). Extinction is a natural process, with over 99% of all species that have ever existed now extinct (Leakey, 1996). However, past and present human activities are causing the continuing disappearance of many species of plants and animals (Chapin et al., 1996). Today, rates of extinction are 100-1,000 times faster than before human existence, and the impending disappearance of currently threatened species could accelerate this rate of loss significantly (Chapin et al. 1998). Furthermore, for every 10,000 species that go extinct, only one new species evolves (Chapin et al., 1998). Thus, the current rate of biodiversity loss greatly exceeds the rate that nature can compensate for, or adapt to.

The most severe threats to our environment and global biodiversity have been categorised into three major classes; habitat destruction, habitat disturbance (including physical disturbance, pollution, climate change and introduced species) and overexploitation of resources (Pullin, 2002). This thesis will treat all three of these threats in relation to egg exploitation and habitat loss to coastal birds against a background of rising sea levels induced by climate change. Habitat destruction is the most direct threat to biodiversity and is probably at its greatest level in Europe; where human population density is amongst the highest and industrial activity widespread and long established (Pullin, 2002). To help mitigate the effects of human population growth and land consumption, many scientists and conservationists urge governments to establish protected corridors, which connect patches of important wildlife habitat. These corridors, if planned correctly, allow wildlife to move between habitats and allow individual animals to move between groups, helping to restore or maintain genetic diversity that is essential both to the long-term viability of populations and to the restoration of functional ecosystems. These are particularly important for migratory species, of which wetland birds are considered such a large component that they were given special protection by the Ramsar Convention as early as 1971. Ramsar seeks to ensure the sustainable, responsible use of wetland resources including designation of wetland sites of international importance and to ensure that all wetland resources are conserved, now and in the future.

Humans not only destroy habitats for development, but also cause disturbance through various industrial and recreational activities. Although human disturbance is recognised to reduce biodiversity and is commonly viewed as negative disruption, the long-term health of most ecosystems depends on a certain level of disturbance. A major effect of disturbance on ecosystem dynamics is a change in species abundance. As a consequence, dominance of a site by one or several individual species can be reduced and diversity increased. Disturbance, which produces empty patches, encourages superior colonisers, which tend to be inferior competitors, while it disfavours superior competitors by reducing competitive exclusion (Kondoh, 2001). Connell's (1978) intermediate disturbance hypothesis predicts that moderate levels of disturbance maximises species diversity. However, empirical work suggests that the disturbance-diversity relationship can be either negative or positive depending on the productivity of the ecosystem (reviewed in Proulx and Mazmuder, 1998). Nevertheless, disturbance from human activities, which are generally at higher levels than natural disturbances, do modify ecosystems and often cause considerable losses of biodiversity. The fundamental understanding of the effects of such disturbances on community processes and biodiversity is essential for the sustainable management of natural resources and spatial planning.

The relatively recent predictions about climate change indicate that human activities will cause massive global changes which will not only have their own long-term effects on biodiversity, but will accelerate other factors such as habitat loss (Galbraith et al., 2002; Thomas et al., 2004). The ability of species to reach new climatically suitable areas will be hampered by habitat loss and fragmentation, and their ability to persist in appropriate climates is likely to be affected by new invasive species (Thomas et al., 2004). Climate change has been predicted to become the greatest threat to biodiversity in many if not all regions of the world (Thomas et al., 2004).

The third major loss of biodiversity, by overexploitation, has gained the world's attention through its impacts on keystone species such as Rhinos and Tigers, which were brought to the brink of extinction through trophy hunting and the trade in animal parts. When the harvesting of a natural resource increases to levels that cannot be compensated by the reproducing population or the natural production of the resource, the harvesting becomes non-sustainable and the resource faces extinction.

The loss of biodiversity is a concern to the human race for three fundamental reasons (Ehrlich and Wilson, 1991). The first is the moral responsibility of humans to protect our living companions and in general the world in which we live. The popularity of ecotourism, bird-watching, wildlife films, pet-keeping and gardening prove that humans gain great aesthetic pleasure from nature (Ehrlich and Wilson, 1991).

The second reason for valuing biodiversity is utilitarian. Humans obtain enormous direct economic gain from biodiversity in the form of foods, medicines, and industrial products. Only a small proportion of plant species has been screened for possible value as providers of food and medicine (Eisner, 1989). Losing species through human activities may hamper our own ability to survive.

The third major value of biodiversity is its ecosystem services, including provision of water, the generation and maintenance of soils for supporting crops and forests, and maintenance of the gaseous composition of the atmosphere which supports the world's organisms. Significant alteration of the atmosphere over the past few decades has exposed the capacity for humans to destroy biodiversity at a colossal scale. The ecosystem services in which biodiversity plays such a critical and intricate role are provided on such a grand scale that there is often no successful substitution for them (Ehrlich and Wilson, 1991). Furthermore, such substitutions often require large amounts of energy, thereby adding to humanity's general impact on the environment (Ehrlich and Mooney, 1983). If the epidemic of extinctions now under way is continued unabated, much of biodiversity and the quality of ecosystem services generated will be lost (Ehrlich and Wilson, 1991)

Summits, conventions and regulations have set targets for countries to try and slow the loss of biodiversity and ensure the sustainable use of natural resources for the health of the planet and ensure that ecosystem services are available for future generations. The Rio Earth Summit 1992 represents a landmark shift in conservation ideals from the public to the political agenda, with government officials from virtually every country in the world represented, and strategic outcomes designed to reverse the effects of environmental degradation.

The Convention of Biological Diversity 1993, which was initiated at the Rio Earth Summit, claims to be the first global, comprehensive agreement to address the conservation of biological diversity within the framework of sustainable development. It has now been endorsed by over 170 governments, and the European Commission, as a legally binding document. Its principles have been adopted by the EC Habitats Directive (92/43/EEC) that encourages sustainable exploitation of wildlife habitats but requires exploiters to demonstrate that they are not disturbing protected habitat and/or species.

The analysis in this thesis of egg harvesting from gull colonies will concern this tension between sustainable exploitation and detrimental disturbance.

The European Commission has shaped the EC Habitats Directive and EC Birds Directive (79/409/EEC) to meet its commitment to the Rio Convention, and has set up the Natura 2000 network of Special Areas of Conservation (SACs) and Special Protection Areas (SPAs). These requirements were transposed into UK law through the Conservation (Natural Habitats) Regulations 1994. SACs are strictly protected sites designated by the EC Habitats Directive, which aims to promote the maintenance of biodiversity, taking account of economic, social, cultural and regional requirements. Article 3 of the Habitats Directive requires the establishment of a European network of important high-quality conservation sites that will make a significant contribution to conserving the 189 habitat types and 788 species identified in Annexes I and II of the Directive (as amended). The listed habitat types and species are those considered to be most in need of conservation at a European level. SPAs are sites that have been identified and classified by Member States of the Council Directive on the Conservation of Wild Birds. Within SPAs, Member States are obliged to take necessary steps to avoid deterioration of natural habitats and disturbance of species, where such disturbance would contravene the objectives of the Directive. Member States are also required to pay particular attention to the protection of wetlands, especially wetlands of international importance. In order to maintain conformity and common standards, the UK has had regard to the internationally agreed guidelines for the selection of wetlands of international importance under the Ramsar Convention (1971). The SPA guidelines make explicit reference to a number of definitions and other principles relating to Ramsar site selection guidance.

In 1995, the UK government consulted over three hundred organisations throughout the UK and launched the UK Biodiversity Action Plan (BAP) for dealing with biodiversity conservation in response to the Rio Convention. UK biodiversity also obtains protection via land areas, which incorporate the diversity and geographic range of habitats, species, geological and geomorphological features in England, Scotland and Wales, being designated as Sites of Special Scientific Interest (SSSIs) under the Wildlife and Countryside Act 1981 (part II). The Countryside and Rights of Way Act 2000 strengthened the law, giving greater power to the designating body to enter into management agreements, refuse consent for damaging operations, and take action where damage is being caused through neglect or inappropriate management. The study areas in this thesis are all SSSIs and SPAs, with the majority also being a Maritime SAC (Fig. 1.1), in consequence it is necessary under European and UK law to assess human activities on these sites to determine the level of disturbance on the habitat, and whether such activities cause significant losses to biodiversity.

The studies presented here represent potential examples of the three major losses to biodiversity, and considers the local and in some cases the wider consequences to coastal bird populations in the UK. The aim of the present study was to assess whether estuarine habitat loss could significantly reduces biodiversity, in terms of the coastal birds that rely on estuaries for food; whether human exploitation of gulls for their eggs is reducing their local abundance and breeding success, and hence could lead to biodiversity loss in the future; and whether physical human disturbance on coastal breeding grounds leads to changes in breeding distributions and abundances, which may ultimately reduce bird diversity at a local and/or global scale.

Coastal habitat loss and disturbance has become a great threat to coastal birds which rely on this valuable habitat for feeding, breeding and roosting. Both saltmarshes and mudflats are UK Priority BAP habitats and are at risk from developments, human disturbance and from sea level rises. English Nature's BAP for mudflats states that 'land claim, for urban and transport infrastructure and for industry, has removed about 25% of the UK's estuarine intertidal mudflats, with up to 80% removal in some estuaries'. The UK BAP aims to halt net loss of mudflats and coastal saltmarshes, create, restore and maintain mudflats and saltmarshes in terms of community and species diversity and to offset predicted losses to rising sea level, and restore estuarine water quality to ensure that existing mudflats and saltmarshes fulfil their important ecological and conservation role.

Human-caused disturbances on coastal bird populations can be direct or indirect. An example of a direct effect is when the presence of humans results in a failed nest through accidental trampling or in a bird starving through exclusion from its feeding grounds. An example of an indirect effect comes from the release of non-native species which result in changes to the ecosystem. For example, American Mink *Mustela vison* that escaped from fur farms in the 1950s (Dunstone, 1993) have caused breeding failure and colony abandonment in populations of coastal bird, especially in Scotland (Craik, 1995; Rae, 1999; Mitchell et al., 2004). Another example was the accidental introduction of Smooth Cord-grass *Spartina alterniflora*, on ship's ballast water, from the east coast of North America to Southampton Water prior to 1870. Its subsequent crossing with the native Small Cord-grass *S. maritima* resulted in the appearance of the Common Cord-grass *S. anglica* (and in the sterile hybrid *S. townsedii* which preceded). *S. anglica* was a successful and aggressive coloniser; and subsequently caused die-back of the native *S. maritima* (Perring and Walters, 1976), loss of habitat for feeding and roosting populations of wintering waders and wildfowl (Davidson et al., 1991), and has altered the course of succession, usually producing a monoculture which has less intrinsic value to wildlife than the naturally species-diverse marsh (Davidson et al., 1991). The spread of *S. anglica* on the south coast of England resulted in a reduction of mudflats which provide food for wintering shorebirds (Goss-Custard and Moser, 1988), and its subsequent dieback has facilitated saltmarsh erosion and the reduction in breeding habitats for coastal and shorebirds.

Populations of coastal birds have also been affected by humans through persecution for their meat, feathers and eggs; the classic example being the extinct Great Auk *Pinguinus impennis* which was first slaughtered for food and bait by local inhabitants, and continued for the bird's fat and feathers. As the bird became scarce, they were collected for a well-paid trade in skins and eggs. Tern populations in northwest Europe were brought to the brink of extinction at the end of the 19th century by egg collection for food and hunting of adults for the millinery trade, but they recovered well in response to protective legislation in the early-20th century (Mitchell et al., 2004). Taking wild birds and their eggs was made illegal in 1954, but unfortunately many birds continue to be illegally persecuted, especially for their eggs.

1.1 Chapter Aims and Objectives

- **Chapter 2** investigates the impact of egg harvesting on the breeding success of the Black-headed Gull *Larus ridibundus* colonies situated on SAC, SPA, Ramsar and SSSI sites in Hampshire, southern England. Given that breeding success has been shown to be related to the colony size and nesting position within the colony (Patterson, 1965), and that tidal washouts have been reported to be common at Hampshire colonies (Taverner, 1966), the impacts of egg collecting may depend strongly on the intrinsic quality of the colony (the mean per capital reproductive success of pairs within the colony before environmental influence) and the timing of washout events. The field study needed to tackle this interaction by comparing breeding success between colonies of various sizes, and with and without tidal influence. Breeding success was measured directly at individual nests by recording variables contributing to egg production, hatching success of eggs and chick survival. The aims were set by the practical objective to establish whether the present level of licensed harvesting on these protected sites is sustainable, or whether this natural resource is being overexploited.

- **Chapter 3** investigates whether egg harvesting and the associated human disturbance has influenced the breeding distribution along the south coast of England of the target species, the Black-headed Gull, and associated non-target breeding seabirds. This was achieved by collating long term data on numbers of breeding pairs and productive at seabird colonies on the south coast of England. The aims were set by the practical objective to establish whether the disturbance caused during the harvest of Black-headed Gull eggs conforms to EC and UK legislation for the protected Mediterranean Gulls *Larus melanocephalus*, Little Terns *Sterna albifrons*, Common Terns *Sterna hirundo* and Sandwich Terns *Sterna sandvicensis*, on an SPA site in Hampshire, southern England.
- **Chapter 4** presents the results of sampling the diversity, abundance and distribution of the macrobenthic invertebrate food supply for wintering shorebirds on the SPA and Maritime SAC of Southampton Water, southern England. This was achieved by designing a sampling method to produce results of comparable efficiency to conventional methods. The aims were set by the objective to identify discrete habitat patches on the basis of the macrofauna present, and to estimate the macrobenthic prey diversity and biomass density for each defined patch. These empirical data informed an individual-based model for Southampton Water, which was designed to predict changes in biological fitness of individual birds and population responses to changes in their environment.
- **Chapter 5** develops an individual-based model of the SPA and Maritime SAC of Southampton Water, in order to evaluate site quality for eight shorebirds: Dunlin *Calidris alpina*, Ringed Plover *Charadrius hiaticula*, Ruddy Turnstone *Arenaria interpres*, Redshank *Tringa totanus*, Grey Plover *Pluvialis squatarola*, Black-tailed Godwit *Limosa limosa*, Eurasian Oystercatcher *Haematopus ostralegus* and Eurasian Curlew *Numenius arquata*. This was achieved by parameterising a model with data on the macrobenthic prey items available to

the shorebirds found in Chapter 4. The model predicts shorebird numbers, mortality rates and body conditions of the foraging birds on Southampton Water throughout the winter season. The aims are set by the objective to determine the effect of habitat loss and changes in the food supply to shorebirds feeding in Southampton Water.

1.1 Study Area

The main study area of this thesis is situated in the Solent. The Solent Marine Site encompasses a major estuarine system on the south coast of England with four coastal plain estuaries and four bar-built. It has the largest number of small estuaries in the tightest cluster anywhere in Great Britain and is located in one of few sheltered channels in Europe, lying between a substantial island (the Isle of Wight) and the mainland. The Solent and its inlets are unique in Britain and Europe for their hydrographic regime of four tides each day, and for the complexity of the marine and estuarine habitats present within the area. There is a wide variety of marine sediment habitats influenced by a range of salinities, wave shelter and intensity of tidal streams. Sediment habitats within the estuaries include extensive estuarine flats, often with intertidal areas supporting eelgrass *Zostera* spp. and green algae, sand and shingle spits, and natural shoreline transitions. Many intertidal areas within the Solent are important for a number of nesting, roosting and feeding sea- and shorebirds (Burges, 2000).

The Solent is designated as a SPA, with the majority of the area also being designated as Solent Maritime SAC, Ramsar and SSSI (Fig. 1.1).

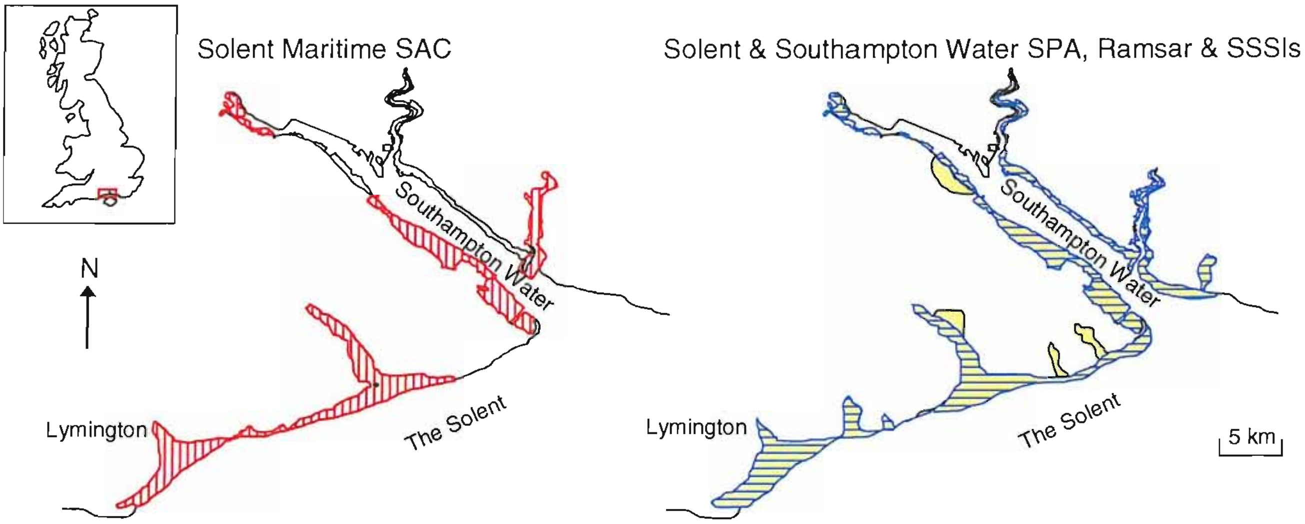


Figure 1.1. Maps indicating the designations placed on the study area from Lymington to Southampton Water. The Solent Maritine SAC is indicated by red vertical hatching

(which extends further east to Chichester Harbour); The Solent and Southampton Water SPA and Ramsar sites are indicated by the blue horizontal hatching; and the SSSIs are indicated by solid yellow.

1.2 Study Species

The primary legislation affecting wild birds in England and Wales is the Wildlife and Countryside Act 1981, with the basic principle of protecting all wild birds, their nests and eggs by law. Rare and declining species, listed in Schedule 1, are afforded additional protection during the breeding season, where it is an offence to intentionally kill, injure, take or damage nests whilst in use or being built, take or destroy eggs, and handle or remove these wild birds.

Birds in Britain also gain protection through the Bird Directive and consequently sites being designated SPAs. Article 4 of the Bird Directive requires Member States to identify areas of the most suitable territories in size and number for rare or vulnerable species listed in Annex I (Article 4.1), and for regularly occurring migratory species (Article 4.2). Under the Conservation (Natural Habitats) Regulations 1994, for Annex I species it is an offence to (a) deliberately to capture or kill a wild animal of a European protected species; (b) deliberately to disturb any such animal; (c) deliberately to take or destroy the eggs of such an animal; or (d) to damage or destroy a breeding site or resting place of such an animal.

Annex II of the Directive lists bird species that, owing to their population level, geographical distribution and reproductive rate throughout the community, may be hunted under national legislation. The species listed in Annex II/1 may be hunted in the geographical sea and land area where the Directive applies; and the species listed in Annex II/2 may be hunted only in the Member States in respect of which they are indicated. The Directive bans certain non-selective methods of hunting and defines the limits within which Member States can set the hunting season.

The conservation status of European species has been recently reassessed (Burfield and van Bommel, 2004), and Species of European Conservation Concern (SPEC) were identified as those that have an unfavourable conservation status in Europe or are secure but concentrated in Europe: SPEC 1 are species of global conservation concern, according to the latest assessments by BirdLife International; SPEC 2 are species with an unfavourable European conservation status, and with more than half of the global breeding or wintering population within Europe; SPEC 3 are species with an unfavourable European conservation status, but with less than half of the global breeding or wintering population within Europe, and SPEC 4 (or SPEC^E) are species with a favourable European conservation status but with more than half the global breeding or wintering population concentrated in Europe. Other species, not considered to be of European conservation concern are designated Non-SPEC species with a favourable European conservation status, and with less than half of the breeding or wintering population within Europe.

The leading governmental and non-governmental conservation organisations in the UK have recently reviewed the population status of the birds regularly found in the UK, and their findings have been published in Gregory et al. (2002). The lists are based on the most up-to-date information available, and will help to guide conservation action between 2002 and 2007. Each species has been placed into a red, amber or green list. Red list species are those that are Globally Threatened (SPEC 1) according to IUCN criteria; those whose population or range has declined rapidly in recent years; and those that have declined historically and not shown a substantial recent recovery. Amber list species are those with an unfavourable conservation status in Europe (SPEC 2 or 3); those whose population or range has declined moderately in recent years; those whose population has declined historically but made a substantial recent recovery; rare breeders; and those with internationally important or localised populations. Species that fulfil none of the criteria are green-listed.

The seabirds and waders that are the focus of the present study are indicated in Table 1.1, with reference to their legal status and European and UK conservation status.

Table 1.1. A list of the coastal birds used in the present studies, and their present legal status and conservation status in Britain.

Bird Species	**Legal status**	**Conservation Status**
Black-head Gull *Larus ridibundus*	Annex II/2, Migratory	Amber,
Mediterranean Gull *Larus melanocephalus*	Schedule 1, Annex I, Migratory	Amber, SPEC 4 Favourable conservation status **(secure)** but concentrated in Europe
Common Tern *Sterna hirundo*	Annex I, Migratory	Green
Sandwich Tern *Sterna sandvicensis*	Annex I, Migratory	Amber, SPEC 3 Unfavourable conservation status **(declining)** and concentrated in Europe
Little Tern *Sterna albifrons*	Schedule 1, Annex I, Migratory	Amber, SPEC 3 Unfavourable conservation status **(declining)** but not concentrated in Europe
Dunlin *Calidris alpina*	Migratory	Amber, SPEC 3 (wintering) Unfavourable conservation status **(vulnerable)** but not concentrated in Europe
Ringed Plover *Charadrius hiaticula*	Migratory	Amber
Ruddy Turnstone *Arenaria interpres*	Migratory	Amber
Common Redshank *Tringa totanus*	Annex II/2, Migratory	Amber, SPEC 2 Unfavourable conservation status **(declining)** and concentrated in Europe
Grey Plover *Pluvialis squatarola*	Annex II/2, Migratory	Amber
Black-tailed Godwit *Limosa limosa*	Schedule 1, Annex I and II/2, Migratory	Red, SPEC 2 Unfavourable conservation status **(vulnerable)** and concentrated in Europe
Eurasian Oystercatcher *Haematopus ostralegus*	Annex II/2, Migratory	Amber
Eurasian Curlew *Numenius arquata*	Annex II/2, Migratory	Amber, SPEC 3 (wintering) Unfavourable conservation status **(declining)** but not concentrated in Europe

CHAPTER 2. IMPACT OF EGG HARVESTING ON THE BREEDING SUCCESS OF THE BLACK-HEADED GULL, *LARUS RIDIBUNDUS*

Contributions: Lord, B. = defining the mission; Doncaster, C.P., Hudson, M.D. = advice on design and assistance in the field; Wood, P.J. = planning design, scheduling and logistics of fieldwork, collecting data (with assistance from people in the Acknowledgements), doing analysis, interpreting and reporting results.

2.1 Abstract

Gull colonies world-wide have been harvested for their eggs for centuries with minimal knowledge of the impacts on breeding. Although most Laridae can replace lost eggs, they have comparatively high energetic demands for egg production. In this chapter we assess the impacts of a licensed egg harvest on the breeding success of black-headed gulls *Larus ridibundus*, which nest colonially in an EU Special Protection Area in Hampshire, Southern England. We compared egg volume, hatching and chick survival from harvested and un-harvested nests in central and fringe positions within colonies of various sizes. Eggs from various laying stages were collected from harvested and un-harvested colonies of similar pre-harvest intrinsic quality, for comparison of their volumes, yolk-to-albumen ratios and eggshell thickness. Egg volume and the yolk-to-albumen ratio depended on laying time and location, with the largest eggs belonging to birds breeding in central positions on large colonies, and laying during the peak period. Peak layers also had the largest yolk-to-albumen ratios. Harvested sites were characterised by reductions in egg volume, yolk-to-albumen ratio and eggshell thickness, which translated to poorer hatching success and chick survival. Harvested sites also had a higher proportion of abnormal eggs, particularly taking the forms of small yolkless eggs and unpigmented eggs. The reduced breeding success on harvested colonies is likely to be linked to depletion of the female's endogenous reserves which can also reduce future survival and breeding propensity.

2.2 Introduction

The eggs of black-headed gulls *Larus ridibundus* L. are harvested from colonies on saltmarshes in Hampshire, Southern England, under licence through the UK Department of the Environment Food and Rural Affairs (DEFRA) for consumption and market. Western European populations of black-headed gulls increased greatly through most of the 20th Century (Cramp, 1983), yet in 2002 the species was added to a UK 'Amber' list, in recognition of its reduced size of breeding population of which more than half is contained in fewer than ten sites (Gregory et al., 2002).

Black-headed gulls typically lay a clutch of three eggs and, like most Laridae, they are indeterminate layers, meaning that they will replace lost eggs (Klomp, 1970). If eggs are lost within a few hours of the first being laid then gulls will add another egg to the same clutch (protracted laying). Black-headed gulls stop protracted laying after losing as many as seven eggs in succession (Weidmann, 1956). If the gull loses an entire clutch it will start again to produce another clutch (replacement laying), however this depends on the time of season and how many clutches have previously been laid. Gulls will relay late in the breeding season, but the 8-13 days of follicle growth require high reserves of energy (Weidmann, 1956).

Replacement laying in ground-nesting gulls functions as an adaptation to unpredictable factors such as floods and predation (Brown and Morris, 1996). Historically, egg harvesting from seabird colonies has been part of various cultures (Burger and Gochfeld, 1994). The few studies of egg harvesting to date have found reduced breeding success in some seabird populations, sufficient either to pose a threat to viability (Haynes, 1987; Burger and Gochfeld, 1994; Feare, 1976a; Vermeer et al., 1991; González, 1999; Zador et al., 2005), or to cause decline (Ainley and Lewis, 1974; de Juana, 1984; Storr et al., 1986; Shannon and Crawford, 1999). Conversely, some gull populations are successfully managed with an egg-harvest (Wanless et al., 1996; Ickes et al., 1998), and in principle regulated harvesting can benefit conservation through raised awareness and possibly protection of the site (Feare et al., 1997). A managed harvest of black-headed gulls' eggs has the potential to be an example of the sustainable use of biological diversity that is one of the principle tenets of Article 10 of the 1993 Convention of Biological Diversity (Sustainable Use of Components of Biological Diversity).

Negative effects of egg harvesting may be inferred from studies that have experimentally induced replacement laying. Egg size has been found to reduce in replacement clutches (Feare, 1976b; Parsons, 1976; Brown and Morris, 1996; Nager et al., 2000; Hipfner et al., 2003), and in some Laridae, replacement clutches contain fewer eggs (Brown and Morris, 1996). Birds use endogenous proteins to form eggs (Carey, 1996; Houston et al., 1995), and they not only show an increased reduction of these proteins with increased egg production (Cooke et al., 1995; Bolton et al., 1993) but protein quantity and quality appears to limit the production of replacement clutches, egg size and egg quality, as measured by the yolk-to-albumen ratio and protein content (Robbins, 1981; Houston et al., 1983; Bolton et al., 1992; Monaghan et al., 1998; Hipfner et al., 2003). Most of the endogenous proteins used in egg production come from pectoral muscles (Houston et al., 1995). Depletion of these muscles reduces flight performance, and thus foraging efficiency and predator avoidance (Veasey et al., 2000, 2001; Kullberg et al., 2005). Moreover, muscle recovery during incubation appears to be slow (Houston et al., 1983), which will influence the trade-off between foraging to maintain parental body condition, and incubation followed by chick provisioning (Monaghan et al., 1998). In some Laridae, the capacity for egg production may be constrained by exogenous food supplies (Oro et al., 1999). For this reason relaying may be more common among females in better feeding condition (Houston et al., 1983; McNamara and Houston, 1996).

In general gulls that lay during the colony 'peak' laying period, when the largest proportion of egg laying is taking place, tend to have higher breeding success than early or late layers (Patterson, 1965; Nisbet and Dury, 1972; Parsons, 1975; Vermeer et al., 1991; Brown and Morris, 1994; Spear and Nur, 1994; Prévot-Julliard et al., 2001). Colonial synchronised breeding probably serves an anti-predator function (Kruuk, 1964), and is thought to be related to food availability (Perrins, 1970). Similarly, the position within a colony can influence breeding success in gulls (Weidmann, 1956; Patterson, 1965; Parsons and Chao, 1983). Patterson (1965) showed that black-headed gulls breeding outside the main colony are less successful, and pairs on the edge of the main colony are slightly less successful, than those breeding in the colony centre.

Black-headed gulls in Hampshire UK have been exploited for their eggs for centuries. The egg-harvest is presently managed through licences, which allow collection from the start of laying until 15th May, with all eggs collected daily from harvested sites (to ensure freshness). The appearance of hatchlings is consequently delayed by at least 3 weeks (Aspinall et al., 1993). High spring tides, which can wash out nests, typically occur at the start of the breeding season during the second week in April, and again in mid to late May. The delay in hatching date caused by harvesting can result in eggs and young chicks being lost to floods in May, to which older chicks are much less susceptible (Aspinall et al., 1993).

Here we describe an empirical study to examine the effects of egg harvesting on the breeding success of black-headed gulls. We measured specific egg components of volume, yolk-to-albumen ratio and eggshell thickness, which have been shown to influence breeding success (Nager et al., 2000; Hipfner et al., 2003), and also hatching success and chick survival. These data were used to determine whether egg harvesting influences these breeding success indicators, over and above effects of colony size and nest position within the colony, and the environmental effect of tidal flooding.

2.3 Methods

2.3.1 Study Sites

Four coastal study colonies in Hampshire and Dorset, Southern England were selected in 2004, and two in 2005 and 2006 (Table 2.1a). In 2004 and 2005 *in-situ* measurements of breeding success indicators were taken within the various colonies (Table 2.1a); and in 2005 and 2006 eggs were taken from the colonies for *ex-situ* measurements of egg components (Table 2.1b). In 2004, two commercially harvested sites were chosen: Pylewell and Lymington, and the research was continued on the Pylewell colony in 2005 and 2006 (Table 2.1a and b). The two large and geographically distinct harvested tidal-marshes, Pylewell and Lymington, lie on opposite sides of the Lymington estuary, Hampshire. These sites are extensively protected by legislation, as part of the extensive Solent Maritime, candidate Special Area of Conservation (under the EU Habitats Directive 92/43/EEC); they are also within the Solent European Special Protected Area (under the EU Directive 79/409/EEC), and are listed as Wetlands of International Importance (Ramsar Site).

Two un-harvested colonies where chosen in 2004: Poole Harbour and Brownsea Island in Dorset, and the research was continued on the Poole Harbour colony in 2005-2006. Egg harvesting in Poole Harbour, which has the same level of legal protection as the Hampshire sites, was prohibited in the early 1990's. The colony here is situated on three islands in close proximity; a larger island straddled by two smaller islands of approximately half the size. This formation and size difference allowed for comparisons of breeding success between island sizes and breeding position (Table 2.1a and b). The second un-harvested colony selected in 2004 was situated on Brownsea Island's non-tidal lagoon in Poole Harbour, which has the same conservation designations as the rest of Poole Harbour (Table 2.1a).

Table 2.1. Experimental designs.

a) Treatment, geographical site, size of study colony and study nest position within the colonies used in 2004 and 2005. * Un-harvested site within a harvested area; † Observed tidal effect after the start of the peak laying period.

Treatment	Site	Predicted Tidal Regime	Observed Tidal Effect†	Colony Size	Nest Position
2004					
Harvested	Lymington	Tidal	Tidal	Large	Central
Un-harvested *	Pylewell	Tidal	Tidal	Large	Central
Un-harvested	Poole Harbour	Tidal	Not Tidal	Large	Central
Un-harvested	Brownsea Island	Not Tidal	Not Tidal	Small	Fringe
2005					
Harvested	Pylewell	Tidal	Not Tidal	Large	Central
Un-harvested	Poole Harbour	Not Tidal	Not Tidal	Large	Central
Un-harvested	Poole Harbour	Tidal	Not Tidal	Large	Fringe
Un-harvested	Poole Harbour	Not Tidal	Not Tidal	Small	Central
Un-harvested	Poole Harbour	Tidal	Not Tidal	Small	Fringe

b) 20 eggs were collected for each egg laying or harvesting stage within the two treatment sites under different harvesting regimes in 2005 and 2006. Predicted peak laying was based on previous years' egg returns from the collectors on the harvested site, and nest densities and laying dates from the previous year on the un-harvested site.

Treatment sites and Harvesting regime	Egg laying/Harvesting stage
Central nests from a Large Harvested site (Pylewell's coastal marshes)	Start of laying Predicted peak laying End of harvest
Central nests from a Large Un-harvested site (Poole Harbour's coastal Islands)	Start of laying Predicted peak laying

2.3.2 Experimental Design

In 2004 and 2005, thirty nests where chosen at random from the full distribution of nests within each treatment site (Table 2.1a). Sites were chosen to test effects of colony size, nest position, tidal flooding and egg harvesting on breeding success. In the event, the un-harvested site in Poole Harbour remained un-flooded during the high spring tides (Table 2.1a). The effects of colony size and nest position within the colony on egg volume were tested within un-harvested sites; and, independently, the effects of harvesting on egg volume were tested from centrally positioned nests on similar sized colonies which were experiencing different harvesting regimes (harvested and un-harvested).

Colonies not experiencing egg-harvest were classed as 'un-harvested' and 'undisturbed', meaning that they were undisturbed by the harvest operation. Harvested colonies were classed as 'harvested' and 'disturbed'. One site could be classed as 'un-harvested' and 'disturbed' because nests here lay in the middle of a harvested area (Table 2.1a). Finally, the combination 'harvest' and 'undisturbed' was impossible to sample, because harvesting inevitably causes disturbance.

Nests were marked with numbered canes and eggs were measured and numbered by a non-toxic waterproof permanent marker in accordance with order of laying when known. This enabled us to follow the life history of each egg to hatching, and to fledging for colour-ringed chicks. The maximum egg width and length were measured with vernier callipers (±0.1mm). Egg volume was estimated to within 2% from maximum egg width and length (Hoyt, 1979):

$$V = K_v \cdot L \cdot B^2 \qquad (1)$$

where V = Volume, K_v = Species specific volume coefficient, L = Length, B = Maximum diameter. We follow Hoyt's (1979) recommendation that $K_v = 0.51$ is applicable to most eggs.

Nest monitoring was initiated on the harvested sites at the end of harvest, and during peak laying on the un-harvested sites, in order to have a comparable record across treatments of parents that would have started laying potentially viable eggs at a similar date within each treatment. Colonies were not entered for data collection during periods of rainfall, or strong or cold winds, and disturbance by researchers was kept to a maximum of 1 hr on each visit in order to reduce chilling of eggs and chicks (in accordance with recommendations in Walsh et al., 1995).

Hatching success was recorded and chicks found in monitored nests were ringed with a colour code to identify the treatment site. Colour ringing permitted the continued monitoring of chicks, dead or alive, on subsequent visits to the colony.

A total of 200 eggs from nests with a single egg were taken for analysis of quality in terms of yolk-to-albumen ratio and shell thickness, on the assumption that the eggs had been freshly laid and were the first eggs of a clutch. These were sampled from two treatment sites under different harvesting regimes in 2005 and 2006, in batches of 20 at various times in the season depending on the treatment (Table 2.1b). Eggs from the start of laying were assumed to be from less competitive birds with an intrinsically lower breeding success than those from the peak laying period, in accordance with data from Weidmann (1956) and Patterson (1965). Eggs taken during the end of the licensed harvest period from central positions were assumed to have been laid by birds that started laying during the peak laying period in accordance to Weidmann (1956) who observed that peak laying birds generally take over early birds' territories in central positions, and defend this territory from late comers. In the event, only 10 of the 20 eggs taken from the predicted peak laying period under the un-harvested regime in 2005 were found to be fresh, the others being addled. Due to egg damage during transportation one egg was unusable from both the start and predicted peak laying periods under the harvesting regime, and two eggs from the start of laying under the un-harvested regime. Eggs were stored in a cold room (4°C) for 28 days, after which their maximum length and width were measured with vernier callipers (±0.1mm) to allow calculation of volume. We used egg component volumes rather than weights in order to minimise underestimation of albumen as a result of water loss (Rahn and Ar, 1974). Eggs were emptied onto a flat glass sheet from which measures were taken with a tripod micrometer (±0.01mm) of maximum yolk height, and albumen height at five points 1-cm out from the yolk. The maximum and minimum diameters of yolk and thick albumen were measured with vernier callipers (±0.1mm). Yolk and albumen volume were estimated zones of a sphere from means of these measures:

$$V_a = \pi \cdot h_a \cdot (3a^2 + 3b^2 + h_a^2)/6, \quad V_y = \pi \cdot h_y \cdot (3b^2 + h_y^2)/6 \qquad (2)$$

where V_a = albumen volume, h_a = height of albumen, V_y = yolk volume, h_y = height of yolk, a = radius of albumen, b = radius of yolk.

The remaining eggshells were washed under cold water to remove excess watery albumen, taking care not to wash away the membranes, then left to dry at room temperature for 15 days. Four dried pieces of shell from the equator of the egg were cut and measured for mean eggshell thickness, using an adapted spring-closing micrometer (±0.01mm) with a rounded tip on the point of contact to fit the curvature of the shell.

Counts of Apparently Occupied Nests (AON) were conducted on each test colony within the first few days of hatching, as described in Walsh et al. (1995). During these counts, records were kept of any egg abnormalities in the form of white eggs with no pigmentation, half-white eggs (with 50% or more of the egg lacking pigment), notably small yolkless eggs (<45mm × 32mm), and failed eggs that took on a 'corroded' and dried appearance (characterised by a cracked and partially collapsed shell and apparently thickened membrane). The occurrence of the corroded eggs was observed to increase during peak hatching, when the largest proportion of hatching in the season was taking place. During this period three transects of 100 nests in 2005 and four such transects in 2006, were established at the larger un-harvested and harvested sites to compare the number of eggs with this abnormality. These transects were also used to count the number of nests with dead chicks (probably starved), which had died without sign of external injury, and together these counts produced the estimate of failed breeding attempts.

2.3.3 Data Analysis

The influence of laying order on egg volume was analysed for those 2004 clutches with identified 1st, 2nd and 3rd eggs. These data allowed us to compare intra-clutch variation within and between study colonies, and to compare with other studies on gulls. Volumes were log-transformed to meet the assumptions of parametric statistical tests. Influences were tested using a fully factorial balanced Analysis of Variance (ANOVA, following Doncaster and Davey 2007), with the random variable 'nest' nested in the fixed treatment 'site' (which included different colony sizes and nest positions: Table 2.1a):

$$\text{Log}_{10}\ \text{Egg Volume} = \text{Site} \mid \text{Nest}'(\text{Site}) \mid \text{Order} + \varepsilon \qquad (3)$$

Separate General Linear Models (GLM) excluding Order (which showed no interaction with Site) allowed all final clutches to be used to test the effect of treatment on whole clutches rather than single eggs. In 2004, the design to measure variation in egg volume in un-harvested sites could not be partitioned below treatment site (which included different colony sizes and nest positions: Table 2.1a):

$$\text{Log}_{10}\ \text{Egg Volume} = \text{Site} \mid \text{Nest}'(\text{Site}) + \varepsilon \qquad (4)$$

In 2005, however, we partitioned un-harvested treatment sites into fixed variables colony size and nest position within the colony using a fully replicated factorial design:

$$\text{Log}_{10}\ \text{Egg Volume} = \text{Size} \mid \text{Position} + \text{Nest}'(\text{Size*Position}) + \varepsilon \qquad (5)$$

Colony size and nest position were found to influence egg volume. For this reason we used a factorial design to test the effect of egg harvesting in 2004 and 2005, using harvested and un-harvested regimes in sites of similar nest position and colony size (Lymington and Poole Harbour in 2004; Pylewell and centrally positioned nests on Poole Harbour's large island in 2005, Table 2.1a):

$$\text{Log}_{10}\ \text{Egg Volume} = \text{Regime} \mid \text{Year} + \text{Nest}'(\text{Year}*\text{Regime}) + \varepsilon \qquad (6)$$

GLM was used to compare the pre-harvest egg volumes, yolk-to-albumen ratios and eggshell thickness at the start and predicted peak laying periods between sites under a harvested and un-harvested regime. This analysis was aimed at comparing the pre-harvest intrinsic quality of the sites, in terms of egg components. One-way ANOVA was used to assess the effect of egg harvesting by testing for differences in egg volumes, yolk-to-albumen ratios and shell thicknesses for eggs having the potential to hatch under the different harvesting regimes (i.e. eggs from start and peak laying under the un-harvested regime; eggs from end of harvest under the harvested regime).

A Binomial exact test was applied to the proportion of nests found to have egg abnormalities (white, half-white and small eggs) on the harvested and un-harvested sites, and also to the proportion of nests with failed eggs and dead chicks found on transects. Logistic regression was used in 2005 to test for an interaction in the effects of egg volume and treatment site on hatching success, and on breeding success. The logistic model used data from the central area on the large un-harvested colony for the control variable, aimed at comparing differences with the spatially similar harvested site.

2.4 Results

2.4.1 Tidal Flooding

Egg laying on all study sites started towards the end of the second week of April in all three study years, and peak laying had commenced by the first week in May. Flooding was recorded on the harvested tidal marshes in 2004 and 2005 in the fourth week of April and again in the first week of May in 2004, during the harvest period. Flooding occurred in the fourth week of May in 2006, after the licensed harvest period, on both the harvested and un-harvested colonies. Whole clutches were lost on the harvested site; however, on the un-harvested site most chicks were at least 10 days old and survived the flooding. The lack of flooding in 2004 on the tidal un-harvested site in Poole Harbour (Table 2.1a) meant that egg volume was uninfluenced by tidal flooding in this year, and this was reflected in the similar egg volumes between tidal and non-tidal large colonies (Fig. 2.1). This comparison of large colonies in 2004 also suggested that egg volume may have been uninfluenced by the disturbance caused by harvesting, since one site was classed as un-harvested and disturbed and the other as un-harvested and undisturbed (Fig. 2.1).

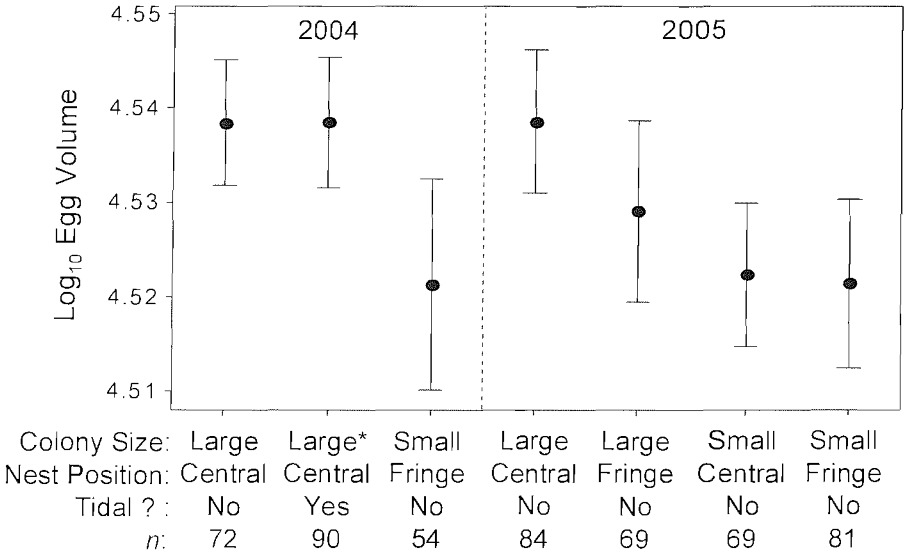


Figure 2.1. Mean egg volumes ±95% confidence intervals at un-harvested sites in 2004 and 2005. * Un-harvested site within harvested area.

2.4.2 Egg Volumes and Yolk-to-Albumen Ratio

Order of laying influenced egg volume, irrespective of treatment site (Order $F_{2,42} = 25.82$, $P < 0.001$, Site $F_{2,42} = 7.21$, $P < 0.01$, Order*Site $F_{4,42} = 1.13$, $P = 0.354$). Holm-

Sidak pairwise multiple comparisons revealed the third egg to be smaller than the first and second, which showed no volume difference (1st vs. 2nd $t = 0.525$, $P = 0.602$, 1st vs. 3rd $t = 3.988$, $P < 0.001$, 2nd vs. 3rd $t = 4.513$, $P < 0.001$). The consistency across sites in these intra-clutch differences enabled us to conduct further analyses on pooled egg volumes within a clutch of three eggs.

Colony size and nest position influenced egg volume in 2004, but not in 2005 (Table 2.2a and b). The post-hoc Tukey test on the 2004 dataset indicated that un-harvested eggs were larger from centrally positioned nests on large colonies compared to those located in both central and fringe position on a smaller colony. Effect sizes are shown in Figure 2.1. A similar (though non-significant) pattern is apparent in 2005, with egg volumes reducing from large to small colonies and from central to fringe nesting positions (Fig. 2.1). Egg harvesting, however, significantly reduced egg volume, with no interaction between years (Table 2.2c). Figure 2.2 shows effect sizes.

Table 2.2. Treatment site influences on egg volume, showing *F* values if $P<0.05$, otherwise n.s. = non significant. R^2-values give the fraction of total variation explained by the model.

a) General linear model (GLM), with un-harvested sites of varying colony size, nest position within the colony and tidal regime in 2004 (see Table 2.1a) as the explanatory variable.

Response (2004)	**Site** d.f. = 2, 98	**Nest'(Site)** d.f. = 98, 202	**R^2 %**
Log$_{10}$ Egg Volume	4.44	1.36	41.90

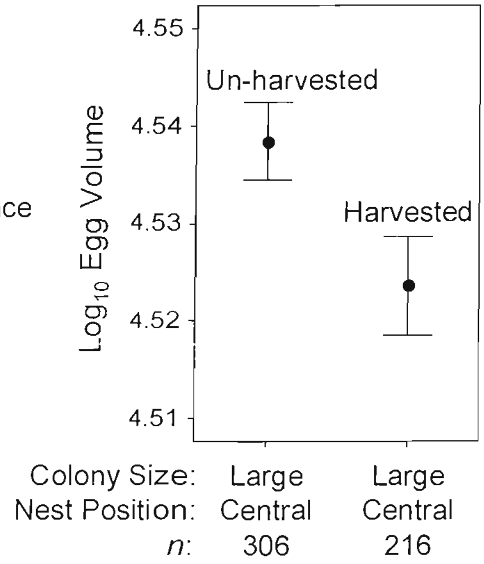
b) Three-factor nested GLM, with colony size and nest position on the un-harvested sites in 2005 as the explanatory variables.

Response (2005)	**Size** d.f. = 1, 97	**Position** d.f. = 1, 97	**Size*Position** d.f. = 1, 97	**Nest'(Size Position)** d.f. = 97, 202	**R^2 %**
Log$_{10}$ Egg Volume	n.s.	n.s.	n.s.	4.84	70.99

c) Three-factor nested GLM, with harvesting regime (harvested and un-harvested) and year (2004 and 2005) as the explanatory variables. Both treatments were situated in central positions on large colonies (Lymington and Poole Harbour in 2004; Pylewell and centrally positioned nests on Poole Harbour's large island in 2005, Table 2.1a).

Response	**Regime** d.f. = 1, 170	**Year** d.f. = 1, 170	**Regime*Year** d.f. = 1, 170	**Nest'(Site Year)** d.f. = 170, 348	**R^2 %**
Log$_{10}$ Egg Volume	12.24	n.s.	n.s.	2.24	54.20

Figure 2.2. Mean egg volumes ±95% confidence intervals at centrally positioned nests on large harvested and un-harvested sites in 2004 and 2005.



Egg volume depended on an effect of harvesting regime that changed between the start and predicted peak laying periods (Table 2.3a). Figure 2.3a shows egg volume under the un-harvested regime increasing slightly from the start to peak laying and egg volumes under the harvested regime increasing greatly over the same period of time. Although nest density had increased on the un-harvested site in 2005, 50% of the eggs collected during the predicted peak laying period were addled containing dead embryos up to 10 days old. The presence of addled eggs suggests that the collection period just preceded the peak of laying, at a time when the more competitive birds were acquiring territories from earlier breeders, resulting in early-laid eggs being destroyed or left unattended to addle (Weidmann, 1956; Patterson, 1965). Egg volume also depended on an overall difference between the start and predicted peak laying periods (Table 2.3a), with eggs from the predicted peak having larger volumes (Fig. 2.3a).

Figure 2.3b shows that similar patterns were observed in the yolk-to-albumen ratio, though these depended on harvesting regime and time effects that both changed between years (Table 2.3a). From 2005 to 2006, the ratio increased under the un-harvested regime and decreased under the harvested regime; also from 2005 to 2006, the ratio increased in the peak eggs and decreased in the early eggs (Fig. 2.3b). The yolk-to-albumen ratio also depended on an overall difference between the start and peak laying periods (Table 2.3a), with peak laid eggs having larger ratios (Fig. 3b).

Eggshell thickness was similar across the harvesting regimes, but depended on a time effect that changed between years (Table 2.3a). Eggs laid during the start of the season changed little in their shell thickness from 2005 to 2006, whilst eggs collected during the predicted peak laying period were thicker in 2006 (Fig. 2.3b). Eggshell thickness also depends on an overall difference between the start and predicted peak laying periods on an overall difference between years (Table 2.3a). Figure 2.3c shows that eggshells were thicker at the start of each season, and generally thicker in 2006.

More pronounced effects of harvesting regime were apparent in the comparison between eggs with the potential to hatch (all unharvested vs. end-of-harvest). For these, yolk-to-albumen ratio depended on an effect of harvesting regime that changed between years (Table 2.3b), with the ratio under the un-harvesting regime increasing from 2005 to 2006, while the ratio under the harvesting regime decreased (Fig. 2.3b). The egg volume, yolk-to-albumen ratio and eggshell thickness depended on an overall effect of harvesting regime (Table 2.3b), with each egg component being smaller under the harvesting regime compared to the un-harvested regime (Fig. 2.3a-c). Effect sizes are shown in Figure 2.3.

Table 2.3. General linear models, with Year (2005 and 2006), harvesting Regime (harvested and un-harvested, see Table 2.1b), and Time (start and peak laying and end of egg harvest) as explanatory variables, showing *F* values if $P<0.05$, otherwise n.s. = non significant.

(a) Comparison of eggs laid at the start of laying and the predicted peak period of laying, d.f = 1, 138.

Response	**Year**	**Regime**	**Year* Regime**	**Time**	**Year*Time**	**Regime *Time**	**Year* Regime *Time**	R^2 **%**
Log_{10} Egg Volume	n.s.	n.s.	n.s.	7.14	n.s.	6.14	n.s.	11.98
Log_{10} Yolk to Albumen Ratio	n.s.	n.s.	15.62	27.22	14.20	n.s.	n.s.	33.29
Eggshell thickness (mm)	6.05	n.s.	n.s.	9.75	6.20	n.s.	n.s.	13.28

(b) Comparison of eggs with the potential to hatch (all eggs laid under the un-harvested regime; eggs laid after egg-harvest under the harvested regime), d.f. = 1, 102.

Response	**Year**	**Regime**	**Year*Regime**	R^2 **%**
Log_{10} Egg Volume	n.s.	20.31	n.s.	19.35
Log_{10} Yolk to Albumen Ratio	n.s.	11.74	11.03	20.03
Eggshell thickness (mm)	n.s.	6.84	n.s.	9.38

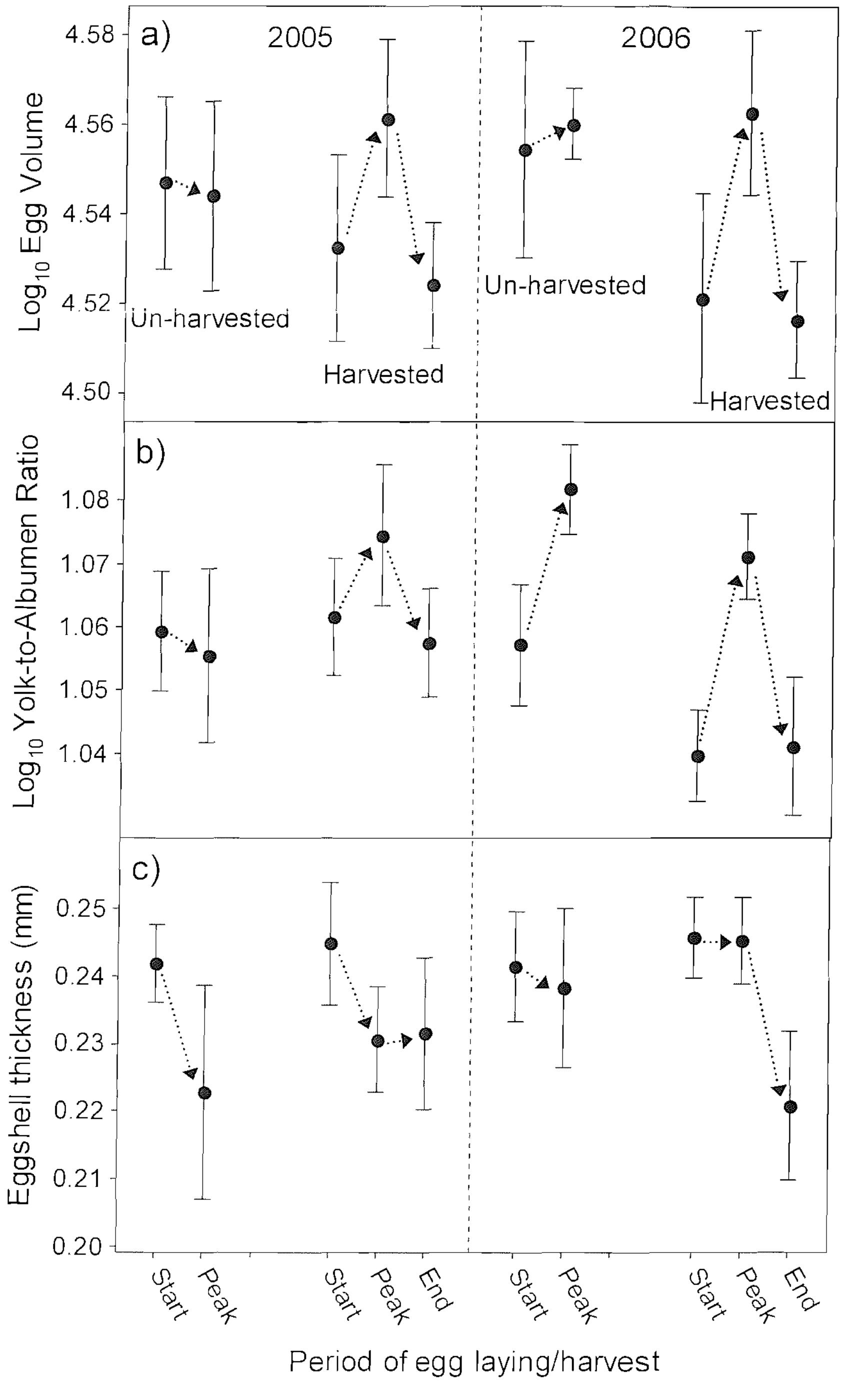


Figure 2.3. Differences in a) mean egg volume, b) mean yolk-to-albumen ratio, and c) eggshell thickness, ±95% confidence intervals, for eggs collected during the start of laying and the predicted peak laying period at the harvested and un-harvested sites, and also during the end of harvest at the harvested site. In 2006 *n* = 20 eggs per sample; in 2005 *n* = 19 for both time periods under the harvested regime, *n* = 18 for the start of laying under the un-harvested regime, and *n* = 10 for the predicted peak laying period under the un-harvested regime.

2.4.3 Egg Abnormalities

Both years had relatively higher numbers of white and half-white eggs, and abnormally small (yolkless) eggs on the harvested sites compared to the un-harvested sites (Table 2.4 and see Appendix A).

Table 2.4. Frequencies of abnormal eggs, failed eggs and dead chicks in Harvested : Un-harvested sites, and binomial exact P values in parentheses, testing the null hypothesis that egg abnormality ratios conform to the ratios of total nests in harvested and un-harvested sites respectively of 5243:9850 in 2005, and 6910:12230 in 2006 (300:300 for dead chicks in 2005 and 400:400 in 2006). In all cases, $P < 0.05$ indicates a significant bias towards abnormalities appearing at the collected site.

	White eggs	Half White eggs	Small eggs	Failed eggs	Dead Chicks
2005	10:3 (<0.001)	62:32 (<0.001)	16:9 (<0.001)	12:3 (<0.001)	16:5 (<0.001)
2006	13:9 (0.002)	54:23 (<0.001)	17:9 (<0.001)	5:2 (0.052)	8:1 (<0.001)

2.4.4 Hatching Success and Chick Survival

Failed (corroded) eggs were relatively more numerous on the harvested site in 2005 at least, with both years having a relatively higher number of dead chicks on the harvested sites (Table 2.4). The proportion of failed eggs and failed breeding attempts varied by egg volume and treatment site (Table 2.5). None of the un-harvested sites differed from the un-harvested control site (the central area of the large un-harvested site) in the logistic regression, whereas the central area of the large harvested site had a higher hatching and breeding failure than the un-harvested control site of similar size and nest position (Table 2.5). Figure 2.4 shows that failed breeding attempts tended to be from smaller eggs regardless of harvesting, and that birds that had experienced egg-harvest produced higher numbers of small failed eggs.

Table 2.5. Binary logistic regression on hatching failure and total failed breeding attempts (failed hatching plus dead chicks) compared to successful hatching and alive chicks from harvested and un-harvested sites of various colony size (large or small) and nest position (central or fringe) and egg volume.The central area of the large un-harvested site (Hatching failure *n* = 66, 7.58% *failed*; Failed breeding attempts *n* = 78, 8.97% *failed*) was used as a control against which to compare all other treatment sites, showing *P*- values, and % *failed* hatching or breeding attempts.

	Site	**Un-harvested Large Fringe**	**Un-harvested Small Central**	**Un-harvested Small Fringe**	**Harvested Large Central**	**Log10 Volume**	**R^2 %**
Hatching failure *n* (*% failed*)	<0.001 *n* = 5	0.420 *n* = 48 (*4.17*)	0.197 *n* = 45 (*2.22*)	0.998 *n* = 18 (*0.00*)	0.002 *n* = 53 (*29.52*)	0.042 *n* = 282 (*13.83*)	24.9
Failed breeding attempts *n* (*% failed*)	<0.001 *n* = 5	0.474 *n* = 69 (*13.04*)	0.105 *n* = 72 (*2.78*)	0.551 *n* = 34 (*5.88*)	<0.001 *n* = 73 (*32.88*)	0.024 *n* = 399 (*17.04*)	21.0

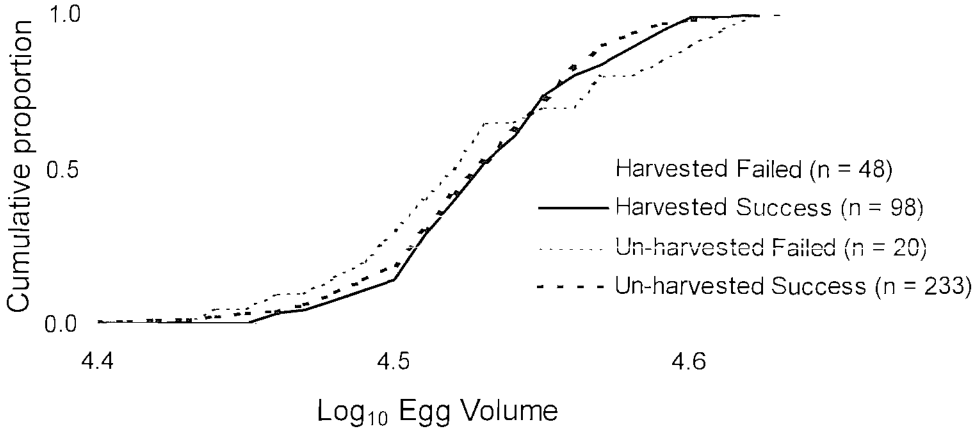


Figure 2.4. Cumulative proportion of egg volumes from harvested and un-harvested sites that either had a failed breeding attempt or were successful; *n* = total number of eggs in the sample.

2.5 Discussion

The principle difficulty with gauging the impact of egg harvesting is to find sufficient replicate sites to avoid confounding influences from tides, colony size and nest position. The reduced geographical range of black headed gulls means that insufficient colonies exist within the same geographical area to estimate interactions between all potential effects. To accommodate this limitation, we were careful in testing effects of harvesting regime to compare nests from similar positions within colonies of similar size, and to test effects of colony size and nest position separately in colonies not experiencing harvesting.

The black-headed gulls in our study laid a significantly smaller last egg (third egg) of a clutch in all situations. This is consistent with the literature for intra-clutch variation in gulls (Parsons, 1976; Houston et al., 1983; Meathrel and Ryder, 1987; Meathrel et al., 1987; Reid, 1987; Kilpi et al., 1996; Ruiz et al., 1998, 2000; Yorio and Garcia Borboroglu, 2002). Various authors describe the cause of the characteristic smaller third eggs as an adaptive mechanism, either to facilitate brood reduction, to act as insurance, or to decrease hatching asynchrony, while others view it as a non-adaptive consequence of the energy constraints experienced during clutch formation (see Reid, 1987; Salzer and Larkin, 1990; Kilpi et al., 1996 for reviews).

Egg volume was influenced by colony size and nest position within the colony in 2004, with egg volume being largest from nests found in a central position within large un-harvested sites. Reduced egg volumes translated to poorer hatching success and increased failed breeding attempts (Table 2.5). These results are thus consistent with Patterson (1965), that breeding success in black-headed gulls is highest in central positions within the main colony compared to the colony fringe and periphery. In addition to spatial influences, both egg volume and the yolk-to-albumen ratio were dependent on temporal factors, with eggs laid during the peak laying period being larger and having a higher yolk-to-albumen ratio at sites under harvested and un-harvested regimes (Table 2.3a). Young inexperienced seabirds breeding outside the peak laying period are well documented to have reduced egg size (Coulson and White, 1958; Lloyd, 1979; Croxall et al., 1992; de Forest and Gaston, 1996; Hipfner and Gaston, 1999; Hipfner et al., 2003), reduced yolk-to-albumen ratio (Hipfner et al., 2003), and chick survival (Patterson, 1965; Nisbet and Dury, 1972; Parson, 1975; Vermeer et al., 1991; Prévot-Julliard et al., 2001).

Egg harvesting reduced both egg volume and the yolk-to-albumen ratio (Fig. 2.2 and 2.3), which translated to a poorer hatching success and chick survival (Table 2.5). Reduced egg and yolk volumes, caused by egg harvesting, is further evident from the higher occurrence of abnormally small yolkless eggs on harvested sites compared to un-harvested sites (Table 2.4). Numerous studies on Laridae have shown that replacement eggs have reduced egg volumes (Parsons, 1976; Brown and Morris, 1996; Nager et al., 2000), lower yolk-to-albumen ratios (Nager et al., 2000), and, because of their lower intrinsic quality, reduced hatching success and chick survival (Nisbet and Dury, 1972; Lundberg and Väisänen, 1979; Monaghan et al., 1995; Nager et al., 2000). Moreover, replacement eggs have shown correlations between reduced egg size and the depletion of the female's endogenous proteins (Robbins, 1981; Houston et al., 1983; Bolton et al., 1992; Hipfner et al., 2003). Reductions in the laying females' condition through replacement laying, has been correlated with reduced ability to rear young (Heaney and Monaghan, 1995; Monaghan et al., 1998), increased susceptibility to disease (Oppliger et al., 1996), poorer adult survival (Visser and Lessells, 2001), and poorer future breeding propensity (Nager et al., 2001). In addition, the extra demands on a female for food to replenish depleted reserves may result in lower quality and even polluted areas being exploited, which can increase the occurrence of developmental defects and mortality in her offspring (Guthovà, 1993).

Eggs from harvested sites also had reduced eggshell thickness (Table 2.3b) and deposition of eggshell pigmentation (Table 2.4) compared to those from un-harvested sites. Deposition of eggshell pigmentation may act as an indication of female health, immunocompetence and stress, especially as the intensity of the two main background colours, blue-green and brown, found on black-headed gulls' eggs are inversely related to cell damage and free radicals (see Moreno and Osorno, 2003). Eggshells and nestling skeletons would appear to depend directly on the amount of foraged calcium (Mänd and Tilgar, 2003), which would potentially reduce in combination with reductions in the female's endogenous reserves and foraging efficiency (see Monaghan and Nager, 1997). Furthermore, an indirect mechanism operating through a trade-off between time spent searching for calcium rich items and time spent foraging for other nutrients, may also mediate calcium availability and thus the breeding performance (Graveland and Berends, 1997; Mänd and Tilgar, 2003). This could explain effect of time of laying and year on eggshell thickness and possibly the yolk-to-albumen ratio (Table 2.3a), as not only the availability of calcium rich items may vary temporally, but so could the time spent searching for such items if other nutritious items needed for yolk production were particularly low in abundance.

The results presented in this chapter are consistent with previous studies (Heaney and Monaghan, 1995; Monaghan et al., 1998), in suggesting that the condition of female black-headed gulls is being depleted on harvested sites to a level that affects the viability of some offspring. Interestingly, the increased occurrence of failed (corroded) eggs on harvested sites may also be influenced by the increase in ambient temperature during incubation, which is at least 3 weeks later in the season than un-harvested sites. Unfavourable humidity and temperature during incubation and hatching can causes the hatchling to stick to the membranes, preventing it from breaking out of the egg (Walsberg and Schmidt, 1992; Wissman, 1996). Furthermore, tidal flooding late in the season was found to affect only the harvested site, causing the loss of whole clutches and young chicks, and not un-harvested sites where the chicks were older and more robust to floods. Both protracted and replacement laying induced by egg harvesting therefore has two components of cost: a direct cost of increased effort in egg formation, and the consequence of being late.

Set against the background of increasing concern about the long-term conservation status of black headed gulls in the UK (Gregory et al., 2002) our findings give cause for a re-evaluation of government policy on commercial egg harvests, particularly as many of the coastal sites where the gulls breed are also threatened by destruction of habitat associated with sea level rise, climate change and the dieback of *Spartina* marsh. The sites around the Lymington Estuary have already lost 81% of marshes since 1921 (Colenutt, 2005).

CHAPTER 3. ASSESSING THE INFLUENCE OF COMMERCIAL EGG HARVESTING AGAINST OTHER ENVIRONMENTAL INFLUENCES ON THE DISTRIBUTION OF GROUND-NESTING SEABIRDS ON THE SOUTH COAST OF ENGLAND

Contributions: Lord, B. = defining the mission; Doncaster, C.P., Hudson, M.D. = advice on design; Wood, P.J. = planning design, scheduling and logistics of fieldwork, collecting data (with assistance from people in the Acknowledgements), doing analysis, interpreting and reporting results.

3.1 Abstract

Little is known of the effects of egg harvesting on breeding distributions of target and non-target species of ground-nesting seabirds. The harvesting of Black-headed Gulls eggs takes place annually under government licence in Hampshire, southern England, on saltmarshes which also provide breeding habitat for Mediterranean Gulls, Common Terns, Sandwich Terns and Little Terns. Evidence presented here suggests that such multi-species colonies are susceptible to site abandonment and that egg harvesting on the south coast of England may contribute to this instability, sometimes acting in concert with predation or other forms of disturbance. Black-headed Gulls and Mediterranean Gulls appear to be affected directly by egg harvesting, which contributes to shaping their breeding distribution. The tern species, which start breeding after the harvesting season, may be susceptible to indirect effects such as abandonment of a harvested site when the number of nesting Black-headed Gulls becomes too low to provide adequate defence against predators. In addition to harvesting, environmental factors such as tidal flooding and predation have caused reductions in the breeding success of seabird species, and are likely to have influence their distributions along the south coast of England.

3.2 Introduction

Eggs have been harvested from seabird colonies world-wide for centuries (Burger and Gochfeld, 1994). The effects of egg harvesting on the target species' breeding success are considered in chapter 2; and the effects on population distribution have not been fully investigated, although egg harvesting has been shown to pose a threat to some seabird populations (Haynes, 1987; Burger and Gochfeld, 1994; Feare, 1976a; Vermeer et al., 1991; González, 1999; Zador et al., 2005), and has been attributed to a decline in others (Ainley and Lewis, 1974; de Juana, 1984; Storr et al., 1986; Shannon and Crawford, 1999). The disturbance associated with egg harvesting on non-target species has also received little attention, and relatively few studies on human disturbance have looked at the effects on multi-species colonies (Blumstein et al., 2005).

Some impacts of harvesting disturbance may be inferred from studies of investigator and recreational disturbance effects on the breeding success of seabirds. Human disturbance has been associated with declines in breeding success in numerous species and is of general concern to conservationists (Carney and Sydeman, 1993). In nesting seabirds, human intrusion has been shown to reduce hatching and fledging success (Hunt, 1972; Roberts and Ralph, 1975; Anderson and Keith, 1980; Burger, 1981; Fetterolf, 1983; Safina and Burger, 1983; Beale and Monaghan, 2004), to reduce population sizes (Hand, 1980), to preclude breeding from certain breeding grounds (Erwin, 1980; Woehler et al., 1994), and to increase nest desertion (Hunt, 1972; Southern and Southern, 1982; Massey and Fancher, 1989).

Birds respond to human disturbance in the same way as they respond to the risk of predation (Beale and Monaghan, 2004), by increasing their heart rate (Wilson and Culik, 1995; Weimerskirch et al., 2002), increasing alarm or defensive behaviours (Kirkman, 1937; Keller, 1989) and ultimately avoiding areas of high risk, either completely or for the period of risk (Gill et al., 1996; Ghalambor and Martin, 2001). During breeding, stress and physiological responses such as increased heart rate result in an increase in metabolic requirements at a time of high energy demands (Fyhn et al., 2001). This may cause the physiological condition of disturbed breeding birds to decline faster than that of undisturbed birds, ultimately resulting in lower attendance and greater nest desertion (Coulson and Johnson, 1993; Cadiou and Monnat, 1996). Nesting colonial seabirds often flush from nests when approached by humans, in an attempt either to intimidate the potential predator or to flee from danger (Anderson and Keith, 1980; Burger, 1982). During flushes, nest contents can be spilled, exposed to intra- and inter-specific predators (Kury and Gochfeld, 1975; Anderson and Keith, 1980; Götmark, 1992; Bolduc and Guillemette, 2003), or perish from exposure to the elements during abandonment (Hunt, 1972). Furthermore, investigator disturbance has been shown to increase fatal attacks on conspecific young (Kirkman, 1937; Fetterolf, 1983), and to increase the attractiveness of an area to opportunistic predators (Gutzwiller et al., 2002).

The current impetus for assessing impacts of human disturbance arises from the growing body of environmental legislation and the increasing importance placed on bird conservation (Hill et al., 1996). As yet, however, there is little guidance as to how such impacts should be assessed (Hill et al., 1997). The European Community Directive on the Conservation of Wild Birds (EC/79/409) refers to the protection, management, and control of all species of naturally occurring wild birds throughout Europe. Member States are expected to secure their obligations to protection of bird habitats by classifying suitable territories as Special Protection Areas (SPAs), in which steps must be taken to avoid habitat degradation and disturbances affecting the birds. The conservation importance of such sites is evaluated in terms of the birds listed in Annex 1 of the Directive. Rare and declining birds designated as Schedule 1 under the Wildlife and Countryside Act (1981 as amended), have further protection during breeding insofar as it is an offence to intentionally (a) disturb the bird while it is building a nest or is in, on or near a nest containing eggs and young, or (b) disturb dependent young of such a bird.

In this chapter, we investigate the influence of an egg-harvest on the breeding distribution of the target Black-headed Gull *Larus ridibundus*, and associated disturbance effects of harvesting on the breeding distribution of non-target seabird species. The study is confined to the south coast of England, a stronghold for black-headed gulls and the front line of northerly colonisation of Mediterranean gulls.

3.3 Methods

3.3.1 Study Sites

Eggs are harvested from Black-headed Gull colonies found on saltmarshes in Hampshire, Southern England, under licence through the UK Department of the Environment Food and Rural Affairs (DEFRA) for consumption and market. Licences are valid from the start of egg laying until 15th May, after which the birds are left to incubate their broods. These coastal colonies are within the Solent's SPAs from the North Solent National Nature Reserve (NNR) on the Beaulieu Estuary westward to Hurst Spit (Fig. 3.1). These colonies also provide breeding areas for Schedule 1 and Annex 1 Mediterranean Gulls *Larus melanocephalus* and Little Terns *Sterna albifrons*, and Annex 1 Common Terns *Sterna hirundo* and Sandwich Terns *Sterna sandvicensis*, along with small numbers of breeding wading birds. Roseate terns *Sterna dougallii* are occasional breeders in southern England but in such small numbers that they are not considered here. We chose to focus on the gull and tern colonies surrounding these harvested colonies along the south coast of England. Egg harvesting on all other Black-headed Gull colonies in the south of England has either never occurred or is now prohibited due to the presence of Mediterranean Gulls (Table 3.1). To establish any effects on population distribution of tern species we included all tern colonies, both mixed and single species colonies, within our study area.

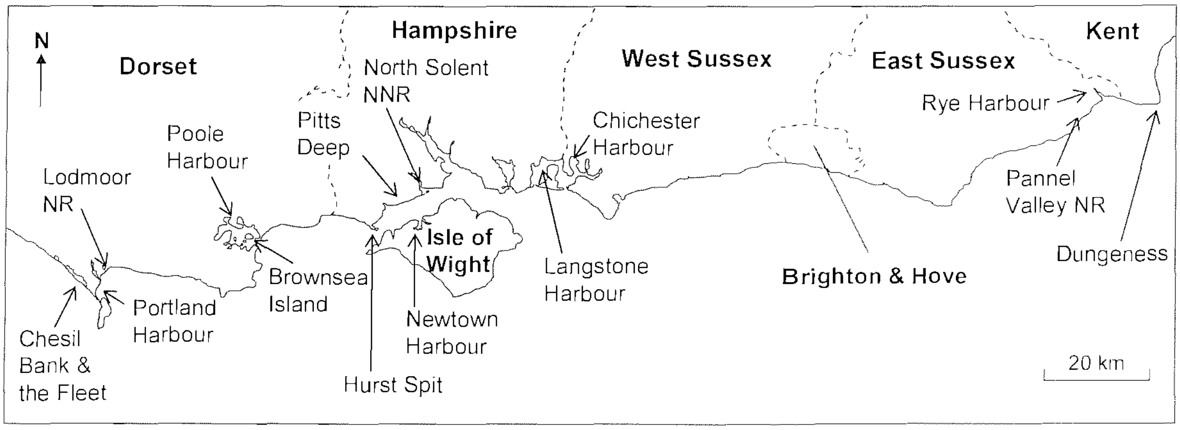


Figure 3.1. Gull and tern colonies on the south coast of England from 1960 to 2006.

Table 3.1. Breeding sites of ground-nesting seabirds on the south coast of England, with the history of Black-headed gull egg harvesting since the 1960s, and present site designations. cSAC = candidate Special Area of Conservation under the EU Habitats Directive 92/43/EEC, SPA = European Special Protected Areas under the EU Birds Directive EC/79/409, Ramsar = Wetlands of International Importance, SSSI = Site of Special Scientific Interest under the National Parks and Access to the Countryside Act 1949.

Site (see Fig. 3.1)	Harvesting History	Designations
Poole Harbour	Harvested to early-1990s	cSAC, SPA, Ramsar, SSSI
Brownsea Island	Un-harvested	
Chesil Bank and the Fleet	Un-harvested	
Portland Harbour	Un-harvested	
Lodmoor NR	Un-harvested	SSSI
North Solent NNR	Harvested	Solent Maritime cSAC, SPA, Ramsar, SSSI
Pitts Deep to Hurst Spit	Harvested	
Langstone Harbour	Un-harvested	
Newtown Harbour	Un-harvested	
Chichester Harbour	Un-harvested	
Rye Harbour	Un-harvested	SPA, SSSI
Pannel Valley NR	Un-harvested	
Dungeness	Un-harvested	SAC, SPA, SSSI

3.3.2 Data collection

Literature was sought for references to breeding seabirds along the south coast of England. Data on breeding numbers and productivity were collated directly from nature reserves, from regional bird reports, from the reports on 'Seabird numbers and breeding success in Britain and Ireland' from 1990 to 2005, and from the Seabird 2000 census (Mitchell et al., 2004). During each breeding season in 2004 to 2006, we conducted counts of Apparently Occupied Nests (AON) on the marshes from North Solent NNR to Hurst Spit and the saltmarsh islands found at the top of Poole Harbour (Fig. 3.1). A group of trained volunteers conducted the AON counts by placing a piece of raw pasta in nests from pasta bags of known quantity. The pasta marker prevented double counting of nests, and provided a nest count from the quantity of pasta used (subtracting the quantity of pasta remaining from the known start quantity).

Collated data, from reserves and reports, on colony numbers were not all conducted in a co-ordinated manner and may have been carried out using various techniques (see Walsh et al., 1995) and during various times during the breeding season. Consequently, both under-counting and over counting may have occurred. Nevertheless, an error of ±12.5% in a population of 20,000 pairs would give a range of 17,500 – 22,500 pairs and in a population of 5,000 pairs a range of 4375 – 5625 pairs. If this is a reasonable achievable level of accuracy, sampling methodology is unlikely to mask any major population changes. Where a colony size was given as a range, the midpoint has been used in subsequent analyses.

3.4 Results

3.4.1 Regional Changes in Seabird Populations

3.4.1.1 Black-headed Gulls

The range of the Black-headed Gull has greatly expanded since the 19th century (Cramp, 1983). The British population of Black-headed Gulls increased exponentially from 1928 to 1973, with the total of 105,200 AON in 1973 being more than double the number found in a survey in 1938 (Mitchell et al., 2004). An influx of birds from Europe boosted the rapid growth during this period, especially in southern England (Aspinall et al., 1993). Further agents of growth may have included climatic amelioration (Reid-Henry and Harrison, 1988), reduced persecution, increased food supplies through opportunistic scavenging, and the development of breeding sites in association with salt marsh expansion during colonisation by *Spartina* (Aspinall et al., 1993). From 1973 to the Seabird Colony Register (SCR) census of 1985-88, the population in England and Wales declined by approximately 20% (Lloyd et al., 1991), alongside a similar reduction in the British breeding (Sharrock, 1976; Gibbons et al., 1993). This trend continued through to the Seabird 2000 census (in conjunction with declines in Denmark: Grell, 1998; Heldbjerg, 2001), with a further 16% reduction in the breeding population in Britain and a 50% reduction in breeding distributions (Mitchell et al., 2004). For these reasons the Black-headed Gull was moved onto the 'Amber' list published in 'The Population Status of Birds in the UK. Birds of Conservation Concern: 2002-2007' (Gregory et al., 2002).

The total numbers on the south coast of England, however, showed little overall change between the 1985-88 SCR and the Seabird 2000 censuses, although some areas declined while others increased (Fig. 3.2).

The harvested colony at North Solent NNR in Hampshire had remained stable at around 1,200 pairs for at least 6 years from the mid-1950s, when an isolated halt on the egg harvest in 1963 coincided with a trebling of the gull population in the subsequent year to 3,900 pairs which consequently triggered a population explosion (Taverner, 1966). The North Solent NNR colony peaked in 1970-72 at 17,000 – 21,000 pairs, making this colony the largest on the south coast of England (Aspinall et al., 1993). Subsequently the colony started to decline and although gull numbers remained relatively stable throughout the first half of the 1980s, averaging 12,500 pairs, after 1986 the colony declined rapidly to extinction by 2006.

North Solent NNR's adjacent harvested colony at Pitts Deep to Hurst Spit (Fig. 3.1) has remained relatively stable since the 1970s with numbers fluctuating around 5,000 – 8,000 pairs (Table 3.2). The un-harvested colonies in Hampshire and the Poole Harbour colony in Dorset, however, have experienced rapid growth since the early 1990s (Fig. 3.2). Harvesting was stopped in the early 1990s in Poole Harbour due to appearance of breeding Mediterranean Gulls. Comparing the average number of pairs from harvested colonies and un-harvested colonies in Hampshire and the Poole Harbour colony, around the date of harvest cessation in Poole Harbour, suggests that the birds from North Solent NNR did not move to the adjacent harvested site, but possibly to Poole Harbour to the west and the un-harvested colony in Lanstone Harbour, Hampshire to the east (Table 3.2).

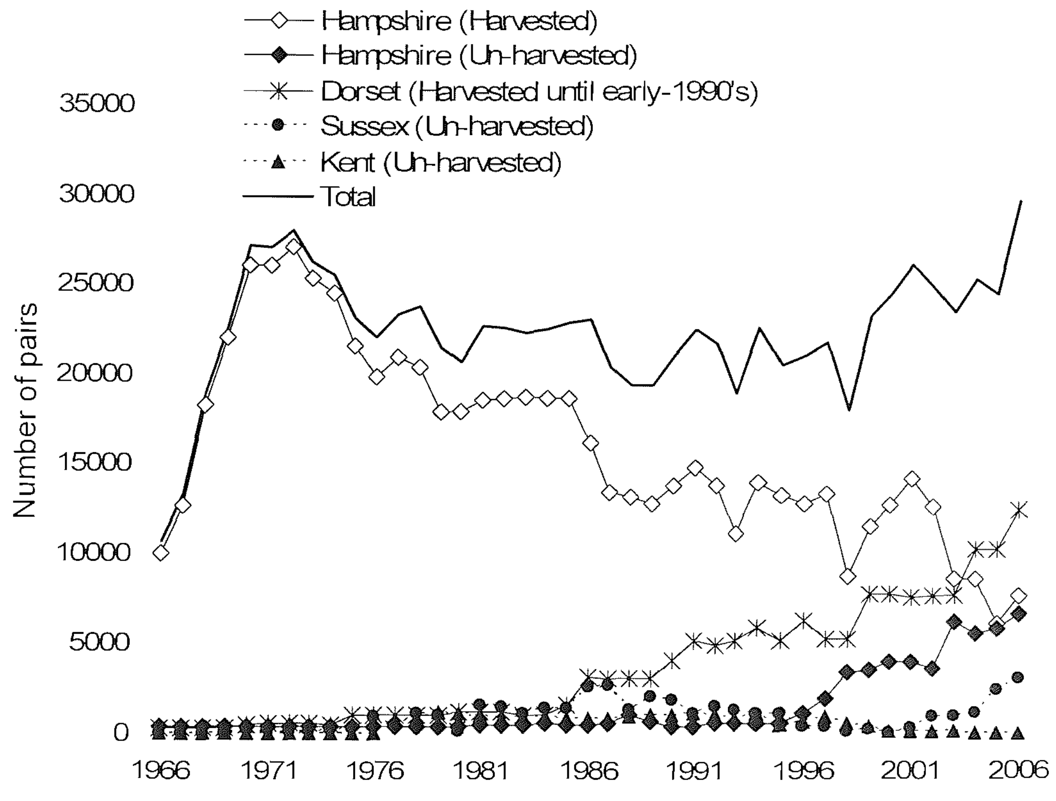


Figure 3.2. Number of Black-headed Gull pairs in harvested and un-harvested regions on the south coast of England from 1966 to 2006.

Table 3.2. Mean numbers of Black-headed Gull Pairs in harvested and un-harvested regional colonies on the south coast of England from 1973 to 1989 and 1990 to 2006, which amounts to 16 year periods around the 1990 cessation of Black-headed Gull egg harvesting in Poole Harbour, Dorset.

Regional colonies	**Mean (±SD) number of pairs between 1973-1989**	**Mean (±SD) number of pairs between 1990-2006**	**Mean change in number of pairs from 1973-1989 to 1990-2006**
Hampshire (Harvested)	*18,606 (± 3,504)*	*11,559 (± 2,663)*	*-7,047*
North Solent NNR	12,721 (±3,479)	4,928 (±3,019)	-7,793
Pitts deep to Hurst Spit	5,885 (±523)	6,631 (±693)	+746
Hampshire (Un-harvested)	*443 (± 167)*	*2,850 (± 2,257)*	*+2,407*
Langstone Harbour	31 (±55)	2,068 (±1,906)	+2,037
Newtown (Isle of Wight)	411 (±119)	782 (±393)	+371
Dorset (Harvested until early 1990's)	*1,490 (± 913)*	*6,921 (± 2,289)*	*+5,431*
Poole Harbour	1,441 (±917)	6,784 (±2,265)	+5,343
Brownsea Island	49 (±68)	137 (±62)	+88
Sussex (Un-harvested)	*1,143 (± 781)*	*1,025 (± 823)*	*-118*
Chichester Harbour	908 (±551)	407 (±574)	-501
Rye Harbour	235 (±343)	507 (±553)	+272
Pannel valley NR	0	111 (±316)	+111
Kent (Un-harvested) - Dungeness only	*704 (± 416)*	*489 (± 433)*	*-215*
		Total south coast change:	+1132

Since the Seabird 2000 census, breeding numbers appear to be increasing on the south coast, dominated by increases at un-harvested colonies in Hampshire, Dorset and Sussex (Fig. 3.2), with the Poole Harbour colony in Dorset now holding the largest Black-headed Gull colony on the south coast of England. This period saw extinctions at two smaller un-harvested sites (Dungeness in Kent and Chichester in East Sussex), as well as the harvested North Solent NNR colony. Figures suggest that the birds from Dungeness and Chichester moved to the adjacent colonies of Rye Harbour and Langstone Harbour, respectively (Table 3.2).

3.4.1.2 Mediterranean Gulls

The Mediterranean Gull is the most recent addition to breeding seabirds of Britain. The currently small and scattered breeding population of Mediterranean Gulls in Britain and Ireland is distributed amongst Black-headed Gull colonies (Mitchell et al., 2004), which have similar laying times from late-April to early-May (Harrison and Castell, 2002). The range of Mediterranean Gulls has expanded greatly over the last 50 years, and the movement into Britain has been part of a wider expansion of the species westward into Europe (Meininger and Bekhuis, 1990; Bekhuis et al., 1997). Breeding numbers in Britain and Ireland have dramatically increased since the mid-1980s, when only a few pairs were recorded, with 224-226 pairs being recorded in 2005, over half of which were nesting in southeast England, a stronghold for the species (Mavor et al., 2006).

Mediterranean Gulls were first recorded breeding in Britain in 1968 at the south coast's largest harvested Black-headed Gull colony, North Solent NNR. They never exceeded 5 pairs, however (Taverner, 1972; R. Lord, pers. comm.). A similar pattern is apparent at the other harvested sites in Hampshire (Fig. 3.3), with low numbers sporadically attempting to breed from Pitts Deep to Hurst Spit (P. Durnell, pers. comm.). Breeding numbers in Britain remained low until the late-1990s, when colonies developed at un-harvested sites in Kent and Hampshire, and the latter population has since rapidly increased (Fig. 3.3). There was a slight dip in the population explosion at the un-harvested Hampshire colony (Langstone Harbour) in 2002 (Fig. 3.3) which coincided with a decrease in Black-headed Gull and tern numbers.

Un-harvested sites in Dorset and Sussex have also seen rapid growth in breeding numbers of Mediterranean Gulls since colonisation (Fig. 3.3). Productivity at the colony in Sussex (Rye Harbour) has been high; averaging 1.1 ± 0.22 fledged young per pair from 2001 to 2006, which is likely to have contributed to the growth. These population increases occurred in conjunction with those seen in their breeding associates, Black-headed Gulls (Fig. 3.2). Similarly, Mediterranean Gulls have mirrored Black-headed Gulls in patterns of site abandonment, as seen at the only colony in Kent (Fig.3.3).

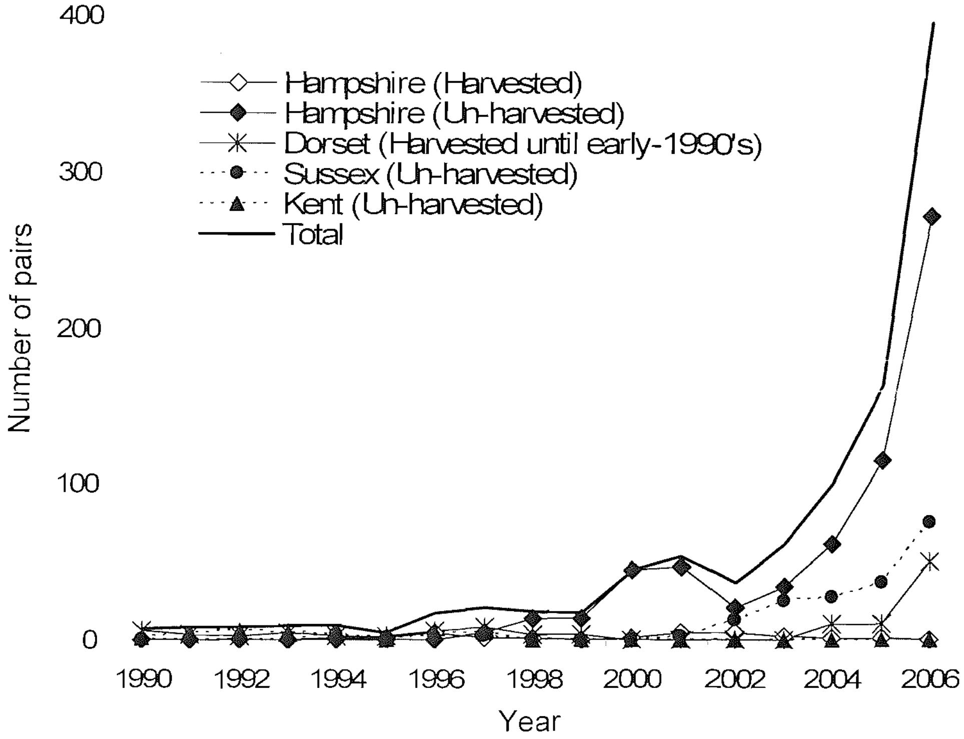


Figure 3.3. Number of Mediterranean Gull pairs in harvested and un-harvested regions on the south coast of England from 1990 to 2006. Note: Harvesting regimes refer to that imposed on Black-headed Gulls, the Mediterranean Gulls' breeding associate.

3.4.1.3 Common Terns

Common Terns have the widest breeding range of seabirds in Britain and Ireland, though they are not the most abundant species (Mitchell et al., 2004). Common Terns start egg laying at similar times to Sandwich Terns and Little Terns, from mid-May to the end of June (Moxom and Burden, 2004). All tern populations in northwest Europe were brought to the brink of extinction at the end of the 19th century by egg collection for food and hunting of adults for the millinery trade, but they recovered well in response to protective legislation in the early-20th century (Mitchell et al., 2004). The breeding population of Common Terns in Britain has remained relatively stable over the last three decades, although there has been great variation between regions (see Mitchell et al., 2004 for details). The population breeding on the south coast of England has mirrored the trends seen throughout Britain, and now appears to be increasing (Fig. 3.4).

Chesil Bank in Dorset (Fig. 3.1) was the stronghold for Common Terns in southwest England during the first half of the 20th century, with approximately 1000 pairs in 1955 (Moxom and Burden, 2004). Numbers declined steeply with low productivity until 1985-88 when a single pair was recorded. Figures suggest that the birds displaced from Chesil Bank moved to the nearby purpose-built islets on Browsea Island and Lodmoor nature reserve in Dorset (Moxom and Burden, 2004), now the stronghold colonies in Dorset. The only colony in Kent, Dungeness has also experienced declines which started in the early 1990s, which have also been attributed to low productivity (Fig. 3.4). It appears from the figures that these birds moved to nearby Rye Harbour and the Pannel Valley nature reserves in Sussex (Fig. 3.1, Fig. 3.4).

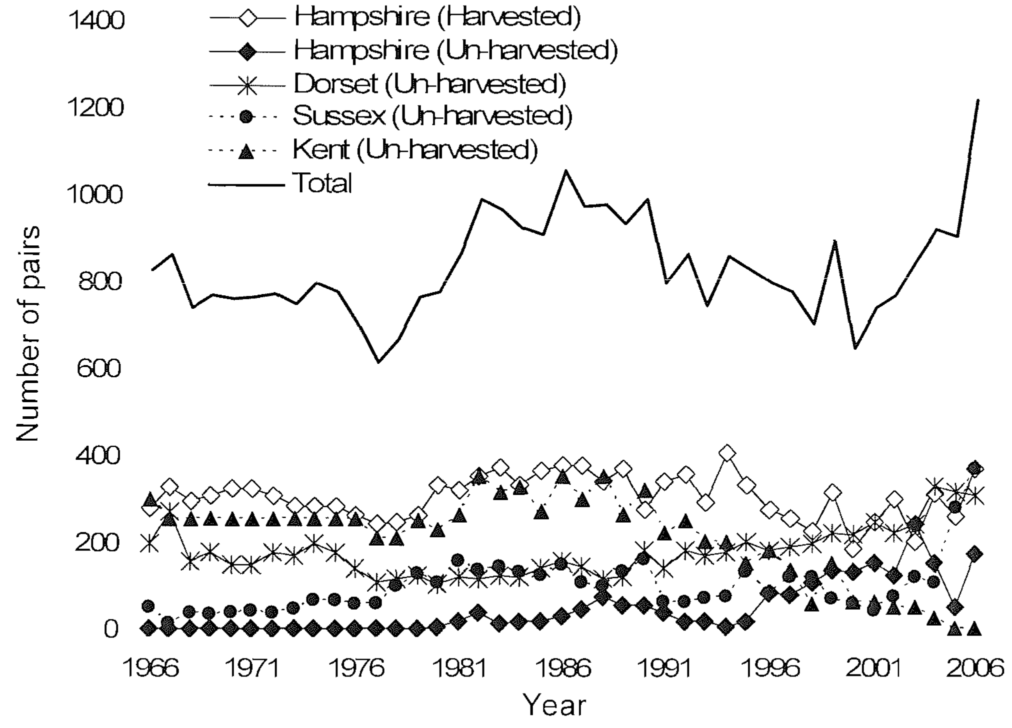


Figure 3.4. Number of Common Tern pairs in harvested and un-harvested regions on the south coast of England from 1966 to 2006. Note: Harvesting regimes refer to that imposed on Black-headed Gulls, where Common Terns are breeding within those colonies.

The decline and subsequent site abandonment at the harvested Black-headed Gull colony at North Solent NNR coincided with the site abandonment by all tern species, which preceded site abandonment by all gull species. Figures suggest that Common Terns from North Solent NNR possibly moved to the nearby harvested area from Pitts Deep to Hurst Spit during this period, causing Common Tern breeding numbers within Hampshire's harvested Black-headed Gull colonies to appear stable since 1966 (Fig. 3.4). However, national or even international immigration cannot be ruled out. Common Terns breeding on the edge of Hampshire's un-harvested Black-headed Gull colony at Langstone Harbour have been increasing since the 1980s (Fig. 3.4). This rapid growth may be attributed to the collapse of the colony at nearby un-harvested colony at Chichester Harbour (A. de Potier, pers. comm.).

3.4.1.4 Sandwich Terns

Sandwich Terns exhibit the most erratic population trends and distributions of any seabird breeding in Britain and Ireland (Mitchell et al., 2004). The population fluctuates dramatically between years in response to large variations in the proportion of mature birds attempting to breed, and the distribution varies in response to mass movements of birds among widely distributed coastal sites (Cramp, 1983; Mitchell et al., 2004). Despite frequent changes in the colony sites used, the broad distribution of Sandwich Terns in Britain and Ireland has remained remarkably similar over the last 30 years (Mitchell et al., 2004).

England's south coast population mirrored the growth seen in the whole of Britain and Ireland from the 1920s to the mid-1980s, and the subsequent decline between the SCR and Seabird 2000 censuses (Fig. 3.5). This decline has been linked to discrete events occurring at individual colonies rather than broader environmental causes, many of which were associated with predation (Mitchell et al., 2004). The British and Irish population appear now to be in a recovery stage (Mitchell et al., 2004), and the population on the south coast of England has been increasing since 2001 (Fig. 3.5).

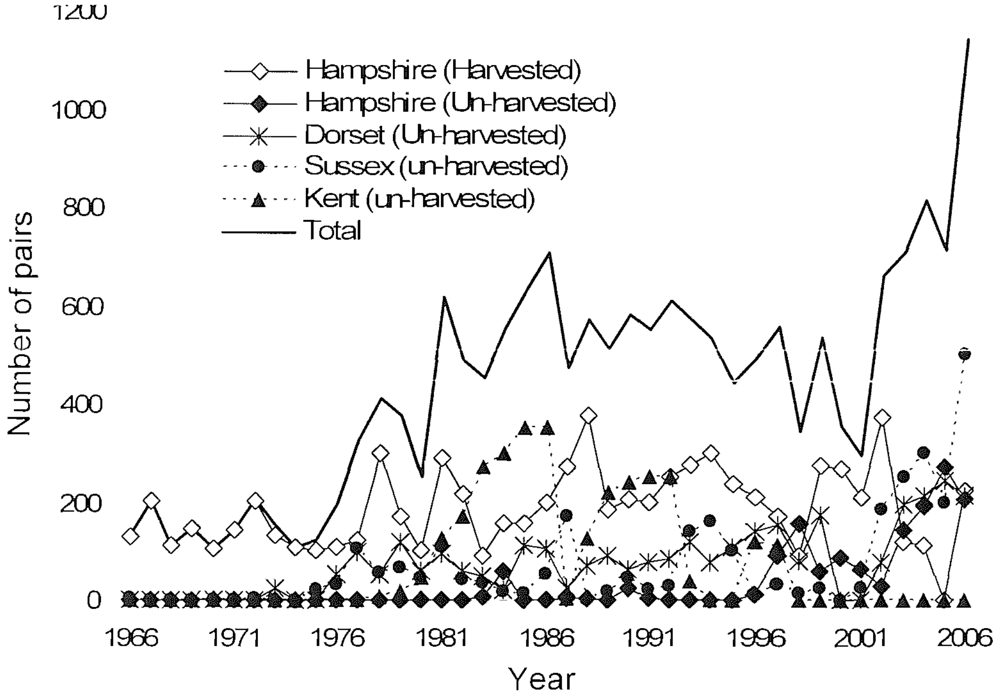


Figure 3.5. Number of Sandwich Tern pairs in harvested and un-harvested regions on the south coast of England from 1966 to 2006. Note: Harvesting regimes refer to that imposed on Black-headed Gulls, where Sandwich Terns are breeding within those colonies.

Sandwich Terns breeding at sites where Black-headed Gull eggs are harvested in Hampshire have remained relatively stable from the mid-1960s (Fig. 3.5). There appears to have been a shift of breeding pairs from North Solent NNR to the nearby Pitts Deep to Hurst Spit region, following the collapse of the Black-headed Gull colony at North Solent NNR. Sandwich Terns abandoned the all harvested sites in Hampshire in 2005, possibly due to total colony failure in 2004, attributed to severe storms (P. Durnell, pers. comm.). These birds may have redistributed to Brownsea Island in Dorset to the west and Langstone in Hampshire's un-harvested Black-headed Gull colony to the east (Fig. 3.5): which both had their highest breeding numbers to date in 2005.

Brownsea Island, the only Sandwich Tern colony in Dorset, saw its first breeding attempts in 1972 and after a few years of unstable breeding, numbers have remained relatively stable (Fig. 3.5). The colony was abandoned from 2000 to 2001, which has been attributed to almost total breeding failure in 1999 (Upton et al., 2000). Total site abandonment of Sandwich terns took place at Chichester Harbour and Dungeness during the mid-1990s, during the rapid decline in Black-headed Gull numbers. Shortly after these site desertions, Rye Harbour in Sussex experienced a rapid population increase (Fig. 3.5). Chichester's birds, however, are more likely to have moved to the nearby un-harvested Hampshire site at Langstone Harbour (A. de Potier, pers. comm.), which has also experienced a rapid increase since the mid-1990s (Fig. 3.5).

3.4.1.5 Little Terns

The Little Tern is the smallest tern breeding in Britain and Ireland. Although colonies can be found around much of the British coastline, breeding is concentrated in the south and east of England, where the species' preference for beaches also favoured by people makes it vulnerable to disturbance (Mitchell et al., 2004).

Following a decline during the 19th century, the Little Tern population in Britain increased during the early-20th century, peaking in the 1930s. Thereafter, numbers fell once again until Operation Seafarer (1969-70; Cramp et al., 1974), after which they then increased to a peak in the mid-1970s, followed by a long-term decline that reached an all-time low in 1998 (Mitchell et al., 2004).

Little Terns nesting on the south coast of England appear, like other terns, to have moved between breeding sites (Fig. 3.6). Since the mid-1960s the Little Tern populations breeding within harvested Black-headed Gull colonies have declined, largely owing to the decline of all species at North Solent NNR (Fig. 3.6). Little Tern numbers at the harvested sites from Pitts Deep to Hurst Spit also declined during the 1980s and 1990s, suggesting that the birds leaving North Solent NNR were not relocating to this neighbouring site. However, numbers have increased slightly at Pitts Deep to Hurst Spit since the abandonment of North Solent NNR. Little Tern numbers at the un-harvested site in Hampshire (Langstone Harbour) increased rapidly during the 1980s, and again after a period of decline in the early-1990s, eventually reaching a record number in 2002 (Fig. 3.6). The first increase at Langstone Harbour has been attributed to a decline at the nearby colony at Chichester Harbour in Sussex (A. de Potier, pers. comm.). The second increase at Langstone Harbour may be a product of the combined losses at North Solent NNR, Rye Harbour (the only remaining colony in Sussex), and Chesil Bank to Portland Harbour (the only colony in Dorset) (Fig. 3.6).

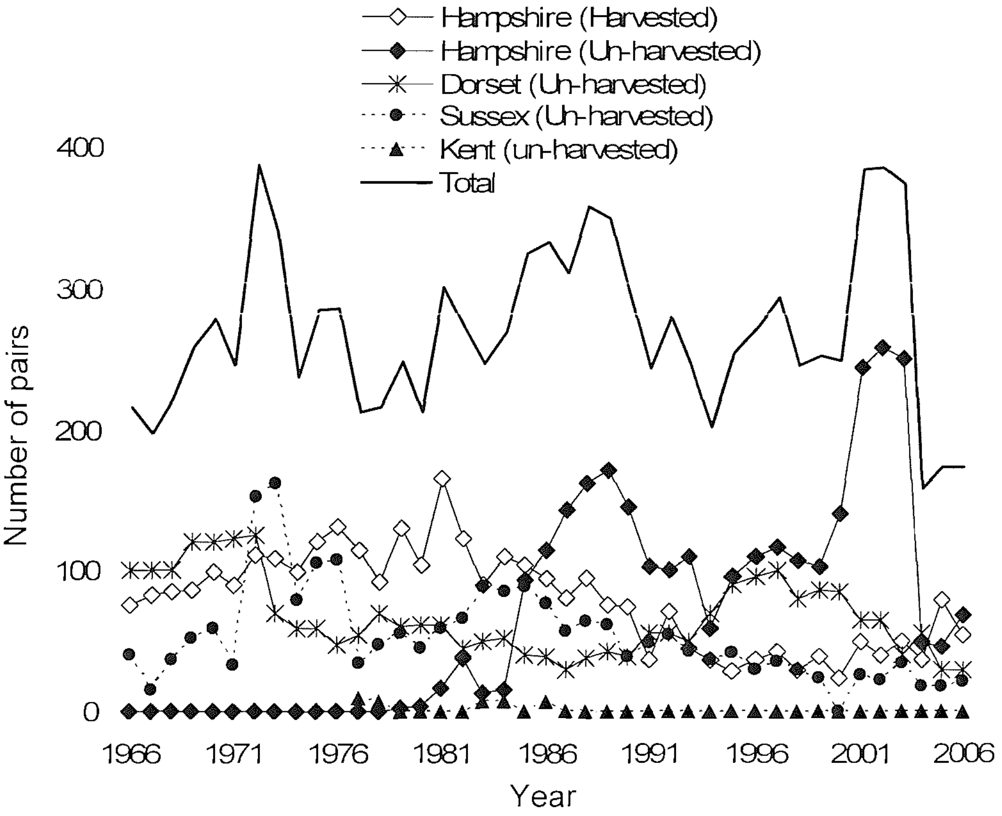


Figure 3.6. Number of Little Tern pairs in harvested and un-harvested regions on the south coast of England from 1966 to 2006. Note: Harvesting regimes refer to that imposed on Black-headed Gulls, where Little Terns are breeding within those colonies.

Little Tern numbers on the south coast of England, unlike the other species studied in this chapter, have dramatically reduced since the Seabird 2000 census (Fig. 3.6). This has been attributed to successive low productivity (Ratcliffe, 2003). From 1989 to 1994 the average productivity for Little Terns breeding on the south coast of England remained below 0.5 fledged young per pair. Productivity generally increased between 1995 and 2001, but then reduced further to <0.2 up to 2005. This low productivity has been attributed to mammalian predation (particularly Foxes), high tides, bad weather and human disturbance (Mitchell et al., 2004).

3.4.2 Causes of Change

3.4.2.1 Predation

At North Solent NNR in 2004-06, we found substantial evidence of heavy predation by Red Foxes *Vulpes vulpes*. Foxes found easy access to the main colony when a shingle bar was constructed in 1986 joining Gull Island with the mainland in an attempt to reduce marsh erosion. Fox predation can greatly reduce the colonies productivity and thus recruitment for the following years. Heavy predation events may also reduce the attractiveness of a site and cause site abandonment. In 2004 we observed Fox predation that caused almost total breeding failure on one of the harvested marshes from Pitts Deep to Hurst Spit. The following year saw a 48% reduction in Black-headed Gull numbers on this marsh, despite a concerted campaign of Fox trapping by the local conservation warden in the area immediately onshore from the colony. By 2006, however, numbers had risen again by 41%. Similarly, the decline in gull and tern numbers at Dungeness and Chesil Bank have been attributed to mammalian predation, mostly from Fox (P. Akers pers. comm.; Moxom and Burden, 2004) with some evidence of American Mink *Mustela vison* predation at Dungeness (P. Akers pers. comm.). Here predation has caused low productivity and in some years total colony failure, and at Dungeness may have halted the growth of the rare breeding Mediterranean Gulls. It has been suggested that the birds displaced from Chesil Bank moved the nearby purpose-built islets on Browsea Island and Lodmoor nature reserve in Dorset, which have lower mammalian predation (Moxom and Burden, 2004).

The rapid growth in Black-headed Gull numbers at the un-harvested colonies in Hampshire (Langstone Harbour) and Dorset (Poole Harbour) coincided with the declines at the harvested colony at North Solent NNR to the west and the un-harvested colony in Chichester Harbour to the east. The growth at Langstone Harbour may have been boosted by the relatively high productivity at 0.70 (±0.11 s.e.) from the mid-1990's to the present day (C. Cockburn. pers. comm.). Although we have no estimates of productivity for Poole Harbour observations during visits in 2004-06 suggest it is relatively high. Both of these sites later experience rapid growths in Mediterranean Gull numbers. Productivity of Mediterranean Gulls in Langstone Harbour has also been reported to have been relatively high productivity over the last 9 years with an average of 0.90 ±0.12 fledged young per pair, which has probably had an influence on the rapid increase in breeding pairs at this colony (C. Cockburn, pers. comm.). Nevertheless, the rapid growth of Mediterranean Gulls breeding in Langstone and Poole Harbour has been part of the wider expansion of the species westward into Europe.

The un-harvested colonies in Langstone and Poole Harbour are situated on small clusters of islands with the nearest island being approximately 0.5km and 0.8 km, respectively, from the mainland. There are no records of any major mammalian predation events on either of these colonies. The absence of mammalian predation is likely to facilitate high productivity and thus recruitment, enabling the colonies to grow. However, these colonies growth may have also been bolstered by birds relocating from inland colonies in England and Wales, which have fared less favourably, with respective declines of at least 14% between the SCR and Seabird 2000 censuses (Mitchell et al., 2004), or even Europe.

3.4.2.2 Tidal Flooding

The mixed species colony decline leading to extinction at Chichester Harbour in East Sussex has been attributed to year-on-year tidal flooding (Thompson et al., 1996). These flooding events lead to low productivity and in some years total colony failure.

Severe storms causing flooding on the lower regions on the harvested sites in Hampshire in 2004 causing all Sandwich Terns to failure, has also been suggested to have caused site abandonment by this species in the following year (P. Durnell, pers. comm.).

3.4.2.3 Marsh Erosion

Habitat reduction caused by marsh erosion has also been suggested to be a factor in the North Solent NNR colony's extinction (J. Taverner, pers. comm.). However, sea defence work to combat erosion appears to have been instrumental in making easy access for mammalian predators to the site.

3.4.2.4 Egg Harvesting and other Anthropogenic Disturbances

Egg harvesting may have assisted the Black-headed Gull decline at North Solent NNR, by adding to the predation effort on eggs. Furthermore, the associated disturbance with egg harvesting may have halted the growth of Mediterranean Gull numbers at North Solent NNR and Pitts Deep to Hurst Spit, both of which had evidence of this species attempting to breed in small numbers before they spread to un-harvested sites along the south coast. Conversely, the lack of Black-headed Gull egg harvesting in Langstone

Harbour, and Poole Harbour after the early 1990s, may have increased the attractiveness to breeding seabirds and facilitated a higher productivity and thus recruitment compared to other harvested sites.

The dip in the gulls' population explosion at the un-harvested Hampshire colony (Langstone Harbour) seen in 2002 (Fig. 3.2 and 3.3.) coincided with increased activities of a group of shellfish gatherers who were operating close to the breeding islands in this year (C. Cockburn, pers. comm.). The Common Tern declines leading to colony extinction at Chesil Bank in Dorset have also bee attributed in part to a surge in marine-related recreation (Moxom and Burden, 2004).

3.5 Discussion

Nesting colonial seabirds, most notably ground-nesters, are thought to be particularly vulnerable to human disturbance (Finney et al., 2005). Human disturbance of ground-nesting Black-headed Gull has received relatively little attention from conservationists, however, despite these colonies harbouring several listed species. The stark declines seen in breeding numbers of Black-headed Gulls in Britain and Ireland should stimulate future interest in this species' breeding activities (Mitchell et al., 2004). This chapter demonstrates their susceptibility to site abandonment after successive seasons of low productivity, which threatens their regional distribution because of an apparent decline in the number of suitable breeding sites (Mitchell et al., 2004).

Egg harvesting has been viewed as not deleterious to the North Solent NNR colony due to the presence of harvesting during the rapid population growth from 1928 to 1970 (Aspinall et al., 1993). However, the population explosions at North Solent NNR after a one year halt on the egg harvest and at Poole Harbour in Dorset after banning the egg harvest in the early 1990's, contradict this view. Furthermore, heavy harvesting of Black-headed Gull eggs in northeast England during the Second World War caused a subsequent dramatic reduction in numbers (Simpson, 2001), and is thought to be one of the factors behind stark declines in Denmark (Møller, 1978). The mass movement of Black-headed Gulls from Europe (particularly Denmark) during the first half of the 20th century, and the more recent national movement of gulls from inland colonies to the coast may have masked any decline in numbers due to harvesting at North Solent NNR and from Pitts Deep to Hurst Spit. Such population movements of common species such as Black-headed Gulls make it difficult to evaluate the true impact of egg-harvesting. Nevertheless, the recent desertion at North Solent NNR, coupled with the growth of surrounding un-harvested colonies, may prove indicative of the impact of egg harvesting on the Pitts Deep to Hurst Spit population. It will be interesting to see whether this population will remain stable, now that the North Solent NNR birds have redistributed, or whether it will subsequently collapse. Furthermore, egg harvesting in Hampshire has been shown to reduce breeding productivity (see chapter 2). Any event that reduces a colony's breeding success to below 0.5 young fledged per pair for consecutive years may result in colony declines and even extinction due to the colony's inabilities to maintain the population by recruitment alone (Mitchell et al., 2004).

Mammalian predation has been suggested to be an important determinant of distribution and population trends of small gulls and terns in Britain and Ireland over the last 15 years (Mitchell et al., 2004). American Mink escaped from fur farms in the 1950s (Dunstone, 1993) and Fox abundance and distribution have increased over recent decades owing to relaxation of control by gamekeepers, especially in East Anglia, southeast England and southeast Scotland (Tapper, 1992). Both of these species predate eggs and chicks, and have caused breeding failure and colony abandonment (Craik, 1995; Rae, 1999; Mitchell et al., 2004), resulting in a decline in regional numbers and the redistribution of the remainder to offshore islands or larger colonies (Craik, 1997; Craik and Campbell, 2000; Clode and MacDonald, 2002; Mitchell et al., 2004). Fox predation may have been a major factor contributing to the decline at North Solent, and has been suggested as the primary cause of colony abandonment at Dungeness and Chesil Bank (Moxom and Burden, 2001; Mitchell et al., 2004). Predation is an important cause of nest failure worldwide (Ricklefs, 1969), and populations risk extinction when predation rates exceed recruitment rates. The harvested colonies from Pitts Deep to Hurst Spit have in the past received less attention from mammalian predators than the neighbouring colony at North Solent NNR. This may have played a part in their continuation as viable colonies.

Site desertion along the south coast has also occurred from tidal flooding and, in part, recreational disturbance, both of which caused reduced breeding success at Chichester Harbour and Chesil Bank, respectively. Tidal flooding has been shown to reduce breeding success at the North Solent NNR colony (Aspinall and Venner, 1991). However, the loss of eggs and young chicks during late season flooding, to which older chicks are less susceptible, can be attributed to a delay in hatching caused by harvesting (Aspinall et al., 1993). The 58% reduction in breeding habitat, due to coastal erosion, at North Solent NNR from 1954 to 2001 (Colenutt, 2005) was also thought to be a factor in the colony's decline (J. Taverner, pers. comm.). However, the remaining breeding habitat area at North Solent NNR is approximately 13% larger than the largest island in Poole Harbour, which held 8290 pairs in 2006 (data from Channel Coastal Observatory). These figures suggest that habitat reduction is unlikely to be a key factor in this particular site abandonment.

Human disturbance associated with egg harvesting appears to directly influence the distribution of breeding Mediterranean Gulls on the south coast of England. Colonisation of Mediterranean Gulls has occurred along the 'frontline' of south and southeast England, and although they were first seen attempting to breed within the harvested Black-headed Gull colony at North Solent NNR in the 1960s, they never established there. This may be attributed to the potential increase in mammalian predation after 1986. However, the harvested colonies from Pitts Deep to Hurst Spit, which is subject to relatively little mammalian predation, has also never established a Mediterranean Gull colony, despite attempts to breed there since the early-1990s. Mediterranean Gulls, however, have colonised and rapidly grown in breeding numbers within un-harvested Black-headed Gull colonies either side of the harvested area, with nearby Langstone Harbour to the east supporting the highest number of breeding pairs in Britain and Ireland, and with rapid increases in Poole Harbour to the west.

The timing of breeding is similar in Mediterranean Gulls and Black-headed Gulls, with possible benefits to breeding success from combined defences against predation (Kruuk, 1964). During egg harvesting, all birds breeding in the colony are flushed from the nest and any eggs not harvested (i.e. Mediterranean Gull eggs) are susceptible to predation or exposure to the elements. Kirkman (1937) found that Black-headed Gulls became more aggressive to neighbouring pairs when returning from a disturbance event, with associated increases in intra-specific egg predation. Black-headed Gulls could potentially behave the same towards Mediterranean Gulls, ultimately reducing their breeding success and increasing nest abandonment. Mediterranean Gulls have been noted in the past for their susceptibility to human disturbance, and such disturbance events have been suggested to be one of the factors in their geographic expansion into Western Europe (Mitchell et al., 2004).

Human disturbance has been identified as the primary cause of a nationwide decline of Little Terns breeding success from 1967 to 1971 (Lloyd et al., 1975). Disturbance caused by egg-harvesting appears to have little direct impact on the distribution of tern species along the south coast of England, probably because the terns generally breed after the cessation of the Black-headed Gull egg harvest. However, the refuge provided by the Black-headed Gull colonies dictates the terns' presence at some sites, as seen at North Solent NNR, Chichester Harbour and Dungeness.

Cumulative disturbance effects on breeding populations of rarer species such as the Mediterranean Gull, or declining species such as Little Terns are generally easy to observe, as displacement by human disturbance can ultimately eradicate them from an area or site (Riffell et al., 1996). However, these impacts can be difficult to see with more common species, such as the Black-headed Gull, where changes may relate to movement between local populations within a wider metapopulation (Hill et al., 1997). Further information is required on inter-colony movements, productivity, recruitment and survival, in order to attain a better understanding of population dynamics and to predict future breeding trends of these species within harvested Black-headed Gull colonies. This study has nevertheless demonstrated possible influences of egg harvesting on the distribution of ground-nesting seabirds on the south coast of England, and that egg harvesting is negatively affecting a Schedule 1 species' breeding success and distribution, with clear implications under EU and UK legislation

Environmental factors such as predation and tidal flooding have also proved to be influential on breeding success and, ultimately distribution. The substantial sea-level rise predicted for the end of the 21st century, especially along the south and east coasts of England will exacerbate the problem of nest flooding (Mitchell et al., 2004) and substantially reduce available habitat. Chichester Harbour appears to have been completely abandoned by breeding seabirds due to consecutive floods at this low-lying site. At present these birds appear to be accommodated elsewhere, but as more sites are lost to flooding events, will there be enough alternative nest sites? Measures should be taken to avoid site abandonment through disturbance, to ensure the survival of ground-nesting seabirds, not just on the south coast of England but across the UK.

CHAPTER 4. METHOD FOR BASELINE MONITORING OF SHOREBIRD PREY IN HETEROGENEOUS ESTUARINE HABITAT: CASE STUDY ON SOUTHAMPTON WATER, U.K.

Contributions: Frost, N. = defining the mission; Doncaster, C.P., Stillman, R.A., Hudson, M.D. = advice on design and analysis; Durrell, S.E.A. le V. dit. = providing invertebrate data for the Exe Estuary and Poole Harbour; Wood, P.J. = planning design, scheduling and logistics of fieldwork, collecting data (with assistance from people in the Acknowledgements), doing analysis, interpreting and reporting results.

4.1 Abstract

Winter survival of many shorebirds depends on the intertidal abundance of macrobenthic invertebrate prey. The ongoing loss and degradation of estuarine feeding areas in the UK places a requirement on statutory bodies involved with marine conservation to anticipate and monitor efficiently changes in shorebird food supplies. In this chapter, we describe a stratified-random sampling strategy for baseline monitoring of shorebird food supplies, which is more sensitive to patchily distributed prey than conventional grid-based monitoring strategies. For the case study of Southampton Water, we sampled from geographically identified habitat patches of different sizes and configurations, using a fully replicated split plot design for ANOVA. The first objective was to compare the relative value of ANOVA to regression analysis, which to date has been the statistical preference alongside grid-based designs, for identifying environmental influences on species abundance, diversity and biomass. We found ANOVA reveals a higher level of heterogeneity within the estuary. The second objective was to identify habitat patches representative of assemblages of invertebrate prey to shorebirds, which can be applied to an individual-based model (see chapter 5) designed to predict shorebird survival over-winter. This was achieved by cluster analysis, which classified sample sites into macrobenthic invertebrate assemblages based on their shorebird prey biomass densities. Stepwise discrimination then determined the key environmental variables influencing the site assemblages. Bootstrap resampling indicated the degree of sampling effort required for future monitoring of shorebird food supplies, and moreover, demonstrated that the ANOVA design produced predictions of adequate precision, and that the grid-based design would have over-sampled certain areas of the estuary ensuing higher sampling efforts and costs.

4.2 Introduction

The seas around the UK contain the greatest variety of marine habitats of any European country with an Atlantic coastline (Laffoley, 2000), and UK estuaries provide an abundance of macrobenthic invertebrate prey species for many resident and migratory shorebirds (McClusky, 1981). Loss or degradation of estuarine feeding grounds has become one of the greatest threats facing shorebirds (Atkinson, 2003). These prime habitats are often susceptible to conflict between conservation priorities and human activities such as waste disposal, land claim, shell-fishing and recreation (Durell et al., 2005b). Many UK estuaries have been designated as Marine and Maritime Special Areas of Conservation (SACs) under the European Union Habitats Directive 92/43/EEC, and as Special Protection areas (SPAs) under the European Directive 79/409/EEC for the conservation of birds, with the objective of protecting and maintaining these essential feeding grounds. The Directives require that Member States take appropriate steps to avoid deterioration of the natural habitats of protected species, which can only be achieved with reliable baseline data on the abundance and diversity of shorebird prey.

The conservation value of estuaries has previously been estimated in terms of the abundance of birds exploiting the mudflats. This method is not predictive, however, so that when a reduction in shorebird abundance has been recorded it is often too late to take remedial action (Stillman et al., 2005a). There is a need for reliable methodologies to anticipate how potential changes to a site may affect the site quality for the shorebird populations. To this end, an individual-based model has been designed to predict changes in biological fitness of individual birds and population responses to changes in their environment, mainly involving changes in the size and quality of feeding areas (Goss-Custard et al., 1995a; Stillman et al., 2001, 2005a; West et al., 2002). These individual-based models aim to predict effects of both long- and short-term changes to feeding areas, by predicting the mortality rate and body condition of the shorebirds throughout the winter.

To apply such a model to any estuary requires a baseline survey to identify discrete habitat patches on the basis of the macrofauna present, and to estimate empirically the macrobenthic invertebrate prey diversity and biomass density for each defined patch. The conventional method of selecting sample sites for a baseline macrobenthic invertebrate survey has been with a geometric grid of sampling points

(McGrorty, 1973; Durell et al., 2005b). The regular spacing of samples has the advantage of systematically covering the whole region of interest, but the potential disadvantage in a landscape of patchily distributed prey that they risk under- or over-sampling patches depending on their size and configuration. In this study, we undertook a baseline survey of the macrobenthic invertebrates on the designated SPA and maritime SAC of Southampton Water, UK using an Analysis of Variance (ANOVA)-based approach which, we argue, better reflects the heterogeneous conditions present.

Our aim was to identify the macrobenthic invertebrate diversity and patch assemblage of Southampton Water, and the key environmental variables determining such assemblages, from stratified-random sampling within relatively homogeneous areas, each containing a recognisably distinct habitat. The stratified-random samples were analysed with a split-plot general linear model (GLM). Model outputs from this ANOVA-based survey were then compared to outputs from multiple regression on the same dataset, which is the conventional analysis applied to grid sampling (Azouzi et al., 2002; Caldow et al., 2005; Durell et al., 2005b). The comparison of methods has limited scope, because multiple regression would conventionally be applied to grid-sampling data, which are not available within Southampton Water. We include it nevertheless, as an approximate comparator of hypothesis-testing ANOVA to parameter-estimating multiple regression. The objectives were: (1) to evaluate the utility of the split-plot ANOVA design for identifying distribution patterns of macrobenthic invertebrates and any environmental indicators of such patterns within the estuary; (2) to quantify the shorebirds' food in terms of habitat patches suitable for predictive individual-based models of shorebird survival using the ANOVA-based survey; and (3) to suggest ways to maximise the efficiency of future monitoring of shorebird food supplies.

4.3 Methods

4.3.1 Study Site

Southampton Water forms the northern extension of the Solent estuarine system in the English Channel between the Isle of Wight and mainland Britain. The tidal regime is unusually complex, controlled by the resonance effect of the eastward narrowing of the English Channel and modified by the hydraulic characteristics of the Solent. The bathymetry distorts the tidal curve with a double high tide and a young flood stand, lasting approximately 2 hours, followed by a normal flood, causing a high water stand of 5 hours and a shorter ebb period of 5 hours (Webber, 1980).

Dyer (1973) defined the hydrodynamics of Southampton Water as partially-mixed, based on an extensive survey of temperature, salinity and currents. The sediments of Southampton Water are predominantly mud and muddy sands, with patches of sandy sediments (Velegrakis, 2000).

The Solent coast supports a particularly high diversity of marine invertebrate species, including numerous scarcer species (Parsons and Foster, 1996), and it constitutes one of the top five sites in the UK in terms of ornithological importance (Burges, 2000). For these reasons, the Solent and Southampton Water are designated marine and maritime SAC and SPA/Ramsar sites (Davis, 1994).

4.3.2 Sampling Design

Macrobenthic invertebrate sampling of Southampton Water was undertaken in September 2003. The whole estuary was partitioned into 'areas', each defined as a discrete region of intertidal habitat suitable for feeding shorebirds. The shorelines of Southampton Water divided into nine relatively homogenous physical units ('areas'), distinguished by easily defined barriers and physical and anthropogenic landscape features (Fig. 4.1). Each area was partitioned into abutting rectangular sections, each of length 500m along the shore and extending from Mean High Water Spring (MHWS) to Mean Low Water Spring (MLWS). Three sections from each area of the estuary were chosen at random for sampling. Each section was approximately divided by Mean Tide Level (MTL), creating subsections at High and Low height of spring tide. Within a subsection, two coordinates were randomly selected as the replicate sample points. Division of sections found in the two eastern tributary rivers do not represent MTL, but simply left and right of the river channel. The elevation (height) of each sampling point was calculated from Admiralty Chart 2036 (2000).

The distribution of 108 sample points was considered more representative of the configuration of Southampton Water, which has sizeable differences in the extent of mudflat either side of the channel, than surveying on a conventional grid of 250×250 m, which would distribute the majority of its 170 sampling points on the western side of the estuary (Table 4.1).

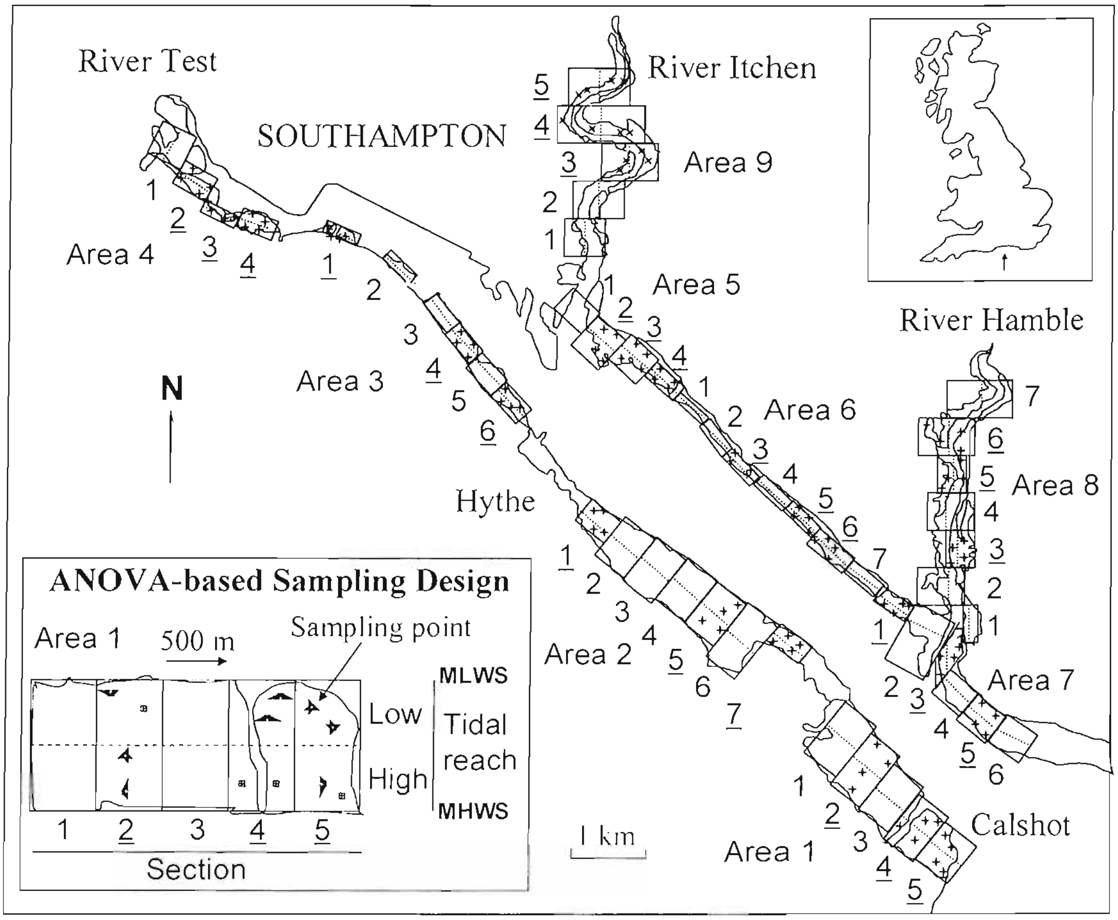


Figure 4.1. Map showing the ANOVA-based sampling design. Each of the nine selected areas are divided into sections each of length 500m along shore and extending from Mean High Water Spring (MHWS) to Mean Low Water Spring (MLWS). Sampled sections numbers are underlined, and randomly positioned sample points are plotted within each of these.

Table 4.1. Number of samples in each discrete area selected for the ANOVA-based sampling design and the corresponding number of samples that would be required when sampling with a conventional 250×250 m grid. The size of each area is given.

General Location		**Area No. (see Fig. 4.1)**	**Size of Area (m^2)**	**No. Samples**	
				ANOVA design	**250x250m Grid**
Western side		1	1569446	12	29
		2	2199213	12	40
		3	858000	12	14
		4	605600	12	15
Eastern side		5	656400	12	16
		6	816400	12	11
		7	657281	12	16
	Rivers	8	557281	12	13
		9	596000	12	16
		Total	8921939	108	170

4.3.3 Invertebrate Survey

Samples were located using a handheld Global Positioning System (GPS), and all except those from Area 8 (River Hamble, Fig. 4.1) were taken at low tide from a hovercraft, using a cylindrical corer (10cm diameter by 30cm height, volume 2356.19cm^3). For logistical reasons, the River Hamble had to be sampled from a boat with a Van-Veen grab (volume 2375.83 cm^3). To ensure consistency of the sample volume, only full grabs were analysed. The small difference in sample volume (<1%), between cores and grabs, was considered negligible.

Each sample was washed through a 0.5 mm sieve. Live whole polychaete worm *Hediste (Nereis) diversicolor* and bivalve mollusc *Cerastoderma edule* were identified, measured (body length for the worm, shell length for the bivalve) and frozen for analysis of ash-free-dry-mass (AFDM). The remaining sample organisms and materials were fixed with 10% formalin in seawater for a period of ~4 weeks, then washed and stored in 70% ethanol for a period of ~6 months, before identification to the lowest possible taxonomic level and measurement to 0.1 mm of length under a microscope. In samples with fragmented or degraded worms, only heads were counted as specimens and global mean lengths were substituted when calculating the AFDM.

AFDM was obtained by procedures described in Durell et al. (2005b). Values were $\log_e$-transformed for linear regression against $\log_e$-transformed live length to obtain a biomass-length ratio for each species. Because regressions for *H. diversicolor* and *C. edule* revealed negligible magnitudes of difference to those previously calculated for the Exe (Durrell et al., 2005b), we used their biomass to length ratios to estimate AFDM from measured lengths of all our preserved specimens (see Appendix E). No biomass-length ratios were calculated for worms <1 mm in width, which were assigned a standard AFDM of 0.344 mg (based on the Exe study of Durell et al., 2005b). Worms that were measured after being fixed were given lengths amplified by 20% when calculating the AFDM, on the basis that *H. diversicolor* reduces in length by 20% after 2 weeks in formalin followed by 6 months in industrial methylated spirits (S. McGrorty pers. comm.). Values of AFDM were summed over each sampling point to produce the total biomass density ($g.m^{-2}$) for each species (or lowest known taxonomic group) at that sampling point.

4.3.4 Surveys of Environmental Variables

Surface sediment to a depth of 5 cm was collected at each sampling point and frozen prior to analysis of particle size distribution in the range 0.2–2000 μm (Mastersizer 2000 Ver. 5.22 analyser) and 1–20 mm (Analysette 3 vibratory sieve shaker). Sample sediments were classified according to the highest proportion of sediment type (following Hallsworth and Knox, 1999), out of clay (grain size <2 μm), silts (fine: <6 μm, medium: <20 μm, coarse: <60 μm), sands (fine: <200 μm, medium: <600 μm, coarse: <2 mm), gravels (fine: <6 mm, medium: <20 mm, coarse: <60 mm), and cobbles (>63 mm). We assumed an inverse correlation of organic content with particle size, as demonstrated in previous studies (Wolff, 1973; Yates et al., 1993; Durell et al., 2005b).

Each sampling point was assigned a distance up the estuary from its mouth using AcrGIS (ESRI® ArcGIS V9.1), and an elevation from Admiralty Charts from which its exposure time was estimated from the average of mean spring and neap tidal curves typical for September 2003.

4.3.5 Data Analysis

The stratified-random sampling was suitable for the fully replicated ANOVA model: Height cross-factored with {Section nested in Area} (Doncaster and Davey, 2007). This design tested for the scale of heterogeneity within and between the pre-defined habitat areas, and the interaction of this horizontal heterogeneity with vertical heterogeneity up the shore, i.e. the spatial variation of environmental variables and the macrofauna, and any correlation therein. Sediment grain size and exposure time were treated as covariates in the general linear model (GLM) of the design.
In addition, we followed the data analysis pathway predominately used with grid-based surveys by applying multiple and stepwise regression to the same dataset (e.g., Yates et al., 1993; Azouzi et al., 2002; Durell et al., 2005b). For these analyses, the covariate of distance up the estuary was substituted for section nested in area. When explanatory variables were correlated, stepwise regression was used in place of multiple regression. Statistical analyses were preformed in Minitab version 14.

The statistical models were applied to five measures of species abundance, diversity and biomass: (i) $\log_e$ number of individuals per core, (ii) $\log_e$ sample biomass, (iii) $\log_e$ number of taxa per core, (iv) Shannon diversity index *H'* (Shannon and Weaver, 1949), and (v) Margalef's diversity index *d* (Margalef, 1958).

To achieve our second objective we used invertebrate biomass density ($g.m^{-2}$) to analyse both the quality and quantity of shorebird habitat assemblages in Southampton Water. Biomass density data were double square-root transformed, and similarities in the biomass and taxa present were calculated between all pairs using the Bray-Curtis similarity index (using PRIMER: Clarke, 1993). Some pooling of samples was required in order reduce noise from small scale variance, so that larger scale shorebird prey assemblages could be distinguished; the two upper-shore samples within each 500 m wide section were pooled together, as were the two lower-shore samples. No account was taken of taxonomic groups with total numerical density below three across the whole of Southampton Water.

The key environmental variables influencing the shorebird prey assemblages were determined by stepwise discriminant function analysis, which assigned each sample to a model-predicted group. The proportion of sampling points assigned to the correct assemblage was estimated by two methods: 're-substitution', where all samples were used to classify all samples, and 'cross-validation', where each sample was left out in turn, a model fitted to the remaining samples and the patch predicted for the missing sample (Krzanowski, 1988). The samples assigned well to one of the environmental variables, and because environmental variables tend to be less patchy and less inclined to sampling error than invertebrate distributions (Durell et al., 2005b), the model-predicted groups were used to identify the habitat patches.

Optimal sampling effort was predicted by calculating the 95% confidence intervals for 1-60 samples using 1000 replications with bootstrap resampling on: (a) the species diversity index (*H'*) and (b) the biomass density of predominant shorebird prey taxa for each habitat patch (Ephron and Tibshirani, 1993). Future surveys can then be designed to produce more precise estimates of invertebrate densities and biomass in a more cost effective way.

4.4 Results

4.4.1 Invertebrates

A total of 71 taxa were distinguished, of which 39 were identified to species and 60 to at least family (see Appendix C, Table C1). The most abundant taxa were the polychaete *H. diversicolor*, the crustacean *Corophium volutator*, and the molluscs *C. edule* and *Hydrobia ulvae*. Of the 32 polychaete taxa, 11 comprised small worms of body width <1 mm, which are largely ignored by shorebirds (Goss-Custard et al., 1977; Pienkowski, 1982), and only make up 1.3% of total polychaete biomass.

The introduced Manila clam *Tapes philippinarum* was also recorded for the first time in Southampton Water during this study. This is not discussed further in this chapter (but see Appendix F, Caldow et al. in press).

4.4.2 Distribution Patterns: Regression vs. ANOVA

Multiple regression analysis revealed an unusual inverse correlation of mean grain size with exposure time, suggesting a general pattern of sediments being muddier upshore and sandier downshore (instead of the usual pattern of sediments getting muddier downshore), but no relation of sediment size to distance up the estuary (Table 4.2a). In comparison, the split-plot GLM showed that the variation in mean grain size depended on area (Fig. 4.2) and on exposure time, though the exposure effect varied between sections within areas (Table 4.2b). Closer inspection revealed that a higher percentage of sections within areas consisted of the usual pattern of sediments getting muddier downshore. Moreover, a single section in Area 5, where a localised patch of very fine mud in relatively homogenous hard sediment was sampled above MTL, was found to be weighting the regression enough to produce the usual inverse correlation. The ANOVA model thus revealed spatial effects on sediment that were not apparent using regression analysis. Furthermore, ANOVA explained a high proportion of the variation in grain size, compared to the much lower proportion explained by the regression (Table 4.2a and b).

Table 4.2. Environmental influences on sediment grain size. R^2-values give the fraction of total variation explained by the model.

(a) Multiple regression, showing partial *t* if $P < 0.05$, otherwise n.s. = non significant.

Response	**Distance up estuary (km)**	**Exposure time (min)**	
	d.f. = 1, 105	d.f. = 1, 105	R^2 %
Log_e mean grain size (µm)	n.s.	-2.78	6.9

(b) General linear model, showing *F* values if $P < 0.05$, otherwise n.s. = non significant.

Response	**Exposed*Area**	**Area**	**Exposed (min)**	**Section(Area)**	**Exposed*Section (Area)**	
	d.f. = 8, 54	d.f. = 8, 18	d.f. = 1, 54	d.f. = 18, 54	d.f. = 18, 54	R^2 %
Log_e mean grain size (µm)	n.s	5.83	n.s.	4.29	2.06	86.6

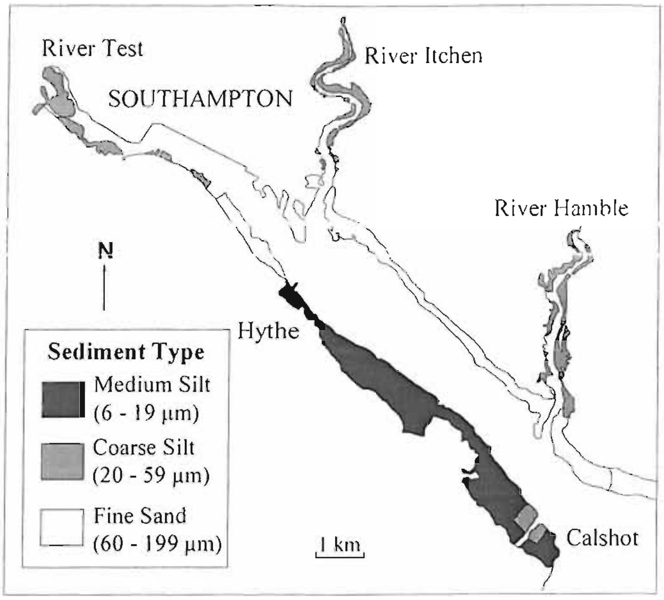


Figure 4.2. Distribution of sediment types from the stratified-random sampling.

Stepwise regression analysis showed no influence of mean grain size on abundance, diversity or biomass distribution (Table 4.3a). In contrast, the ANOVA model indicated an effect of mean grain size on biomass and diversity, again with a many-fold higher proportion of total variation explained (Table 4.3b). The influence of mean grain size on biomass depended on area (Grain*Area interaction in Table 4.3b), reflecting an increase in biomass with increasing grain size in Areas 1, 5, 6 and 7 and a decrease in biomass in Area 3, while all other areas changed very little (Fig. 4.3a). The nature of this interaction suggests a spatial influence on biomass that is independent of the distance up the estuary. Stepwise regression, however, indicated distance up the estuary to positively influence biomass, abundance and diversity, albeit explaining a small proportion of total variation compared to ANOVA (Table 4.3a and b).

Because of the correlation between grain size and exposure time (Table 4.2a) the hypothesised influence of exposure time was tested in a separate model (Table 4.3c). Results were similar, with stepwise regression indicating that exposure time negatively influences diversity, albeit with only 4-5% of the variation of responses explained (Table 4.3a), compared to 67-69% for the GLM analyses (Table 4.3c). Exposure time also influenced diversity through an interaction with area (Table 4.3c), reflecting an increase in diversity with increasing exposure time in Areas 2 and 5 and a decrease in diversity in all other areas (Fig. 4.3b), and moreover, reflecting a spatial influence on diversity that is independent of the distance up the estuary.

Table 4.3. Environmental influences on biomass and species diversity indices. R^2 values give the fraction of total variation explained by the model.

(a) Stepwise regression, showing partial *t* if $P < 0.05$, otherwise n.e = not entered into model, n.s. = non significant. $N = 108$.

Response	**Mean grain size (μm)**	**Distance up estuary (km)**	**Exposure time (min)**	R^2 **%**
Log_e Biomass/core ($g.m^{-2}$)	n.e.	2.62	n.e.	6.1
Log_e no. individuals/core	n.s.	2.62	n.e.	10.3
Log_e no. taxa/core	n.e.	2.07	n.e.	3.9
Diversity index *H'*	n.e.	n.e.	2.05	3.8
Species richness *d*	n.e.	n.e.	-2.41	5.2
MDS Axis 1	n.e.	n.e.	n.e.	1.8
MDS Axis 2	n.e.	n.s.	-2.00	5.9

(b) General linear model, with mean grain size as an explanatory variable, showing *F* values if $P<0.05$, otherwise n.s. = non significant.

Response	Grain*Area	Grain (µm)	Area	Section (Area)	Grain*Section (Area)	
	d.f. = 8, 54	d.f. = 1, 54	d.f. = 8, 18	d.f. = 18, 54	d.f. = 18, 54	**R^2 %**
Log$_e$ Biomass/core (g.m^{-2})	2.31	10.36	n.s.	2.98	1.90	72.3
Log$_e$ no. individuals/core	n.s.	n.s.	n.s.	1.98	n.s.	65.2
Log$_e$ no. taxa/core	n.s.	5.71	n.s.	2.26	1.83	66.7
Diversity index *H'*	n.s.	5.56	n.s.	2.38	n.s.	63.7
Species richness *d*	n.s.	5.47	n.s.	2.35	1.85	65.8
MDS Axis 1	n.s.	6.40	n.s.	n.s.	2.21	61.7
MDS Axis 2	n.s.	n.s.	4.06	n.s.	n.s.	58.2

(c) General linear model, with Exposure time as an explanatory variable (correlated to mean grain size in (b)), showing *F* values if *P*<0.05, otherwise n.s. = non significant.

Response	**Exposed*Area**	**Exposed (min)**	**Area**	**Section (Area)**	**Exposed*Section (Area)**	
	d.f. = 8, 54	d.f. = 1, 54	d.f. = 8, 18	d.f. = 18, 54	d.f. = 18, 54	R^2 **%**
Log_e Biomass/core (g.m^{-2})	n.s.	n.s.	n.s.	2.42	n.s.	68.4
Log_e no. individuals/core	n.s.	n.s.	n.s.	n.s.	n.s.	64.6
Log_e no. taxa/core	2.34	5.35	n.s.	2.07	n.s.	67.1
Diversity index *H'*	2.64	7.10	n.s.	2.50	n.s.	68.5
Species richness *d*	3.26	8.21	n.s.	2.40	n.s.	69.1
MDS Axis 1	n.s.	n.s.	n.s.	n.s.	n.s.	53.2
MDS Axis 2	2.27	n.s.	3.58	n.s.	n.s.	64.3

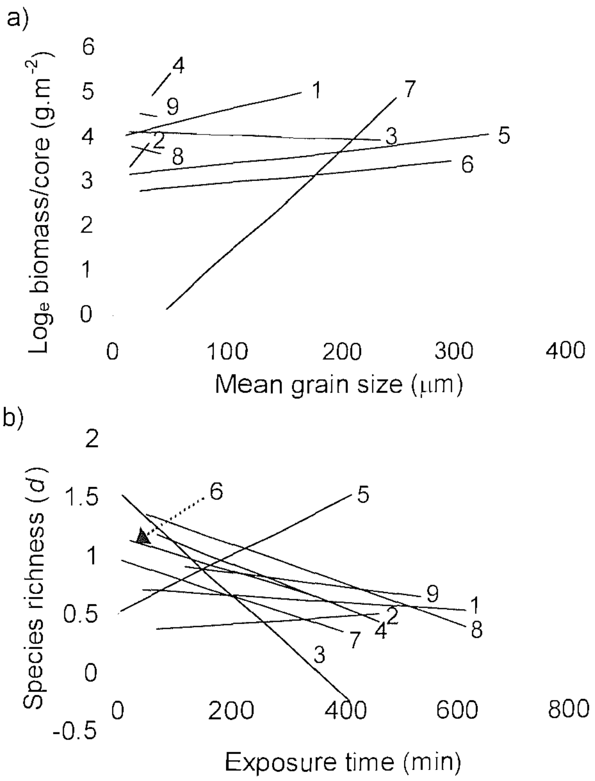


Figure 4.3. Interaction plots showing significant interaction between the effects of area and a) mean grain size on $\log_e$ Biomass/core ($g.m^{-2}$); and b) exposure time on species richness *d*. Area numbers are indicated at the end of each regression line.

4.4.3 Determining the Macrobenthic Invertebrate Assemblages

Cluster analysis of the biomass densities of 17 principal prey families generated three main site assemblages at a lower level of similarity (Fig. 4.4). Assemblage 2 holds the majority of the samples (78%), however, further grouping at a higher level of similarity subdivided it to create five assemblages in total.

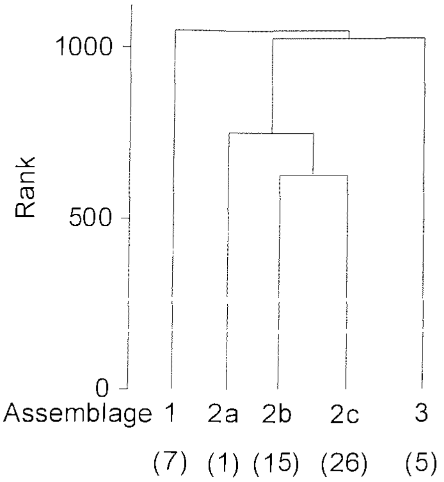


Figure 4.4. Simplified dendrogram of a cluster analysis of samples based on a Bray-Curtis similarity matrix of invertebrate biomass densities. Numbers in brackets give the number of samples assigned to each assemblage.

A 2-d Multi-Dimensional Scaling (MDS) ordination did not show clear separation of samples into assemblages. In previous studies, MDS axes have been subjected to multiple regression to quantify the correlation of assemblages to environmental variables (Durell et al., 2005b). The design of our study permitted comparison of regression to GLM analysis. Stepwise regression showed an effect of exposure time on MDS Axis 2 (Table 4.3a). However, GLM showed an effect of mean grain size on MDS Axis 1 and an interaction of area with exposure time on MDS Axis 2 again with a higher proportion of total variation explained compared to regression (Table 4.3b-c). Thus, the ANOVA-based design found assemblage 1 to be in sandy sediments mostly situated in Area 6 and 7; assemblage 2a, being only one sample site in Area 1, to be in a muddy sediment; assemblage 2b is found in muddy sand sediments and mostly situated in Area 3; assemblage 2c to be in a muddy sediment and mostly located in Areas 1, 2, 4, 8 and 9; and assemblage 3 in sediments mostly comprised of a sandy sediment and located in areas only on the eastern side of the estuary (Fig. 4.5a).

4.4.4 Predicting Invertebrate Assemblages from Environmental Variables

Of the four environmental variables: distance up the estuary ($\log_e$), exposure time ($\log_e$) and mean grain size ($\log_e$), and the spatial variable area, only grain size showed influence, with stepwise discriminant function analysis, on the invertebrate assemblages. Mean grain size predicted the classification of samples into assemblages to a high level of confidence (Fig. 4.5b), with 60% of the 53 samples being classified correctly using the re-substitution method and 59% by the cross-validation method. Assemblages 1 and 3 had the most misclassifications, being placed relatively evenly into the other assemblage. This is most probably due to the predicted assemblages 1 and 3 having similar mean grain sizes.

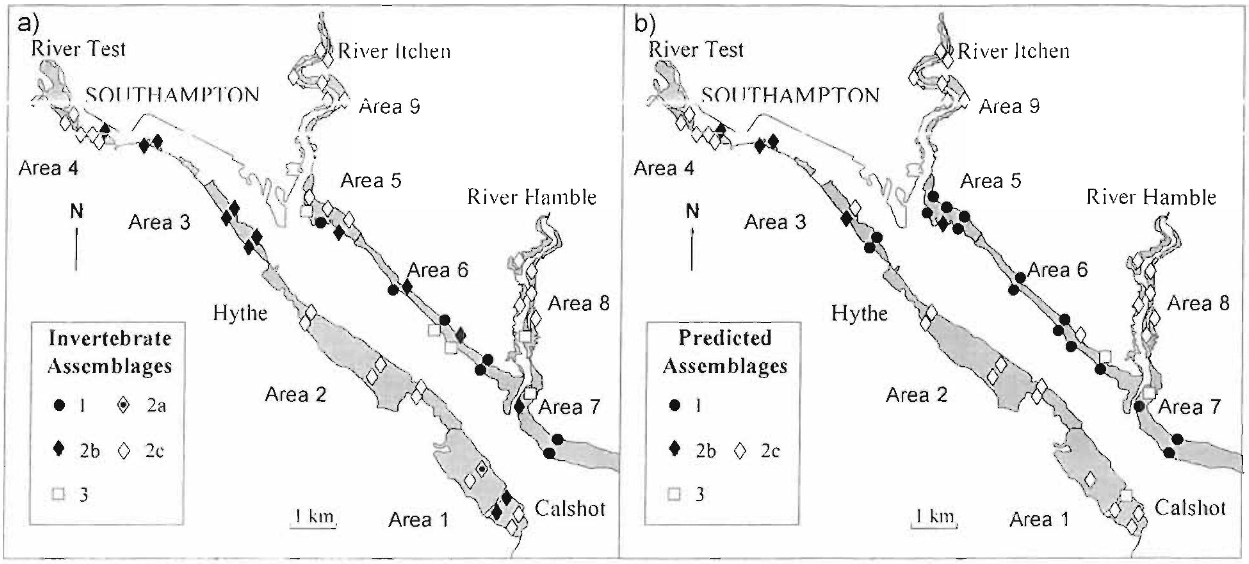


Figure 4.5. (a) Observed distribution of the invertebrate assemblages from cluster analysis, and (b) the predicted distribution produced by stepwise discriminant function analysis.

4.4.5 Determining Habitat Patches from Assemblages

The habitat patches generated by the three dominant model-predicted groups classified by sediment type in stepwise discriminant function analysis, are mapped in Figure 4.6. The characteristics of the three habitat patches are shown in Table 4.4. The muddy habitat patch is defined by the presence of Hydrobiidae, Nereidae, Scrobiculariidae, and Tellinidae (Table 4.4), all of which are found commonly in soft substrata and often in black-muddy sand under brackish condition (Hayward and Ryland, 2000). The mixed muddy sand habitat patch is defined by the presence of Cardiidae (Table 4.4), which are associated with sandy mud, sand, or fine gravel (Hayward and Ryland, 2000); whilst the sandy habitat patch is defined by the presence of Terebellidae (Table 4.4), which prefer sandy beaches and muddy sand (Hayward and Ryland, 2000).

Figure 4.6. Distribution of habitat patches.

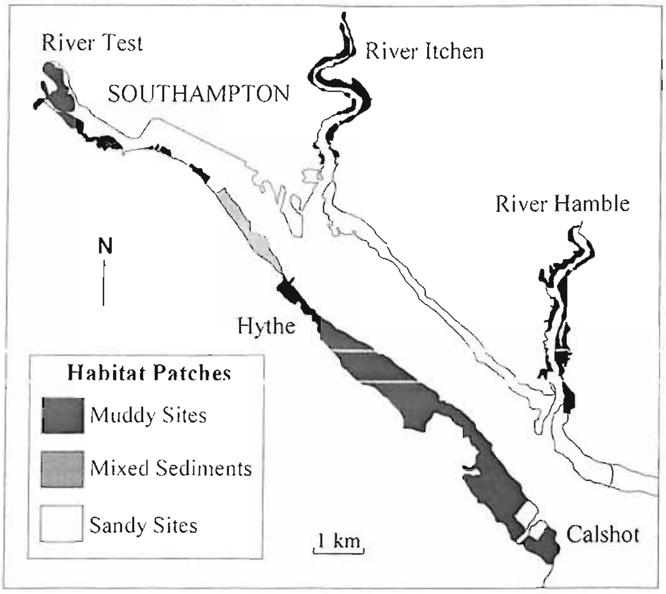


Table 4.4. Key characteristics of habitat patches within Southampton Water. Values given are means with standard errors in brackets. n = the number of core samples within each patch. Values in bold were significantly (one-way ANOVA, P < 0.05) higher than those for other patches.

	Muddy Habitat Patch (predominately assemblage 2c) $n = 29$	**Mixed Muddy Sand Habitat Patch** (predominately assemblage 2b)	**Sandy Habitat Patch** (predominately assemblage 1 and 3)
Number of animals/core	**20.12 (4.31)**	7.83 (3.49)	4.13 (0.58)
Number of taxa/core	2.57 (0.20)	2.50 (0.51)	1.89 (0.23)
Species diversity (*H'*)	-0.51 (0.06)	-0.57 (0.18)	-0.49 (0.08)
Species richness (*d*)	0.62 (0.07)	0.74 (0.25)	0.65 (0.11)
Total invert biomass (g.m^{-2})	173.40 (32.28)	159.42 (47.39)	105.41 (29.74)
Biomass densities (g.m^{-2})			
Ampharetidae	5.53 (3.51)	5.04 (1.89)	4.05 (1.87)
Aphroditidae	0.00 (0.00)	1.75 (1.75)	1.18 (0.91)
Cirratulidae	0.68 (0.47)	3.19 (2.07)	2.24 (1.95)
Nephtyidae	4.97 (2.37)	5.23 (2.39)	3.28 (1.24)
Nereidae	**61.69 (12.83)**	30.21 (20.21)	44.19 (23.76)
Phyllodocidae	0.33 (0.19)	0.07 (0.07)	0.51 (0.13)
Terebellidae	0.00 (0.00)	0.77 (0.77)	**15.58 (5.97)**
Amphipoda	1.45 (1.32)	0.00 (0.00)	1.50 (0.55)
Isopoda	0.24 (0.19)	0.00 (0.00)	0.11 (0.08)
Portunidae	2.01 (1.80)	2.39 (1.52)	0.22 (0.22)
Cardiidae	53.36 (27.15)	**104.27 (49.92)**	29.18 (14.05)
Hydrobiidae	**19.10 (5.67)**	4.25 (3.95)	0.12 (0.12)
Littorinidae	2.54 (1.74)	0.28 (0.18)	2.82 (1.96)
Polyplacophora	0.00 (0.00)	0.00 (0.00)	0.41 (0.32)
Scrobiculariidae	**17.93 (5.41)**	0.00 (0.00)	0.00 (0.00)
Tellinidae	**2.67 (1.01)**	0.00 (0.00)	0.00 (0.00)
Veneridae	0.91 (0.69)	1.94 (1.94)	0.00 (0.00)

4.4.6 Maximising Monitoring Efficiency

Figure 4.7 shows how the precision of the survey decreased rapidly with small sample sizes, indicated by the 95% non-parametric confidence intervals. It is clear from bootstrapping that future surveys would need to take more samples in the mixed habitat patch but fewer in the muddy and sandy habitat patches (Fig. 4.7). Bootstrapping predicts that the rate of precision increase is low after 20-25 samples per habitat patch; thus making it uneconomical sampling above this number of samples. Taking 20-25 samples from each habitat patch would reduce the number of samples taken from 108 in the present survey to 60-75, and saving approximately a half to a third of the sampling effort and cost.

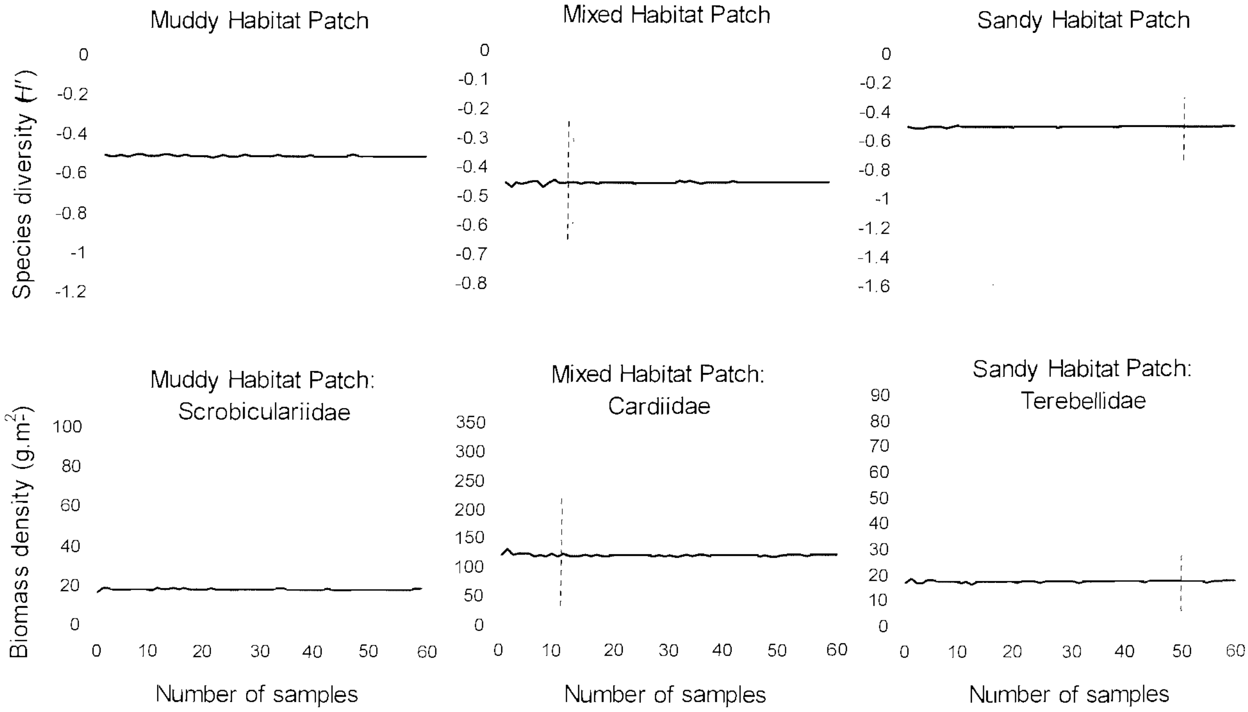


Figure 4.7. Mean species diversity index (*H'*) and mean biomass density (g.m^{-2}) for predominant shorebird prey family in each habitat patch, each showing the 95% confidence interval and against the number of samples taken using bootstrap resampling. The vertical solid line indicates the number of samples actually taken during the present survey, and the dashed line the number of samples needed for a 250x250m grid survey. For the muddy habitat patch the number of sampling points needed for a grid survey is 109, and therefore off the scale of the graph.

4.5 Discussion

In this chapter we compared the measured variation of Southampton Water's macrobenthic invertebrate communities using a stratified-random sampling design suitable for ANOVA with the variation produced when using regression analysis predominately used with grid-based surveys. Although a better comparison of designs could have been obtained by applying the regression analysis to data from grid-based sampling, the sampling points from the stratified-random sampling design arguably represented the profile of Southampton Water more precisely. We demonstrated that the nested ANOVA design can yield more powerful predictions than regression based models. This is consistent with findings by Underwood and Chapman (1996) on rocky shores. Furthermore, due to the sensitivity to the patchiness of the habitat, this design can reduce initial sampling effort and cost by reducing the number of sample sites compared to a 250×250 m grid survey. The assumption behind the ANOVA model, that areas within the estuary can be reliably identified pre-sampling, which are more homogeneous within each area than between areas, was satisfied in Southampton Water but may not be possible for all study sites, in which case we advise using conventional grid-based surveys.

Sampling effort is an important consideration for the design of estuary surveys, because of the large amount of time required to sort and identify invertebrate samples. Any method that can reduce the number of samples for processing, whilst nevertheless maintaining power to explain variation in prey abundance and diversity, should be of interest to those concerned with monitoring estuary SPAs (Durell et al., 2005b). Bootstrap resampling indicated that the precision of our sampling was sufficient, and in most cases more than sufficient to produce reliable information for a baseline survey, and moreover, that both the sandy and muddy habitat patches would have been considerably over-sampled if a 250 x 250 grid survey had been used (Fig. 4.7).

Within intertidal habitats, invertebrates show great variation in distribution and biomass (Woodin, 1974; Goss-Custard et al., 1977; Thrush et al., 1989; Turner et al., 1995), and this variation appears to be determined by external variables (e.g., Peterson, 1991; Warwick et al., 1991; Yates et al., 1993; Azouzi et al., 2002; Durell et al., 2005b). Adopting a grid-based survey limits the spatial test variables to distance up the shore (or exposure time) and distance up the estuary. Although we found an influence of distance up the estuary on taxa abundance, diversity and biomass when testing with stepwise regression analysis, no such simple relationship was apparent in the ANOVA. The ANOVA had much greater power to explain variation in the taxa measures, and it revealed an influence of geographical area that was independent of the distance up the estuary.

Mean exposure time can also influence macrobenthic invertebrate distribution (Bertness and Grosholz, 1985; Peterson and Black, 1987; Peterson, 1991; Warwick et al., 1991; Yates et al., 1993; Beukema and Flach, 1995; Durell et al., 2005b), and was measured in our study simply from topography and tidal data. Both stepwise regression and ANOVA revealed influences of exposure time on the taxa measures, but ANOVA showed that the influence of exposure time depended on area, which could not be tested using a grid-based survey.

Sediment composition is often considered to be the most important variable affecting macrobenthic invertebrate distributions (Longbottom, 1970; Boyden and Little, 1973; Gray, 1974; Green, 1975; Azouzi et al., 2002). Our results for Southampton Water support this, indicative of the particle size distribution being the only variable influencing the estuary's macrobenthic invertebrate assemblages in cluster analysis. The ANOVA revealed influences of mean grain size on taxa abundance and biomass, which were not apparent when testing with stepwise regressions. These results demonstrate the higher level of estuary-wide heterogeneity that can be achieved using a sampling strategy applicable for ANOVA modelling.

Cluster analysis and MDS were used to identify differences between macrobenthic invertebrate communities. These techniques are widely used for such purposes, and also to monitor changes over time (Clarke and Warwick, 1994; Dernie et al., 2003; Junoy and Vieitez, 1990; Parry et al., 2003; Warwick et al., 2002; Durell et al., 2005b). By identifying the environmental variables that correlated with macrobenthic invertebrate communities within an estuary, we were able to predict the distribution of estuary-wide habitat patches. For Southampton Water, macrobenthic invertebrate distribution was well predicted by sediment composition. These results suggest the possibility of efficiency savings in future monitoring effort by either measuring the changes in the sediment composition, which is generally less time consuming to process, or by optimising the sampling effort needed within each habitat patch. We demonstrated that fewer samples would be needed in the dominating muddy habitat patch. However, the spacing of samples within this habitat would have to be considered as the patch is not located in one area but split up around the estuary (Fig.

4.6). The risk generated by reducing the number of samples within an estuary is the increased chance of missing very localised and/or rarely occurring species. This is unlikely to be critical, however, when surveying for the purpose of assessing shorebird food, unless they are important shorebird prey species (Durell et al., 2005b).

Grid-based systems of surveying baseline macrobenthic fauna have previously been considered the most efficient and systematic way of selecting sample sites (McGrorty, 1973; Durell et al., 2005b). We have demonstrated that in estuaries that can be divided into more or less discrete areas based geographical features, this may not be the case and that stratified statistical designs can provide more information about the heterogeneity of the estuary. Macrobenthic invertebrate and environmental information sampled by stratified-random designs yield powerful and precise predictions that are suitable for applications to models of bird feeding behaviour. These individual-based models can predict the effects on shorebird survival of any changes to the macrobenthic invertebrate biomass densities caused by habitat degradation over and above seasonal processes of depletion. Such predictions are essential for shorebird and estuarine conservation. The next chapter demonstrates how the data provided here were applied to an individual-based model.

CHAPTER 5. MODELLING THE EFFECTS OF HABITAT LOSS FOR WINTERING SHOREBIRDS IN SOUTHAMPTON WATER, U.K.

Contributions: Frost, N. = defining the mission; Stillman, R.A. = advice and parameterisation of the model; Doncaster, C.P., Hudson, M.D. = advice on design; Wood, P.J. = planning design, doing analysis, parameterisation of the model, interpreting and reporting results.

5.1 Abstract

European conservation law now requires environmental impact assessments of estuary sites of importance to over-wintering shorebirds. Reliable methodologies are consequently needed to monitor site quality and assess impacts of habitat loss. We developed an individual-based model of Southampton Water to evaluate site quality for eight shorebirds: dunlin *Calidris alpina*, ringed plover *Charadrius hiaticula*, ruddy turnstone *Arenaria interpres*, redshank *Tringa totanus*, grey plover *Pluvialis squatarola*, black-tailed godwit *Limosa limosa*, Eurasian oystercatcher *Haematopus ostralegus* and Eurasian curlew *Numenius arquata*. Over-winter survival was predicted both with and without 7% habitat loss for the proposed construction of a port terminal at Dibden Bay. The model accurately predicted the observed shorebird distribution if non-starving birds were assumed to move within restricted sections of the site, consuming any prey which yielded a threshold energy assimilation rate. In contrast, the model predicted that too few patches were occupied if birds were assumed to consume only those prey that maximised energy assimilation rate. All species except turnstone and oystercatcher were reliant on the consumption of annelids to maintain high survival rates. Dunlin and curlew were predicted to be the species most likely to have reduced survival if either prey biomass or overall habitat area were reduced. In some simulations, the habitat loss caused by the Dibden Bay port terminal was predicted to decrease the survival rate of dunlin by 2.7%, turnstone by 0.9% and curlew by 1.7%, but did not effect the survival of any other species. The effect of habitat loss on these species was eliminated by the proposed mitigation of a tidal creek. The predicted success of the mitigation, however, did not account for the years required to construct the mitigation habitat, or any accumulative effects on the mortality of shorebirds which would be forced to feed from other sites within the estuary.

5.2 Introduction

Environmental-impact assessment has become mandatory in determining whether certain human activities should be permitted, especially in areas with European designation such as Special Protection Areas (SPAs) under the EU Directive 79/409/EEC for the conservation birds, and Special Areas of Conservation (SACs) under the EU Habitats Directive 92/43/EEC. These Directives require that Member States take appropriate steps to avoid deterioration of the natural habitats of species as well as disturbance of species within designated areas. Many of Britain's intertidal estuaries, which provide food for wintering shorebirds, have now been assigned such European designations. Proper assessment of these estuaries now requires reliable methodologies to monitor site quality for shorebird populations and to estimate impacts of habitat loss.

The quality of estuary SPAs is often measured in terms of bird numbers, but this has two major drawbacks particularly for migratory species. Firstly, the numbers of birds using a site depends not only on the condition of the site, but also the condition of other sites both within the non-breeding and breeding season (Goss-Custard, 1993; Goss-Custard et al., 1995a; Gill et al., 1997). For example, a reduction of birds at one site may have resulted from an increase in quality at another site or an overall reduction in reproductive rates or increased morality within the whole population. Secondly, this method is not predictive and the observation of reduced bird numbers often comes too late for remedial action (Stillman et al., 2005a).

A series of individual-based models have been designed to predict changes in biological fitness of individual birds and population responses to changes in their estuarine environment, mainly in relation to human activities such as shellfishing (Caldow et al., 2004; Stillman et al., 2001, 2003; West et al., 2003), disturbance (West et al., 2002), habitat quality (West et al., 2005), habitat loss (Durell et al., 2005a; Stillman et al., 2005b) and climate change (Durell et al., 2006). The simulated birds are allowed to maximise their individual chances of survival and reproduction in response to changes in the environment. Behavioural decisions are based on optimal foraging theory and game theory, which are considered to provide realistic predictions (Goss-Custard, 1993; Sutherland, 1996; Goss-Custard and Sutherland, 1997). Population change is predicted at the end of winter from the fates of all individuals that either starved to death, or experienced reduced energy reserves which may impinge on migration, or sustained adequate fat stores.

In this study, we further developed the latest individual-based model, MORPH (Grimm et al., 2006), in order to assess the quality of the designated SPA and maritime SAC of Southampton Water, UK for eight over-wintering shorebird species, and to assess the potential impact of habitat removal and consequent mitigation associated with the rejected proposal for construction of a new port (Dibden Terminal, Associated British Ports, 2000a). We extend previous applications of the model by incorporating restricted dispersal of shorebirds within the study site, and by comparing the predictions of alternative model versions based on different shorebird decision rules.

5.3 Methods

5.3.1 Study Site

The Solent and Southampton Water are designated SPA/Ramsar sites (Davis, 1994). The Solent is one of the most important areas of estuarine habitat in southern Britain, containing over 9000 hectares of intertidal sediments including mudflats, sandflats, shingle and saltmarshes (Tubbs, 1990). The Solent's coast supports a particularly high diversity of marine invertebrate species, including numerous scarcer species (Parsons and Foster, 1996). The densities of birds using the Solent estuaries are amongst the highest recorded in northern Europe (Tubbs, 1999), making the Solent an internationally important site for waterbirds (Burges, 2000). During the winter months of the five-year period 1999/2000 – 2003/4, the Solent was internationally important for ringed plover *Charadrius hiaticula*, grey plover *Pluvialis squatarola*, dunlin *Calidris alpina*, black-tailed godwit *Limosa limosa*, bar-tailed godwit *Limosma lapponica*, and redshank *Tringa totanus*, while in the same period it was nationally important for Eurasian curlew *Numenius arquata*, greenshank *Tringa nebularia*, and avocet *Recurvirostra avosetta* (Musgrove et al., 2001; Pollitt et al., 2003; Collier et al., 2005). During the same period, Southampton Water itself was internationally important for black-tailed godwit and nationally important for dunlin and greenshank (Musgrove et al., 2001; Pollitt et al., 2003; Coller et al., 2005).

Southampton Water (Fig. 5.1) forms the northern extension of the Solent estuarine system in the English Channel between the Isle of Wight and mainland Britain. The tidal regime is unusually complex, controlled by the resonance effect of the eastward narrowing of the English Channel and modified by the hydraulic characteristics of the Solent. The bathymetry distorts the tidal curve with a double high tide and a young flood stand, lasting approximately 2 hours, followed by a normal flood, causing a high water stand of 5 hours and a shorter ebb period of 5 hours (see Webber, 1980).

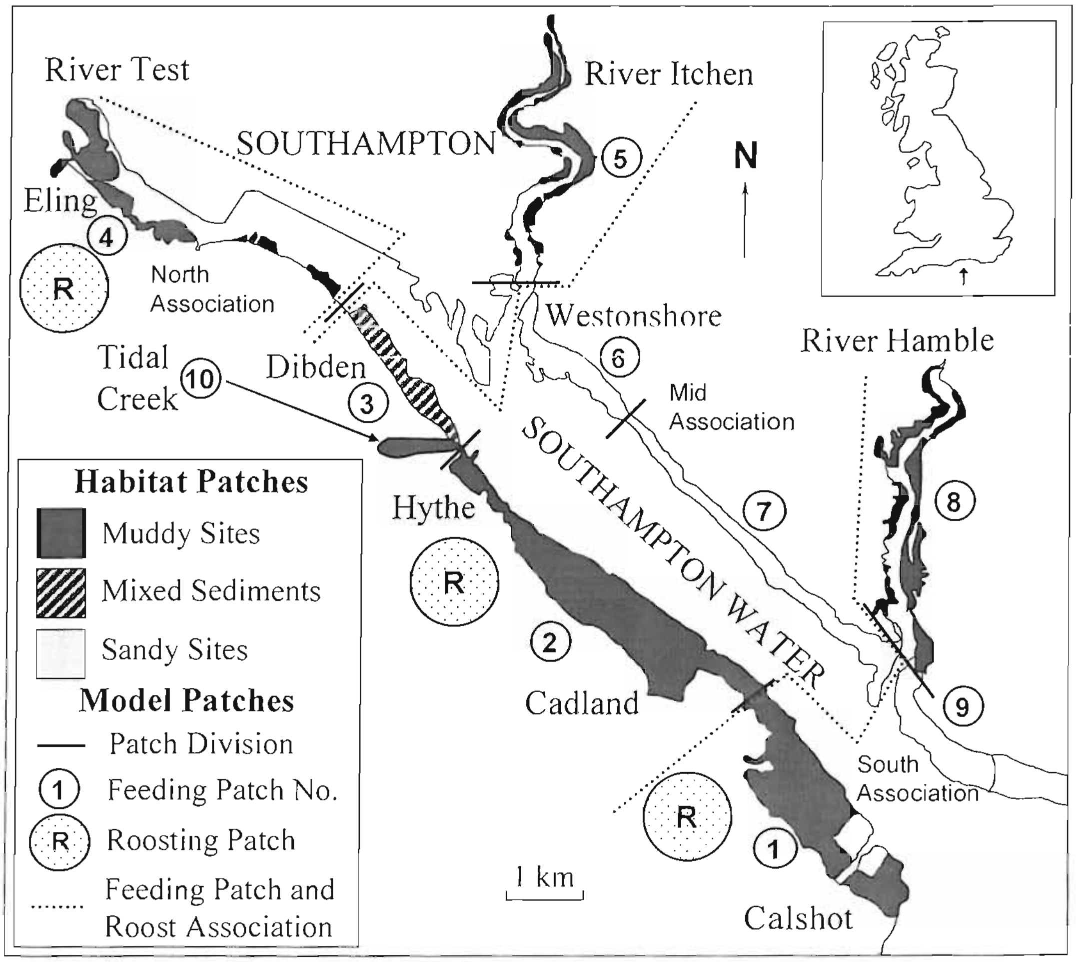


Figure 5.1. Map showing the habitat patch and model feeding and roosting patch distribution around Southampton Water.

5.3.2 Dibden Terminal Proposal

The proposals by Associated British Ports (ABP) for a port terminal at Dibden Bay were rejected after public inquiry in 2003. The primary proposal entailed the loss of 76 ha of intertidal (7% loss of shorebird feeding habitat) and 52 ha of adjacent shallow subtidal areas (Fig. 5.1), by quay construction and capital dredging (ABP, 2000a). The secondary proposals included two mitigation measures intended to reduce or avoid ecological impact (ABP, 2000a): (a) recharge of the Hythe to Cadland foreshore to create an additional 22 ha of mud down to Mean Low Water (MLW) and to improve the quality of the 137 ha of existing but contaminated mudflat (Fig. 5.1); (b) construction of an intertidal creek to provide approximately 32 ha of intertidal habitat to MLW of which 30 ha is intertidal mud (Fig. 5.1).

5.3.3 The Model

The individual-based model, MORPH, is described in Grimm et al. (2006) (p55 of online appendix), and is based on earlier models (Goss-Custard et al., 2000; Stillman et al., 2000, 2001, 2003; West et al., 2003, 2005; Caldow et al., 2004; Durell et al., 2005a). As with previous models, MORPH tracks the location, behaviour and fate of each individual in a population as it attempts to meet its daily energy requirements. Simulated individuals were allowed to differ in their feeding efficiency and dominance which determine intake rate in the absence of competitors, and the influence interference competition from competitors on intake rate respectively. Individuals that exceeded their daily maintenance requirement increased their fat store, whilst those that did not could only survive by drawing on their fat stores and they died when these fell to zero. This was the only source of predicted mortality and thus true mortality may be underestimated since raptors can influence distribution and survival in some estuaries (Whitfield, 1985, 2003; Quinn and Cresswell, 2004). Conversely, true mortality may be overestimated if shorebirds emigrate as conditions deteriorate, since the model predictions are based on a closed site system.

MORPH predicted how individuals respond to environmental change by varying their feeding location and diet (Durell et al., 2006). Model birds could feed on a number of food types, within their specific diets, which were distributed across feeding patches within the estuary in accordance with baseline surveys of macrobenthic invertebrates. Each prey type contained nutrient components that were assimilated into the bird upon consumption. Birds could only feed on patches that were exposed by the tide; otherwise they moved to a roost containing no food. The predictions of the model varied slightly each time it was run due to stochastic variation in the characteristics of the individuals. For this reason we present the mean of either ten (habitat loss from Dibden Bay simulations) or five (all other simulations) runs for each combination of parameter values. Ten replicates of the Dibden Bay simulations were run to increase the probability of detecting the impact of the development on survival.

The following sections and Table D1 in Appendix D describe how MORPH's five sets of parameters were parameterised for Southampton Water.

5.3.3.1 Global Parameters

The model simulated the winter feeding period from the beginning of September 2003 to the end of March 2004, divided into hourly time steps (Table D1a, Appenix D).

Seasonal change in the duration of daylight hours was calculated for Southampton Water allowing bird behaviour to differ between day and night.

5.3.3.2 Patch Parameters

The macrobenthic invertebrate prey of shorebirds was surveyed in Southampton Water in September 2003 and again February 2004 using a novel survey design applicable for analysis of variance (chapter 4). Cluster analysis (PRIMER, Clarke, 1993) and stepwise discriminant function analysis of prey invertebrate biomass densities identified three habitat patches based predominantly on sediment composition. These habitat patches were further divided for the model into nine discrete feeding patches (Fig. 5.1), based on geographical position, to increase the resolution of the model. For testing the removal of Dibden Bay and the proposed mitigations, a further patch was created for the creek and a substitute patch for the recharged Hythe to Cadland area (Fig. 5.1). We used the same model patch resource and component parameters for the creek as the River Hamble, based on our prediction that the tidal creek substrate would be most similar to the soft substrates of this tidal river. The biomass density data for patch 2 (Esso to Hythe, Fig. 5.1) was used for the recharge.

The invertebrate survey revealed that 29% of samples taken between the Esso Terminal and Cadland (Fig. 5.1) were extremely polluted with oil, and hence any prey from these samples would likely have been toxic to the birds. To account for this pollution, we reduced the area of Esso Terminal to Hythe (Modal Patch 2; Fig. 5.1) by 29%, assuming that birds would not consume prey from such polluted sediments.

The maximum exposed area of each feeding patch was calculated from the difference between Mean Low Water Spring (MLWS) and Mean High Water Spring (MHWS) and the exposed area of each patch every hour over the winter was calculated using a numerical hydrodynamic model developed using the 2D modelling package MIKE21 (Danish Hydraulic Institute) (Table D1b, Appendix D). Exposed patch areas were predicted by calculating the water depth within each grid cell of the hydrodynamic model (cells were considered dry if the water level was <1cm) and summing the areas of all cells within a patch for each time step. The hydrodynamic model predicted the exposed areas over an average spring and neap cycle, and was run for three scenarios; (a) the existing or baseline conditions of the estuary; (b) Dibden Bay removed and the tidal creek added; (c) Dibden Bay removed and the tidal creek added plus the recharge of material on the Hythe foreshore.

Three large roosts were incorporated into the model, each with a central coordinate representative of numerous small roosts identified by local ringing groups. Birds were assumed to use the roost nearest to their feeding patches with a maximum distance of 3.5km from the patches central coordinate, creating feeding patches-roost associations (Fig. 5.1). The River Itchen's feeding patch is not associated with a roost, owing to the surrounding area being heavily industrialised and not supporting any roost sites within the 3.5km circumference. The industrial nature and the associated disturbance of this site according to the Wetland Bird Survey (WeBS) Low Tide Counts translates to a relatively low number of birds. For further details on the WeBS Low Tide Counts please visits www.bto.org/surveys/webs.

5.3.3.3 Resource Parameters

Prey species from the intertidal survey of September 2003 were grouped into 5-mm size classes for each of the following types: annelids, hard bivalves, soft bivalves, *Hydrobia*, crustacea and crabs (Table D1c, Appendix D). Mortality of prey not attributable to birds was calculated from the difference between prey densities at the end of a model run and densities found in the February 2004 survey. Only *Hydrobia* differed, and we therefore assumed that bird depletion was the only source of mortality for all prey species except *Hydrobia*, which had an overwinter mortality of 40.1% due to factors other than the birds, occurring at a constant daily rate.

5.3.3.4 Component Parameters

The model had one resource component, ash-free dry-mass (AFDM) (Table D1d, Appendix D). Prey AFDMs were calculated from the prey length-AFDM relationships of individuals collected during the autumn from the Exe estuary (Durell et al., 2005b), as AFDM could not be measured for all species in Southampton Water, and tests showed that values did not differ significantly between the sites (see Appendix E). Initial numerical and AFDM densities for each prey type and size class were calculated for each feeding patch. Individual mass of molluscs has been shown to decrease during the winter (Zwarts, 1991; Zwarts and Wanink, 1993), and although it was not measured throughout the winter in Southampton Water we decided to include this mass reduction from the nearest suitable site: the Wadden Sea. The model therefore assumed that the mean AFDM of all molluscs decreased by 28% (Zwarts, 1991; Zwarts and Wanink, 1993), at a constant daily rate throughout the winter, while the AFDM of all other prey types remained constant (Table D1d, Appendix D).

5.3.3.5 Forager Parameters

Forager parameter values used to apply MORPH to Southampton Water are summarised in Table D1e in Appendix D. The model included the eight species of shorebirds found in the highest numbers in Southampton Water, based on the WeBS Low Tide Counts during the winter 2003/04: dunlin, ringed plover, ruddy turnstone *Arenaria interpres*, redshank, grey plover, black-tailed godwit, Eurasian oystercatcher *Haematopus ostralegus* and Eurasian curlew. Except for black-tailed godwits, population size was based on the mean number counted for the whole of Southampton Water during the winter WeBS Low Tide Counts 2003/4. We estimated that black-tailed godwit numbers were higher than the observed WeBS Low Tide Counts, based on our observations during hourly counts from high to low water on a spring and neap tide each month at four main feeding areas: Calshot, Eling, Westonshore and the mouth of the River Hamble (Fig. 5.1). For the initial population size of black-tailed godwits we took an average between the WeBS and our counts. All shorebirds apart from dunlin and grey plover were considered present at their maximum population size at the start of September (Day 1); dunlin and grey plover immigrated into the system at a constant rate until mid December (Day 107), based monthly data from WeBS Low Tide Counts.

The mean body mass for each dunlin, turnstone, grey plover and oystercatcher at the start of winter was determined from measurements taken by Farlington Ringing Group in Southampton Water during the winters 2000/1 – 2003/4 (Potts, P. pers. comm.). Initial body masses for the remaining species were calculated as 94% of mass on the Wash (Johnson, 1985), as dunlin, turnstone, grey plover and oystercatcher masses in Southampton Water were 94% of masses on the Wash. Model birds attempted to maintain a constant body mass throughout winter (i.e. their target body mass equalled their initial body mass). Forager diets and size of consumed prey, and starvation masses were obtained from previous empirical data (Stillman et al., 2005a; Goss-Custard et al., 2006; Goss-Custard, J.D., unpubl. data). Previous individual-based models (e.g. Stillman et al., 2005a) assumed that several bird species consumed diets comprised of the same prey types and the same size classes; more realistically this model allowed each forager to feed from its own specific diet.

Shorebird intake rates were determined by the abundance of food in a patch and the strength of interference from other competitors. The influence of food abundance on the model bird's intake rate in the absence of competitors was calculated from the following Holling Type II functional response (Stillman et al., 2005a):

$$IFIR = f\,\frac{IFIR_{\max}B}{B_{50} + B} \qquad (1)$$

where $IFIR$ = interference-free intake rate (mg s^{-1}), f = foraging efficiency of the individual, B = patch biomass density of prey within the individuals specific diet (mg m^{-2}), $IFIR_{\max}$ = maximum intake rate when prey are superabundant and B_{50} = prey biomass density at which intake rate is 50% of its maximum. The foraging efficiency for each individual was drawn from a normal distribution, with a mean of 1 and a standard deviation of 0.125 (Goss-Custard et al., 1995c). $IFIR_{\max}$ and B_{50} were estimated from previous empirical data (Goss-Custard et al., 2006). $IFIR_{\max}$ was related to shorebird body mass and prey mass by the following equation (Stillman et al., 2005a):

$$\mathrm{Log}_e\,(IFIR_{\max}) = -2.802 + 0.2451\log_e(M_{\mathrm{spec}}) + 0.365\log_e(rM_{\mathrm{prey}}) \qquad (2)$$

where M_{spec} = average body mass (g) of the shorebird at the start of the winter, M_{prey} = mean AFDM (mg) of prey within the shorebirds specific diet, and r = ratio of size of prey consumed to size in patch. Birds generally select the larger sized prey within their specific diets, yielding a value of r = 1.05 (Goss-Custard et al., 2006).

The influence of conspecific competitors on a bird's intake rate was incorporated using an interference function (Stillman et al., 1996):

$$IR = IFIR\left(\frac{gD+1}{D_0+1}\right)^{-(m_{\max}-(m_{\max}-m_{\min})d)} \qquad \text{if } D \geq D_0 \qquad (3)$$

$$IR = IFIR \qquad \text{if } D < D_0$$

where IR = intake rate (mg s^{-1}), D = conspecific competitor density in patch (ha^{-1}), D_0 = con-specific competitor density above which interference reduces intake rate, g = aggregation factor, d = dominance of the individual (0-1), m_{max} = susceptibility to interference of least dominant individual (d = 0), and m_{min} = susceptibility to interference of most dominant individual (d = 1). The threshold for D_0 was set at 100 birds ha^{-1} for all foragers. This figure is based on approximate thresholds from empirical studies in which interference occurs either through prey stealing among foragers ('kelptoparasitism'), such as oystercatchers feeding on mussels *Mytilus edulis* and cockles *Cerastoderma edule* (Stillman et al., 1996; Triplet et al., 1999) or through prey-avoidance behaviour to the presence of foragers ('prey depression'), such as redshank feeding by sight on the amphipod crustacean *Corophium volutator* (Yates et al., 2000). An aggregation factor incorporated into the interference function allows for the model shorebirds to aggregate in a patch, rather than being spread uniformly, as would occur in nature. The aggregation factor was set at 10 for all species, in accordance with cockle-feeding oystercatchers on the Burry Inlet, UK (West et al., 2003) and the Humber estuary (Stillman et al., 2005a). The susceptibility to interference of the least (m_{max}) and most ($m_{\min}$) dominant individuals for each species were predicted from previous studies and our observation during this study on the foraging behaviour of individual species and the mobility and predator responses of different prey. As in previous models interference was assumed to be absent for *Hydrobia*, which are consumed quickly (Stillman et al., 1997) and can not rapidly escape from the approaching birds. Mobile prey such as annelids and crustacea which have the ability to rapidly escape into the sediment were assumed to induce prey depression interference which is independent of the foragers' dominance, and assigned an interference value (0.48) of the same strength as redshank feeding on *Corophium* (Yates et al., 2000). For all other types of interferences we made some changes to previous models (see Stillman et al., 2005a), based on our foraging behaviour observations in Southampton Water during the winters 2003-05. For non-mobile larger prey such as bivalves, and for crabs which are mobile only on the surface of the intertidal substrate, interference was assumed to occur through kelptoparasitism dependent on dominance, being absent in the most dominant and strongest in the least dominant. For all species except cockle-feeding oystercatchers and crab-feeding oystercatchers, curlew, turnstone and redshank, relatively small prey were consumed in a short period of time (<10s). The strength of interference was weak (0.08) in these systems and predicted from an interference model (Stillman et al., 2002). Cockle-feeding oystercatcher and crab-feeding species were assigned a larger strength of interference (0.5) dependent on dominance, based on empirical studies (Triplet et al., 1999).

The amount of energy assimilated from consumed prey depends on the energy density of the prey and the efficiency with which energy is assimilated from the prey. Energy density was assumed to be 23.5kJ g^{-1} in annelids and crustacea, including crabs, and 22k J g^{-1} in all bivalves and *Hydrobia* spp. (Zwarts and Wanink, 1993).

Assimilation efficiencies, based on previous empirical data (J. D. Goss-Custard unpubl. data), were assumed to be 0.85 for all species consuming annelids and crustacea, including crabs; and 0.75 for species, except oystercatchers, consuming hard and soft bivalves. Oystercatchers have higher assimilation efficiency (0.85) when consuming bivalves because they remove the shell before consumption. Assimilated energy was converted into body mass from the assumption that 33.4KJ of energy was stored in each gram of storage tissue (Kersten and Piersma, 1987). The body mass of each species was used to calculate species specific daily energy requirements using the 'all bird species' equation of Nagy et al. (1999). Maximum daily energy assimilation for each species was calculated from their initial body mass (Kirkwood, 1983). The maximum amount of energy assimilated during each one hour time step was calculated as the daily figure divided by 12, assuming that birds fed for 12 hours per day, the approximate time for which their intertidal feeding areas are exposed. Birds limited the proportion of time feeding during time steps to prevent their maximum assimilation being exceeded.

We developed 2 versions of the Southampton Water model which differed in the decision rules birds used to decide which prey and patches to feed on; the 'rate-maximising' model assumed that birds always fed in the patches and on the prey that maximised their energy assimilation rate, whereas the 'satisficing' (e.g. Ward, 1992) model assumed that the feeding decisions of the birds depended on whether or not they were losing body mass (Table 5.1). Shorebirds use several roosts throughout Southampton Water, and individuals tend to forage on habitats relatively close to their roost site, rather than moving freely throughout the site (P. J. Wood, Pers. Obs.), most likely to minimise travel costs, and due to their greater experience of the relative quality of local habitats. This realism was incorporated into some simulations (termed "restricted dispersal simulations") by dividing the site into four regions, south, mid and north, and Itchen (Fig. 5.1; Table 5.1). The south, mid and north regions had an associated roost, and it was assumed that birds remained in these feeding patch and roost associations, unless they were losing mass. Birds that were losing mass moved to any patch within the site. The Itchen region did not have an associated roost and was only occupied by birds that were losing mass by feeding in other regions. The initial number of birds of each species in each region was determined from the distribution of birds recorded in the WeBS low tide counts, but changed when starving birds moved between regions.

Table 5.1. Decision rules used in model evaluation of bird distribution and prey selection of shorebirds in Southampton Water.

Decision Rule	Rule Description
1. Satisficing with restricted dispersal	Non-starving birds only move within their feeding patches-roost association. Starving birds (i.e. those that are losing mass) feed anywhere. Non-starving and starving birds feed either (i) in any patch and on any prey which yields an energy assimilation rate over twice their energy expenditure rate, or (ii) in the patch and on the prey that maximises energy assimilation rate if the criterion in (i) is not met. This ensures that birds attempt to meet their daily requirements by feeding for no more than 50% of the time (i.e. the approximate time for which their intertidal feeding areas are exposed).
2. Rate-maximising with restricted dispersal	Non-starving birds only move within their feeding patches-roost association. Starving birds feed anywhere. Non-starving and starving birds feed in the patch and on the prey that maximises energy assimilation rate.
3. Satisficing without restricted dispersal	Birds can move anywhere. Birds feed either (i) in any patch and on any prey which yields an energy assimilation rate over twice their energy expenditure rate, or (ii) in the patch and on the prey that maximises energy assimilation rate if the criterion in (i) is not met.
4. Rate-maximising without restricted dispersal	Birds can move anywhere. Birds feed in the patch and on the prey that maximises energy assimilation rate.

5.3.4 Model Evaluation and Simulations

Model predictions of survival rate could not be evaluated as no empirical data were available on survival. Instead, we evaluated the model by comparing predicted prey selection of each shorebird from our four decision rule models (Table 5.1), with observations from Goss-Custard et al. (1991) on the proportion of prey species being eaten by shorebirds at five estuaries in south-west England, including Southampton Water. The second model evaluation compared the predicted distribution of the shorebirds from our four decision rule models (Table 5.1), with the WeBS Low Tide Counts during the winter 2003/04.

We used the model to predict site quality in terms of prey biomass, taking into account the likely accuracy of the biomass densities of the different prey species estimated from the survey and various nighttime feeding efficiencies. To determine the relative effects of different prey species on site quality we ran a set of simulations in which one prey type was removed from the estuary. Each model bird could consume any other prey from its specific diet, so that if their most profitable prey species was removed it could switch to consuming one or more other prey species to compensate. To determine the vulnerability of each species to habitat loss, we ran simulations in which the areas of all patches were reduced simultaneously. To determine the effect of habitat loss and mitigation in association with the proposed construction of the Dibden Bay Terminal, we ran simulations in which (a) the intertidal area at Dibden was removed, (b) Dibden was removed and the intertidal mitigation creek at Dibden added, and (c) Dibden was removed and the intertidal creek and the recharge at Hythe added. These simulations were run using the 'worst-case' estimate of the prey-biomass density set by the lower 99% confidence limit, and with 50% night-time feeding efficiency for all foragers, and are termed "worst-case simulations".

5.4 Results

5.4.1 Model Evaluation

The best fit to the observed prey selection by grey plover, black-tailed godwit and curlew was obtained from the satisficing model with restricted dispersal (Fig. 5.2). The best fit to the observed prey selection by redshank and oystercatchers was obtained from the satisficing model without restricted dispersal, closely followed by the satisficing model with restriction (Fig. 5.2d and g). For oystercatchers, the satisficing model with restriction may have predicted lower prey selection for bivalves compared to that observed (Goss-Custard et al., 1991), due to the lack of mussel *Mytilus edulis* beds in Southampton Water compared to the other sites in their study. No observations were available for dunlin, ringed plover and turnstone, which all rapidly eat small prey making it difficult to record the prey type before being swallowed (Goss-Custard et al., 1991). However, as predicted by all four models, dunlins have been found to predominately feed on annelids and *Hydrobia* (Goss-Custard et al., 1977, 1991; Pienkowski et al., 1984).

The satisficing model with restriction best predicted the observed distribution (sum of squared residuals (predicted minus observed percentage of species population on a patch) 5901; Fig. 5.3). In particularly, the rate-maximising without restricted dispersal model poorly predicted the distribution of all species (sum of squared residuals 56048), with over 75% of the total population for all species except dunlin and oystercatcher being placed in one feeding patch, which had few or in some cases no observed birds. The satisficing model without restricted dispersal and rate maximizing model with restricted dispersal predicted species distribution with intermediate accuracy (sum of squared residuals 12854 and 17661 respectively).

Given that the satisficing model with restricted dispersal fitted most closely to the observed distributions of all shorebirds and the prey selection for most shorebirds, all further results were derived from this model.

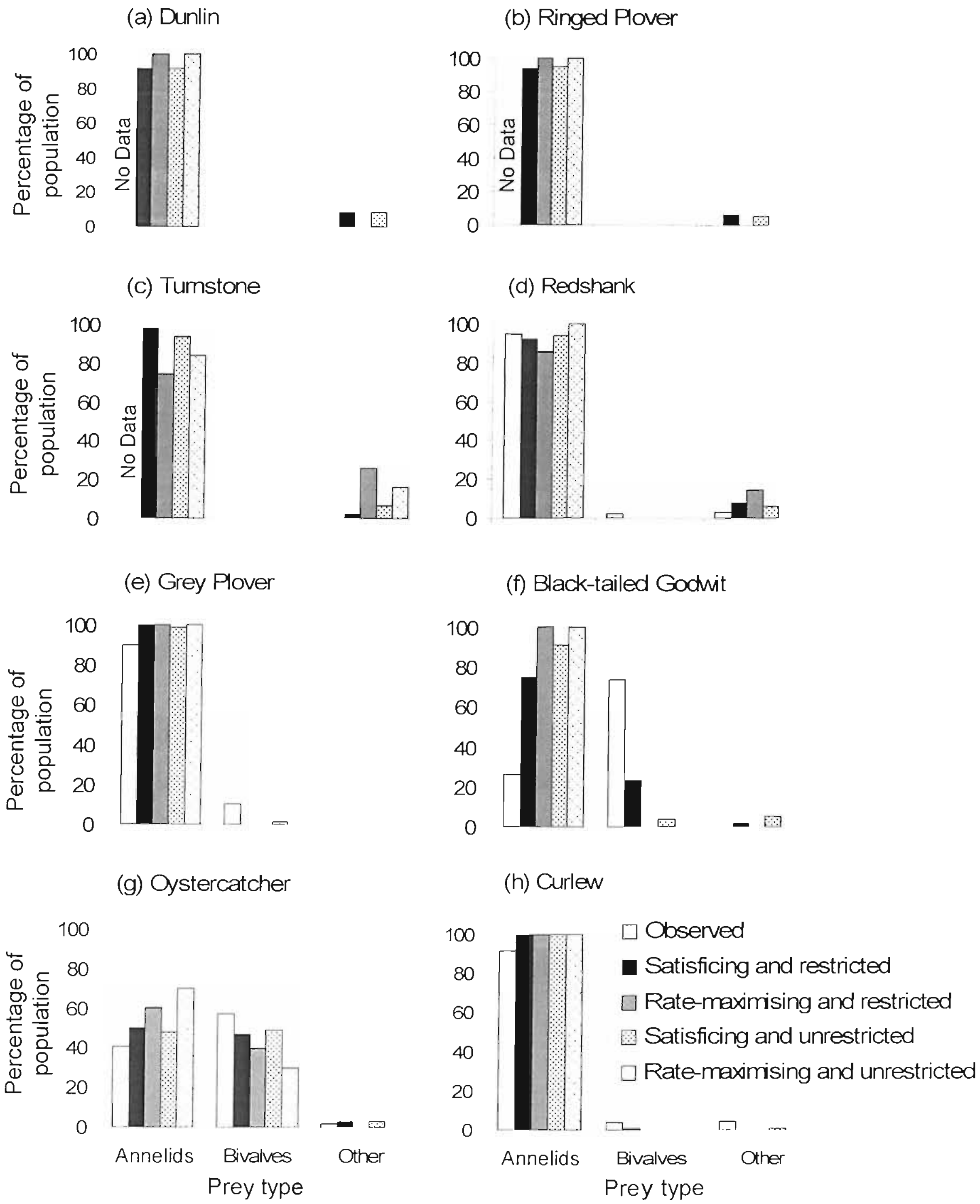


Figure 5.2. Predicted prey selection of shorebirds on Southampton Water from four decision rule models (Table 5.1), compared to that derived from observations on the proportion of prey types being eaten by shorebirds at five estuaries in south-west England (Goss-Custard et al., 1991). Predictions are September to March averages of the percentage of time spent feeding on the different major prey types.

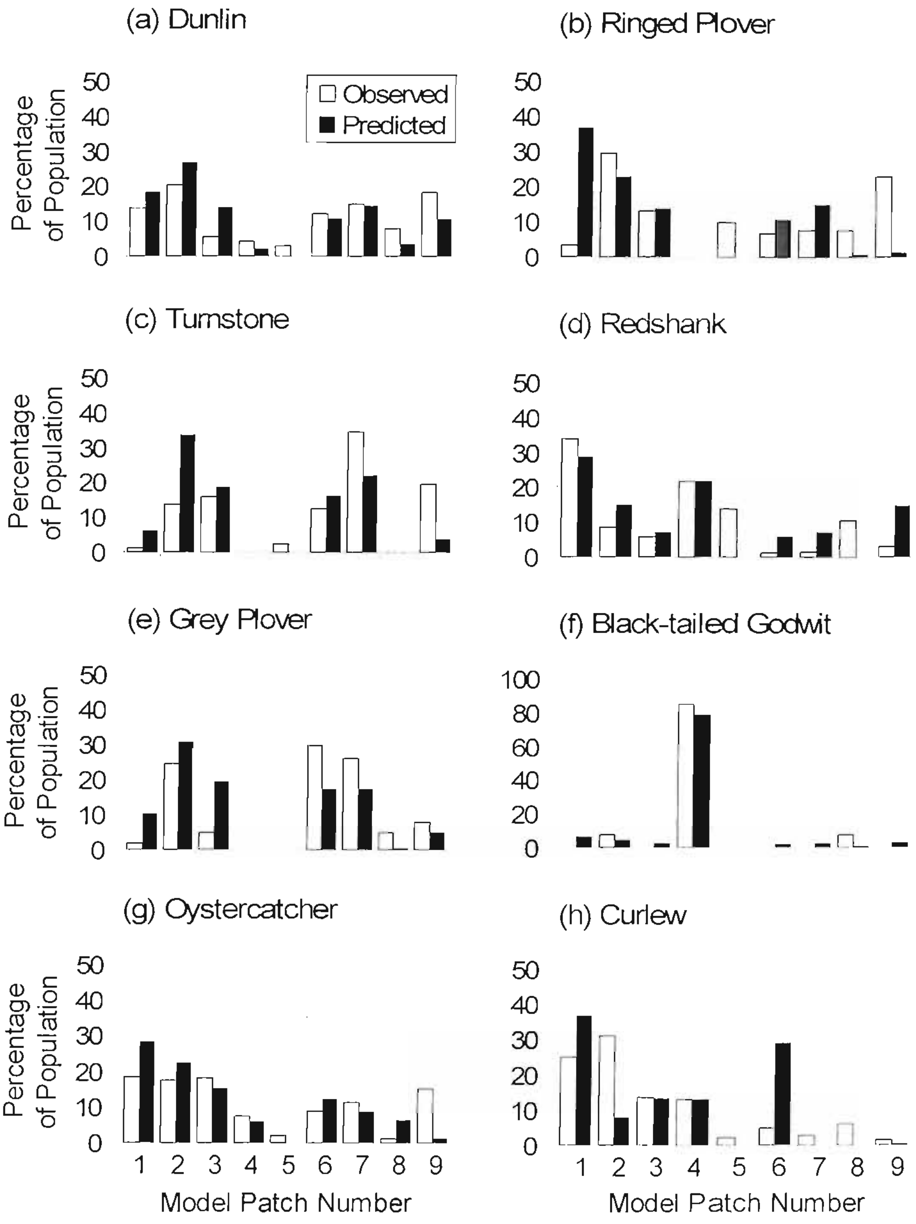


Figure 5.3. For shorebirds throughout Southampton, observed and predicted distribution from the satisficing model with restricted dispersal decision rule (Table 5.1). Observations are September to March averages from WeBS Low Tide Counts during 2003/04. Predictions are September to March averages of percentage of time spent feeding in different patches. Orientation of patch numbers in Fig. 5.1.

5.4.2 Prey Biomass and Site Quality

Prey biomass densities were highest for oystercatchers, which feed on larger annelids and molluscs, and lowest for ringed plovers, which feed on smaller classes of annelids, *Hydrobia* and small crustacean (mainly *Corophium* spp.) (Fig. 5.4). With the exception of dunlin, the model predicted 100% survival of all species when nighttime feeding efficiency was equal to that of daytime feeding efficiency, even when the survey was assumed to overestimate prey biomass (shading to the left of the vertical black lines in Fig. 5.4). Reducing nighttime feeding efficiency to 50% of daytime feeding efficiency resulted in a reduction in the survival of dunlin, redshank and curlew, even when the survey was assumed to overestimate true biomass density (Fig. 5.4). At this reduced nighttime feeding efficiency, the survival of all other species remained high at between 98-100% across the full 99% confidence limits of the survey.

Curlew, which feed by touch, are reported to feed almost entirely by day, and redshank feeding on intertidal mud change their feeding behaviour from sight feeding on *Corophium valutator* during daylight hours to feeding on *Hydrobia* spp. by touch at night (Hammond and Pearson, 1994). However, reducing the feeding efficiency of curlews to zero at night caused all individuals to die, and allowing redshank to feed only on *Hydrobia* at night caused their mortality to increase to 50%. These reductions in survival suggest either that the model overestimated mortality for these species, or that the survey underestimated the biomass density of their prey. Alternatively, these high mortalities may mean that curlew do feed at night and redshank feed on more than *Hybrobia* at night, or that they are reliant on terrestrial fields around the estuary for supplementary feeding when their intertidal prey are covered by the tide (shown to be important in other estuaries: Durell et al., 2006). Although little else is known on the nighttime efficiency of shorebirds, birds that feed by sight such as grey plover and turnstone would be expected to have lower efficiencies at night. We reduced nighttime efficiency to 50% of daytime efficiency based on an estimated average for all shorebirds combined, and so represent a 'best case' scenario for curlew, but possibly an underestimated efficiency for other shorebirds.

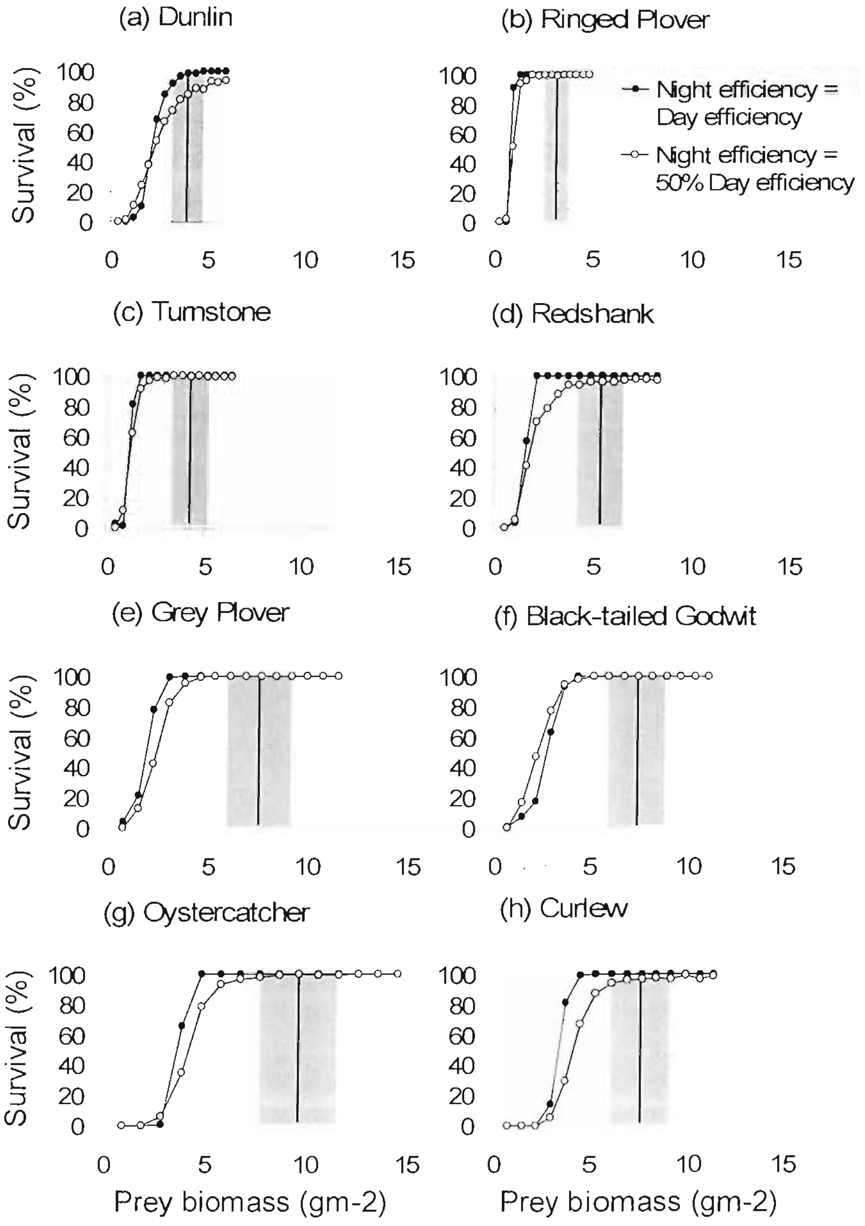
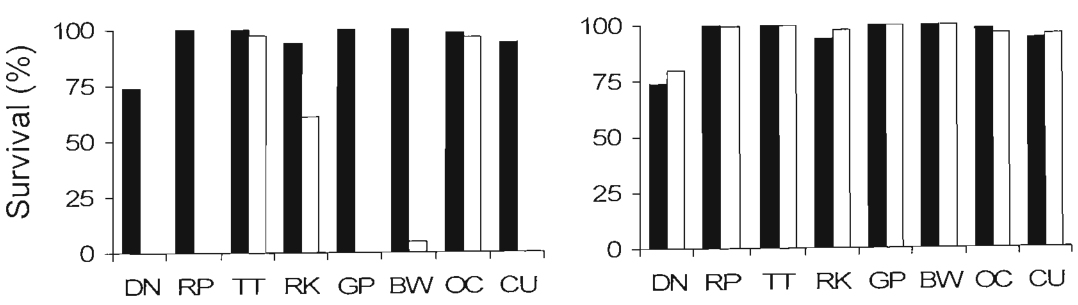


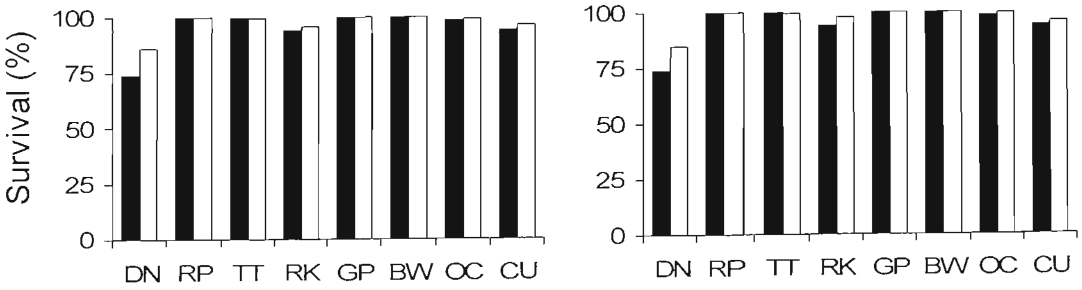
Figure 5.4. Predicted effect of changes in prey-biomass density on percentage overwinter survival of shorebirds in Southampton Water. Two models show percentage overwinter survival where nighttime feeding efficiency is equal to daytime feeding efficiency and where nighttime feeding efficiency is half daytime efficiency. For each shorebird, prey biomass is the estuary-wide mean within their specific diets. Black vertical lines = mean prey biomass estimated by survey, grey shading = 99% confidence limits of survey (calculated following Stillman et al., 2005a).

5.4.3 Prey Species and Site Quality

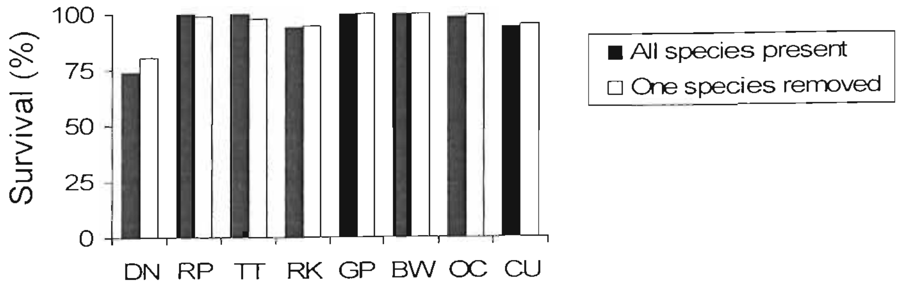
Removing annelids from the worst-case simulations greatly reduced the survival of all species except turnstone and oystercatcher (Fig. 5.5a), indicating the importance of this prey type for the majority of the birds feeding in Southampton Water. The removal of bivalves, *Hydrobia*, crabs and crustacea had no effect on the survival of any of the foragers (Fig. 5.5b-e).



(a) Annelids (b) Bivalves



(c) Hydrobia (d) Crabs



(e) Crustacea

Figure 5.5. Predicted effect of removing prey types on percentage overwinter survival of shorebirds in Southampton Water. Prediction are for 'worst-case' estimates of prey biomass (80% of observed) and nighttime feeding efficiencies (50% of daytime efficiencies). Where DN = dunlin, RP = ringed plover, TT = turnstone, RK = redshank, GP = grey plover, BW = black-tailed godwit, OC = oystercatcher, CU = curlew.

5.4.4 Habitat area and Site Quality

In order to determine the vulnerability of different species to habitat loss we ran a set of worst-case simulations in which the area of all patches was reduced simultaneously. These simulations therefore represent the loss of average quality habitat throughout the site, rather than the specific habitat that would have been lost due to the Dibden Bay development. The survival rates of dunlin and curlew were decreased when total habitat area was reduced by 5-10% (i.e. the approximate amount of loss that would be caused by the development) (Fig. 5.6a and h). The survival rates of the remaining species were unaffected by this magnitude of habitat loss, although the next most vulnerable species were redshank, black-tailed godwit and oystercatcher, each having reduced survival rates when more than 30% of the habitat was lost (Fig. 5.6d, f and g). The survival rates of ringed plover, turnstone and grey plover were unaffected by up to 50% habitat loss (Fig. 5.6b, c and e).

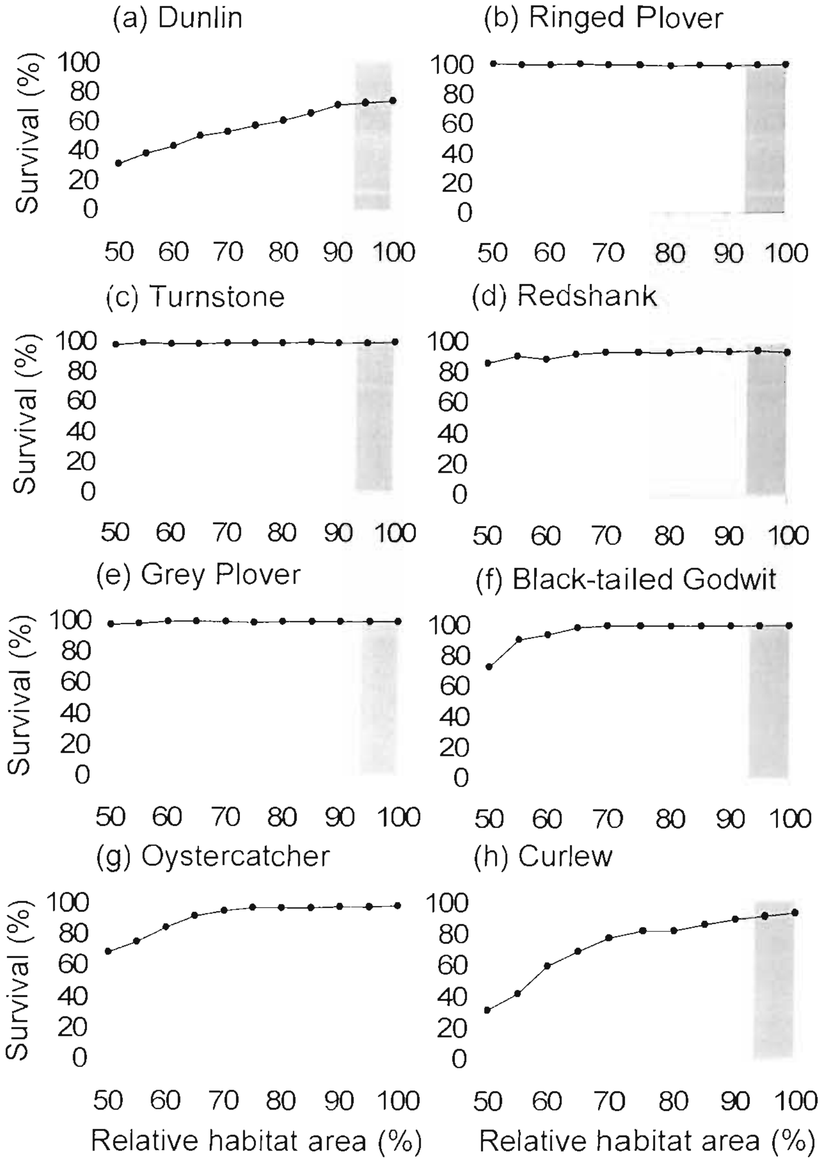
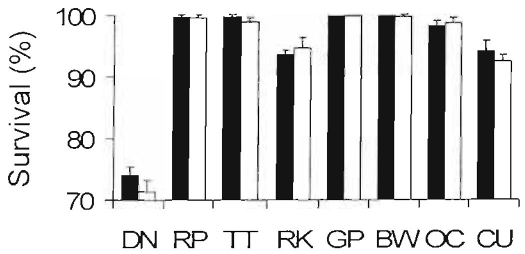


Figure 5.6. Predicted effect of changes in habitat area on percentage overwinter survival of shorebirds in Southampton Water. Prediction are for 'worst-case' estimates of prey biomass (80% of observed) and nighttime feeding efficiencies (50% of daytime efficiencies). Habitat was removed from all patches simultaneously. Grey shading = 7% habitat loss equal to that lost to the proposed Dibden Bay development.

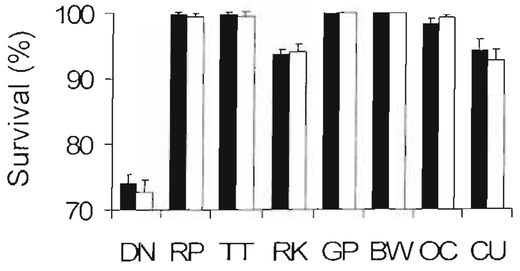
5.4.5 Habitat Loss and Site Quality

The loss of Dibden Bay from the worst-case simulations significantly decreased survival in dunlin by 2.7% (t-test comparing predicted dunlin survival with and without habitat loss, t=2.37, n=10 simulations, p=0.030) and turnstone by 0.9% (t=2.60, n=10, p=0.024). This habitat loss also decreased the survival in curlew by 1.7%, although at a lower significance level (t=1.80, n=10, p=0.093). Habitat loss had no significant effect on the survival of any other species (t-tests comparing predicted survival with and without habitat loss, n=10, p>0.10 in all cases) (Fig. 5.7a). Habitat loss in association with the mitigation measures of either adding the creek (Fig. 5.7b), or adding the creek and recharging the sediments at Hythe (Fig. 5.7c) had no significant effect on the survival of any species (t-tests comparing predicted survival with and without habitat loss and mitigation, n=10 simulations, p>0.10 in all cases).

(a) Dibden loss



(b) Loss plus creek



(c) Loss plus creek and recharge

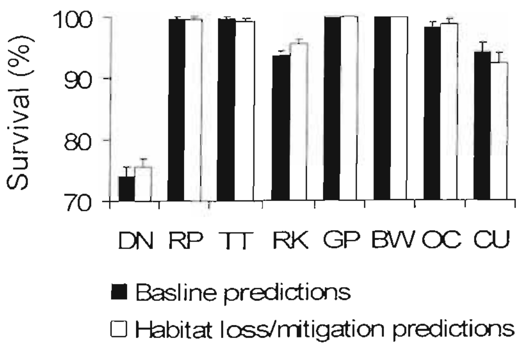


Figure 5.7. Predicted effect of removing Dibden Bay and adding the proposed mitigations, the tidal creek and the Hythe to Cadland recharge, on the percentage overwinter survival of shorebirds in Southampton Water. The bars show the mean predicted survival from ten replicate simulations with associated 95% confidence limits. Prediction are for 'worst-case' estimates of prey biomass (80% of observed) and nighttime feeding efficiencies (50% of daytime efficiencies). Where DN = dunlin, RP = ringed plover, TT = turnstone, RK = redshank, GP = grey plover, BW = black-tailed godwit, OC = oystercatcher, CU = curlew.

5.5 Discussion

A growing body of evidence suggests that individual-based models can provide vital prediction of site quality for winter feeding shorebirds. To date, little was known on the winter survival of wintering shorebirds on Southampton Water, or on the potential impacts to shorebirds survival of habitat removal. Direct measures of survival would be of little use in predicting how future environmental changes to the estuary may affect its quality, in terms of shorebirds. In this chapter, we have shown how site quality can be measured from the predicted survival rates of shorebirds and how the effect of environmental change in Southampton Water will influence these survival rates. We achieved this by parameterising the recently developed MORPH model (Grimm et al., 2006) using data from an estuary-wide macrobenthic invertebrate survey (chapter 4) and data obtained from WeBS Low Tide Counts.

The model was extended for Southampton Water to test four decision rules which incorporated rate-maximising or satisficing rules, and dispersal restrictions. Previous models have used either rate-maximising (Stillman et al., 2001, 2003; West et al., 2002, 2003, 2005; Caldow et al., 2004; Durell et al., 2005a, 2006) or satisficing (Stillman et al. 2005a) decision rules without restricted dispersal. However, we have shown that satisficing decision rules with restricted dispersal more accurately predicted the observed distribution of all shorebirds and the prey selection for most shorebirds. Unless they were losing mass, the birds in the satisficing models consumed any prey which provided an energy-assimilation rate greater than double their energy-expenditure rate, to ensure they met their daily requirements by feeding for 50% of the time (i.e. the approximate time for which their intertidal feeding areas are exposed). Such decision rules are likely to be more appropriate to large spatial scales where it is unlikely that birds have the perfect knowledge of the quality of each feeding patch required to move to the patch in which their intake rate would be maximised (Stillman et al., 2005a). We achieved restricted dispersal by limiting the dispersal of non-starving birds to sections of the study site comprised of feeding patches and an associated roost. The restricted dispersal rule possibly predicted shorebird distribution more accurately due to most shorebird species developing social flocks when feeding and roosting, which are thought to reduce predation risk and increase foraging efficiency (Eiserer, 1984; Ydenberg and Prins, 1984; Cresswell, 1994; Krause and Ruxton, 2002). Communal roosts and feeding flocks act as information centers for food-finding (Ward and Zahavi, 1973; Krause and Ruxton, 2002). Social interactions of flocks may result in the relative dominance status of foragers to be so well established that little agonistic behaviour is required (Balph, 1977). Furthermore, social flocks may have preferred feeding areas and roost patches, which are in close proximity to reduce commuting costs (Caccamise and Morrison, 1988).

As with any model, the accuracy of our predictions will depend on the accuracy with which each parameter was measured, especially the abundance and the distribution of the macrobenthic invertebrate food supply. We used a range of simulations which incorporated the full range of possible prey-biomass densities. We also used a range of nighttime feeding efficiencies, based on the literature suggesting that certain species reduce or change their feeding behaviour during the night (Hammond and Pearson, 1994). Using the worst-case estimate of the prey-biomass density and nighttime feeding efficiency half of that in the day we were able to predict which shorebird species would be the most vulnerable to environmental changes in Southampton Water. Annelids were predicted to be the major component of diet of all species except oystercatchers, and due to their predicted equal dependence on annelids and bivalves, this species did not suffer when annelids or bivalves were removed. Turnstones also showed no predicted reductions in survival when annelids were removed from their specific diets, suggesting that they were able to compensate by feeding from other prey types. The predicted dominance of annelids and bivalves in the diets occurred because these prey types were present at the highest biomass densities and were generally larger than the other types of prey. Most of the prey selection predictions accorded with a review of the diets of shorebirds in the south-west of England (Goss-Custard et al., 1991). Oystercatchers, which feed on larger prey items, had the highest prey-biomass densities and were the least likely to be affected by habitat loss. Smaller species such as ringed plover and dunlin, which feed on smaller prey items, had the lowest prey-biomass densities. Dunlin, turnstone and curlew were the most likely species to be affected by the loss of Dibden Bay. Any negative effects of habitat loss on the survival of these species were eliminated with the addition of the tidal creek.

Although our simulations suggest that the mitigation would offset the removal of Dibden Bay, our model does not account for the years during removal and construction of the mitigation proposals. ABP predicted that Dibden Bay would be unavailable to shorebirds from the onset of dredging and the tidal creek would take at least nine years to provide alternative shorebird habitat (Associated British Ports, 2000b; Drewitt, 2001). Furthermore, the recharge from Hythe to Cadland would result in a temporary reduction in the extent of feeding habitat, and the 22 hectares of additional mudflat, following the recharge, was predicted to take 8 years to reach its optimal ecological function (Associated British Ports, 2000b). It is reasonable to expect a gap of up to 9 years of lower prey-biomass densities than present estimates would have an accumulated effect on shorebird mortality, especially as Dibden Bay and the Hythe to Cadland foreshore provides habitat for a large proportion of the total population of dunlin, ringed plover, grey plover, curlew and oystercatcher in Southampton Water (Fig. 5.3). This emphasises the dangers associated with using models to predict future environmental changes. To maximise their usefulness models must be run for the worst-case scenario and incorporating accumulative effects for each consecutive year of predicted change. Nevertheless, these model predictions have been useful in showing which shorebird species are most sensitive to habitat loss, and based on shorebirds preferred diets the model can predict which species would be most affected by the loss of specific areas of intertidal feeding areas in Southampton Water.

The quality of SPAs for shorebirds not only depends on the biomass of prey, but the availability of prey (Durell et al., 2006). Intertidal exposure time in Southampton Water is already brief, due to the unusual double high tide, and is likely to reduce further with predicted sea-level rise or sediment loss (Bray et al., 2000). We advise that future estuary monitoring to determine whether prey biomass densities fall to values at which shorebird survival was predicted to decrease is essential for the maintenance of the SPA and maritime SAC of Southampton Water.

CHAPTER 6. GENERAL DISCUSSION

This thesis has examined how examples of threats to our environment and global biodiversity can be assessed within a local scale and how implications of such threats can accumulate to a national and even a global scale. Data chapters have dealt with how the overexploitation of a natural resource can affect populations in the short term (chapter 2) and long term (chapter 3), how the effects of physical human disturbances (chapter 3) and habitat loss (chapter 5) can change population dynamics and the distribution of species, and how climate change will potentially exacerbate these effects (chapter 2-5). This thesis evaluates impacts in the context of European legislation concerning biodiversity, and seeks to provide information required for future developments.

The Solent has been acknowledged to provide prime habitat for coastal birds (Tubbs, 1999; Burges, 2000), and this thesis has demonstrated how these species are can be negatively affected by human actions. Thus, the security of the Solent's coastal bird species will depend on their protection from detrimental human actions and the protection and management of their habitats, especially as they are dependent on lowland coastal habitats that will be most affected by sea level rise.

The potential implications for effective management of the ornithological resources of the Solent are evident. The health of the breeding coastal birds depends on the saltmarsh habitat on which they nest which needs management to minimise coastal erosion from sea level rise. However, this thesis has demonstrated that factors such as egg harvesting, human disturbance, predation and tidal flooding influence the breeding success, and ultimately the population sizes and distributions of these species. All of these factors can be managed, with scope to reduce or even prevent the anthropogenic impacts. The health of the wintering coastal birds of the Solent, which rely upon the invertebrate food provided by the estuaries and mudflats, depends on the maintenance of this food supply. The present study has demonstrated how we can predict effects of habitat loss and disturbance on wintering shorebirds by assessing the food supply within an estuary and applying those data to an individual-based model. This method also allows us to predict how well measures proposed to mitigate habitat losses will fare into the future. Such predictions are essential for shorebird and estuarine conservation. Nevertheless, chapter 5 emphasised that the utility of model simulations to conservation depends on thorough assessment of the parameters entered into models and any accumulation effects.

In this discussion, I will draw together and evaluate some of the key findings from data chapters. I will point to some likely implications, and formulate questions that should be addressed by future studies.

6.1 Impacts of egg harvesting

In chapter 2 and 3 the impacts of exploiting a local wild population were assessed in order to provide advisory data to which governmental organisations can review the licensing of such an activity. The target resource, Black-headed Gulls' eggs, have been harvested from the study area in Hampshire for centuries (B. Lord, pers. comm.), and since the Wildlife and Countryside Act (1981) and the requirements therein, this activity has been managed by issuing licences. However, to date there have been no empirical studies to assess the impacts on breeding success incurred by the Black-headed Gulls from an annual egg-harvest or the implications on their breeding distribution and population size; and even less is known on the impact to the breeding distributions of seabirds which experience the disturbance associated with an egg-harvest.

The key finding from chapter 2 was that the breeding success, measured by indicators such as egg volume, yolk-to-albumen ratio, hatching success and chick survival (Nager et al., 2000, Hipfner et al., 2003), was lower for harvested than non-harvested breeders, over and above the effects of colony size and nest position within the colony. Based on previous studies (Heaney and Monaghan, 1995; Monaghan et al., 1998) we concluded that the lower breeding success on harvested colonies is likely to be linked to depletion of the female's endogenous reserves through repeated laying. Reductions in breeding success indicators have been observed in other seabird species when experimental inducing individuals to lay replacement eggs (Feare, 1976b; Parsons, 1976; Robbins, 1981; Houston et al., 1983; Bolton et al., 1992; Brown and Morris, 1996; Monaghan et al., 1998; Nager et al., 2000; Hipfner et al., 2003). Thus, the results presented in chapter 2 are not surprising considering the egg-harvest occurs for approximately 4 weeks of the breeding season. What was surprising and, as far as I am aware, unknown before this study was the negative effect on hatching success from excess egg water loss incurred from delaying incubation through egg harvesting, evident from the failed 'corroded' eggs.

Eggs that lose abnormal amounts of water during incubation frequently do not hatch (Snyder and Birchard, 1982; Carey, 1986). Nest microclimate is particularly important, with eggs being exposed to high temperatures or low nest water vapour pressure losing large amounts of water (Lundy, 1969; Webb, 1987). This results in the hatchlings sticking to the membranes of the egg, preventing them from breaking out (Walsberg and Schmidt, 1992; Wissman, 1996). As natural environments rarely provide exactly the correct conditions for the embryos, parents must regulate nest microclimate by incubating the eggs (Reid et al., 2000). I hypothesise three mechanisms by which the occurrence of failed 'corroded' eggs increase at harvested sites. The first simply being the increase in ambient temperature during incubation, which is at least 3 weeks later in the season than un-harvested sites. This increase in temperature may prove difficult to regulate for the incubating parents. The second is that parents will spend more time foraging, thus leaving the microclimate of their nest unregulated for longer, allowing eggs to equilibrate with ambient temperatures. The energetic demand upon the female increases with relaying (Heaney and Monaghan, 1995; Oppliger et al., 1996; Monaghan et al., 1998; Visser and Lessells, 2001). Thus parents incubating replacement eggs may have been forced to forage more in order to maintain their energy balance. The third is that the shell structure of the replacement eggs may have changed so that egg water loss increased. The rate at which eggs lose water has also been shown to depend on shell structure (Packard and Packard, 1993), especially shell thickness (Ar et al., 1974). The present study demonstrated that both the shell thickness and the deposition of pigmentation were lower on harvested than un-harvested sites, both of which suggest negative impacts on females' health (Monaghan and Nager, 1997; Moreno and Osorno, 2003). In chapter 2, I hypothesised that the thinner eggshells could be explained by a constraint on the females' ability to forage for calcium rich items. However, egg shells have been shown to thin when the females are laying in high ambient temperatures, apparently due to alkalosis of the blood caused by excessive loss of carbon dioxide in panting (Smith, 1974). I certainly observed Black-headed Gulls panting during incubation on hot sunny days at the harvested sites.

It would be interesting to compare the shell structure and occurrence of 'corroded' eggs from Black-headed Gulls breeding at high ambient temperatures from un-harvested sites with that of birds breeding on the present harvested sites, to determine which factor is causing excess egg water loss. Nonetheless, it remains the case that thinner shells and failed 'corroded' eggs, plus un-pigmented eggs and small yolkless eggs, all increased in occurrence on harvested sites.

The principle difficulty when designing how we were going to gauge the impact of egg harvesting was finding sufficient replicate sites to avoid confounding influences from tides, colony size, nest position and predation. The first design incorporated all combinations of three test variables: egg harvesting, egg harvesting associated disturbance and tidal flooding, except the impossible combination of harvesting without disturbance. The first year of study demonstrated significant effects of colony size and nest position within the colony for some of these breeding success indicators. These effects were confounded with treatment effects, because not all the available harvested and un-harvested colonies were of similar size. Furthermore, not all of the colonies that were designated as tidal actually flooded during the breeding season; also one of the small harvested colonies was abandoned by breeders before final egg measurements could be made, following substantial losses to mammalian predators. For these reasons, the design was adapted to that described in chapter 2. Ideally the same sites and thus analysis would have been used for all years of study, but due to site abandonment and the uncertainty of some sites being used after the first year owing to foxes causing total chick loss late in the season, five study areas were chosen based on colony size, nest position and harvesting regime for the 2005 (see Chapter 2). Two similar study areas, one harvested and the other not, were studied in both years, which allowed analysis of the effect of year and harvesting, and year-by-harvesting interactions.

A further limitation was encountered in 2005 when half of the eggs collected as peak laid eggs from the un-harvested site were found to be addled. The presence of addled eggs suggested that the collection period just preceded the peak of laying, at a time when the more competitive birds were acquiring territories from earlier breeders, resulting in early-laid eggs being destroyed or left unattended to addle (Weidmann 1956, Patterson 1965). This shed doubt on the origins of the remaining fresh eggs, which could have been re-laid eggs from early laying birds, or first laid eggs from peak laying birds, or both. The latter seems more probably, as the yolk-to-albumen ratio did not differ significantly between these eggs and those laid earlier in the season, while there was a significant increase from early laid eggs to peak laid within the same site the following year and in both years on the harvested site (Fig. 2.3, chapter 2).

These complications are likely to contribute to raising the error variation in tests of treatment effects. Nevertheless, egg volume and the yolk-to-albumen ratio were found to be influenced by laying time and location, and most importantly, negatively influenced by egg harvesting.

The lack of flooding on proposed tidal sites resulted in tidal flooding being excluded from the ANOVA design. However, our observations indicated that late season flooding events caused whole clutches to be lost on harvested sites, whereas on the un-harvested site most chicks were at least 10 days old and able to survive the flooding. The lack of flooding in 2004 enabled us to compare two similar un-harvested sites, excluding the flooding regime. This comparison indicated that egg volume was uninfluenced, in this year, by tidal flooding (Fig. 2.1, chapter 2). The same comparison of sites also suggested that egg volume may have been uninfluenced by the disturbance caused by harvesting, since one site was classed as un-harvested and disturbed and the other as un-harvested and undisturbed. However, these results were from one year only, and would statistically benefit from further studies. Furthermore, in Chapter 3 disturbance from egg harvesting appears to have restricted the breeding distribution of the UK's relatively recent breeding associate of the Black-headed Gull, the Mediterranean Gull.

The key findings in chapter 3 were that mammalian predation, of which egg harvesting is an example, and tidal flooding have caused major reductions in breeding success of all study seabird species and influenced their distributions along the south coast of England. The breeding distribution of both Black-headed Gulls and Mediterranean Gulls appear to be affected directly by egg harvesting and its associated disturbance. Other ground-nesting seabird species such as terns, which general start laying when egg harvesting has ceased, don't appear to be directly effected by the egg-harvest. Although the refuge provided by the Black-headed Gull colonies has dictated the terns' presence at some sites, whereby terns abandon a harvested site when the number of nesting Black-headed Gulls have diminished to a level that cannot provide adequate defence against predators (Kruuk 1964).

It would be interesting to see whether natural and/or anthropogenic sourced food supplies influence the breeding distribution of any of the study seabird species in chapter 3. We assumed that food supply was constant between sites due to their relatively close proximity to each other and landfill sites along the south coast of England. However, food quantity, quality and accessibility could potentially be a confounding factor when assessing impacts of egg harvesting.

Changes in the reproductive success of several fish-eating seabirds have been linked to prey shortages due to over-fishing (Crawford and Shelton, 1981; Furness, 1982; Poole, 1985). Furthermore, supplementary feeding and proximity to a plentiful resource such as a landfill site are also known to affect breeding success (Martin, 1987; Boutin, 1990; Nilsson and Svensson, 1993; Duhem et al., 2002; Prévot-Julliard et al., 2001). Black-headed Gulls are opportunistic foragers and it is well documented that they forage on landfill sites. One of the largest landfill sites along the coast of Hampshire, which is in close proximity to the harvested marshes from Keyhaven to Lymington, is in the process of closing (P. Durnell pers. comm.); it will be interesting to see whether there is a further movement of gulls away from Hampshire towards the surrounding counties which have large landfill within close proximity to breeding habitat, such as Beacon Hill landfill, near Poole Harbour, Dorset.

Foraging on landfills can also have highly detrimental effects on breeding success (Guthová, 1993), and cause higher adult mortality (Ortiz and Smith, 1993). We assumed that foraging on landfills would be similar in all study sites. Further studies would benefit the present study that assessed the differences in breeding success of gulls that receive various combinations of harvesting vs. un-harvested and foraging on landfill vs. not foraging on landfill. However, the scope for the site selection needed for such a comparison is very limited, especially as all other variables (e.g. colony size, tidal effect and predation) would need to be constant.

A scoping study in collaboration with Philippa Hudson of Bournemouth University (Appendix B) revealed that eggs collected on the harvested sites had very high numbers of *Escherichia coli*, *Salmonella* and *Campylobacter* on the exterior shell and in much lower numbers within the egg contents. The implications of these findings are of significance to the food standards of the commercial harvest; especially as anecdotal evidence suggests that such eggs are usually consumed 'soft', implying that these eggs may not receive the sorts of heat treatments which would kill these pathogens. Moreover, if further studies with larger replication significantly confirmed the presence of these pathogens within eggs, the licence to harvest the eggs would need reviewing by DEFRA and the Food Standards Agency.

In light of the observed detrimental effects of harvesting on breeding success and distributions of seabird colonies in the Solent, it is apparent that the present commercial licence to harvest Black-headed Gulls eggs would benefit from urgent review. Without change to this commercial egg harvest in Hampshire, the continuation of the Solent's seabird breeding populations is uncertain, especially as the breeding range and numbers of Black-headed Gulls have been in decline since the late 1970's (Mitchell et al., 2000). Furthermore, evidence suggests the present levels of harvesting are preventing Mediterranean Gulls from colonising or even breeding successfully on harvested sites. Mediterranean Gulls are protected as Annex 1 birds under the EC Birds Directive (EC/79/409) and as Schedule 1 birds and under the Wildlife and Countryside Act 1981. Regulations state that is an offence under these legislations to disturb such designated birds while building a nest or is in, on or near nest containing eggs and young. If the lack of Mediterranean gulls on harvested sites is due to egg harvesting and its associated disturbance within the Solent, the harvest will be violating EU and UK legislation. These results should be considered as potentially applicable to other harvested populations, where harvesting may reduce breeding success to an unsustainable level or may affect rarer species that breed in the colony. The damaging impacts reported in chapter 2 and 3 were incurred by a commercial harvest that involved removal of all eggs on a colony every day for a substantial fraction of the breeding season. Small-scale egging should be encouraged in accordance with the sustainable-exploitation principles of the Biodiversity Convention, and can have added benefits of informal policing of the area and monitoring of predation (which can have just as devastating an impact as harvesting). However, if breeding numbers continue to reduce in Hampshire and/or within the UK, it would be advisable to halt egg harvesting.

6.2 Impacts of habitat loss on winter shorebird populations

Models are becoming more desirable to assess the impact of anthropogenic activities on sensitive habitats and species, and provide future predictions. The Centre for Hydrology and Ecology (CEH) has been developing an individual-based model which can be applied to any habitat in which the target species are dependent. The models produced to date by CEH have mainly been aimed at estuaries which provide food for wintering shorebirds (Goss-Custard et al., 1995a, b, c, Stillman et al., 2000, 2001, 2005a, b; West et al., 2002, 2003; Durell et al., 2006). These models predict the intake rates of birds, and ultimately body conditions and mortalities, which have been forced by disturbance, habitat loss or climate change to alter their diet and/or to redistribute themselves over resource patches of varying quality (Goss-Custard et al., 2000).

Chapter 4 demonstrated how the baseline measurements can be obtained in order to parameterise an individual-based model. In this study, we used a stratified-random sampling design to identify discrete habitat patches on the basis of the macrobenthic invertebrates present within an estuary, and to estimate empirically the macrobenthic prey diversity and biomass density for each defined patch. This design also allowed us to identify macrofauna distribution and any environmental influences on species abundance, diversity and biomass.

Chapter 4 had two key findings. Firstly, our ANOVA on the sampling design revealed a higher level of heterogeneity within the study estuary (Southampton Water) than could be resolved from the multiple regression techniques that are normally applied to grid-based designs. Secondly, our stratified-random sampling design had a lower initial sampling effort and cost than a conventional 250×250 m grid survey, by virtue of a smaller number of more efficiently distributed sample sites . Although a more formal comparison of designs could have been obtained by applying the regression analysis to data from grid-based sampling, the sampling points from the stratified-random design indisputably represented the asymmetrical profile of Southampton Water more precisely than could have been achieved by the alternative of a grid (Fig. 4.1). Although the comparison of analyses is limited when applied to the same data set, it has provided a useful approximate comparator of hypothesis-testing ANOVA to parameter-estimating multiple regression.

This stratified sampling method could be applied to other estuaries and habitats where biological information is required. However, its utility depends on the assumption behind the ANOVA model that areas within the habitat can be reliably identified pre-sampling, which are more homogeneous within each area than between areas, needs to be satisfied. If this is not correctly satisfied then the model will have reduced ability to determine biological patterns within the habitat. If the habitat cannot be divided into areas pre-sampling then we advise using a random geometric sampling design, as described in Durell et al. (2005b).

The key finding in Chapter 4 of biological interest was that the macrofauna of Southampton Water is most influenced by the sediment composition, which is often considered the most important variable affecting macrobenthic invertebrate distributions (Longbottom, 1970; Boyden and Little, 1973; Gray, 1974; Green, 1975; Azouzi et al., 2002). These findings suggest the possibility of efficiency savings in future monitoring effort within Southampton Water by measuring the change in sediment composition.

It would be interesting to compare what environmental factors most influence the macrobenthic invertebrate distribution within various UK estuaries. For instance, the macrofauna of Poole Harbour, which is approximately 40km west of Southampton Water, is also influenced most by sediment composition (Caldow et al., 2005); whereas the macrofauna of the Exe, which is approximately a further 100km west, is most influenced by distance up the estuary (Durell et al., 2005b). However, these results may have been influenced by different sampling designs and statistical analyses.

An interesting result from the invertebrate survey was the presence of the introduced species, the Manila clam *Tapes philippinarum* indigenous to the western Pacific Ocean. This is the first record of this species in Southampton Water and evidence that it has spread from Poole Harbour, where it has naturalised since its introduction in the late 1980s for the purpose of aquaculture (Jensen et al., 2004, 2005). Introductions of non-native species have been classified as one of the major threats to our environment and global biodiversity (Pullin, 2002). However, the evidence provided in Appendix F (Caldow et al. in press), shows how this introduced species is providing Oystercatchers in Poole Harbour with a new food resource and resulted in a previously unknown predator-prey interaction between these species. This study used an individual-based model to demonstrate that the presence of the Manila clam is predicted to cause a decrease in over-winter mortality of Oystercatchers, even at the currently low clam density found in Poole Harbour. Furthermore, if the Manila clam were to spread around the British coasts, a process which is likely to be facilitated by climate change, shellfish-eating shorebirds are likely to benefit considerably on a national scale.

In chapter 5 we applied the macrobenthic invertebrate data from the survey described in chapter 4 to an individual-based model for Southampton Water to evaluate site quality for eight shorebirds. The key findings in chapter 5 were: Firstly, that the shorebirds using Southampton Water appear to be influenced by a decision rule on which prey and area within the estuary to feed on. We found that if model non-starving birds were assumed to move within restricted areas of the estuary, which were closest to their roosting locations, and consume any prey which yielded a threshold energy assimilation rate, then model birds behaved in way which distributed them within the estuary similar to that of the observed birds and also consumed similar prey species to observed birds. This may have implications for future models of shorebirds feeding in estuaries, especially as previous models have not considered this decision rule. Efforts could be made in the future to empirically test the restricted dispersal decision rule.

Colour-ringing or radio tracking birds can provide ways to follow a birds movements from feeding areas to roosting areas.

The second key finding was that the majority of the shorebirds depend on annelids for survival, with Oystercatchers utilising both annelids and bivalves. Similar results were found on the Humber estuary (Stillman et al., 2005a). This implies that if survey resources are limited, it would be more important to estimate the biomass densities for annelids and bivalves, than to estimate the densities for *Hydrobia*, crabs and crustacea. Further studies on other estuaries are required to determine whether these conclusions are more widely applicable.

The third key finding was that Dunlin and Curlew would be most affected by habitat loss when the loss was spread throughout the estuary. Turnstones were also affected when the habitat loss was restricted to the proposed Dibden Terminal site. These shorebirds are protected as migratory species (Article 4.2) under the EC Birds Directive, and are also listed on the UK 'Amber' list (Gregory et al., 2002). Dunlin's conservation status is of particular interest within the present study, as the UK non-breeding population has experienced a moderate (25–49%) decline over the 25 years and more than 50% of the UK non-breeding population is found in 10 or fewer sites. Thus the implications of losing feeding habitat in Southampton Water for Dunlins would be seen at a national level. Furthermore, losing habitat within Southampton Water may have accumulation effects within the Solent. Shorebirds may be forced to move to other estuaries and mudflat, which may subsequently exceed their carrying capacity resulting in a prompt depletion of the invertebrate food supply. If this was to occur the survival of many shorebirds within the Solent would be at risk.

The survival rate of Curlews, at least, may have been increased if terrestrial fields were included in the model. Curlews are known to supplement their estuarine diets by feeding extensively in nearby fields, water meadows and recreational grassland (Goss-Custard and Durell, 1984; Pickess and Underhill-Day, 2002). Previous models that included terrestrial habitats found that the survival rates of Curlew were influenced by the area of supplementary feeding fields (Stillman et al., 2005a; Durell et al., 2006b).

Further refinement of the model to increase the precision of the prediction could be looked at for the future, such as empirically finding each shorebird specific aggregation factor, con-specific competitor density, nightime feeding efficiencies, and assimilation efficiencies for consuming species specific prey items.

Our model predicted survival rate from food availability, however other factors such as disturbance or raptor predation may also be important. Disturbance from humans is likely to be high along the eastern side of the estuary due to industry and recreation, and relatively low on the western side of Southampton Water due to the large, muddy and mostly inaccessible tidal flats. Human disturbance can be included into the model (e.g. Stillman et al., 2001; West et al., 2003; Durell et al., 2006), and could enhance the precision of the predictions.

Predation by raptors can be a key factor determining the distribution and survival of shorebirds (e.g. Whitfield, 1985, 2003; Quinn and Cresswell, 2004). We cannot rule out the possibility that survival rates for Southampton Water will be lower than predicted due to raptor predation, or that starving birds will be forced to feed in areas with a higher predation risk, further decreasing survival rates (e.g. Whitfield 1985, 2003; Quinn and Cresswell, 2004).

The main limitation, however, in our simulation of habitat loss and mitigation associated with the Dibden Terminal proposal was the lack of accumulated effects. Although our simulations suggest that the mitigation would offset the removal of Dibden Bay, our model did not account for the years during removal and construction of the mitigation proposals. The biomass and densities of invertebrate prey within the estuary would be greatly reduced by the construction process. For this reason, the predictions presented in Chapter 5 for the effect of mitigating the loss of the habitat at Dibden, should not be used to justify the removal of intertidal habitat. New predictions should be sought that incorporate accumulative effects for each consecutive year of predicted change. Model predictions without such accumulative effects, in my opinion, should not be used within any decision making framework concerning development, especially in areas with European designations such as SPA and SAC. However, if accumulative effects are incorporated along with all the parameters described in chapter 5, then individual-based models provide a valuable tool in which governmental authorities can assess the impact of future developments or anthropogenic disturbances.

6.3 Conclusions

Climate change has been recognised to have the potential to accelerate other factors causing biodiversity loss (Galbraith et al., 2002; Thomas et al., 2004). Sea level rise is predicted to exacerbate habitat loss of saltmarshes and tidal flats. This will have implication for the Solent's breeding populations of seabirds and wintering shorebirds.

The harvested sites around the Lymington Estuary have already lost 81% of marshes since 1921 (Colenutt, 2005) and substantial sea-level rise predicted for the end of the 21st century will further diminish this habitat. Thus, measures should be taken to avoid site abandonment through anthropogenic activities, to ensure the survival of ground-nesting seabirds, not just within the Solent but globally. Similarly, if proposed developments within the Solent's intertidal areas are not assessed thoroughly and prediction of impacts to shorebirds sought, then habitat loss could be disastrous, especially with predicted habitat loss from sea level rise (Bray et al., 2000).

Finally, the EC Habitats Directive now puts the burden of proof on applicants to show that their operations within SPAs do not cause significant disturbance (Regulation 48). EU law does not define precisely what constitutes 'significant disturbance', and this is a key question that needs to be resolved. However, I believe that the current commercial egg harvest amounts to significant disturbance within the Solent's SPAs. Furthermore, any habitat loss within the Solent's SPAs which is not fully mitigated for before the construction process would also amount to significant disturbance, thus both of these activities are infringing EU legislation.

APPENDIX A – ABNORMAL EGGS

Figure A1. Examples of white eggs found on a harvested site.

Figure A2. Example of a half-white egg (left) and a 'corroded' egg with a dead chick inside (right), both of which were found on a harvested site.

Figure A3.Examples of abnormally small yolkless eggs; one which was found in a nest on a harvested site alongside a small egg and a normal sized egg (left), and two abnormally shaped small yolkless eggs (right) also found on a harvested site.

APPENDIX B - EXAMINATION OF GULLS' EGGS FOR *SALMONELLA* SPP., *CAMPYLOBACTER* SPP. AND *ESCHERICHIA COLI.*

Introduction

Access to fresh recently laid gulls' eggs destined for the human food chain provided an opportunity to examine these products for pathogens of human significance. Whilst the collection of such eggs is regulated via licensing, the transport and sale into the human food chain is not, and such products are considered likely to be a potential source of microbiological contamination. Anecdotal evidence provided by experienced chefs working in the catering industry suggests that such eggs are usually consumed 'soft' as any additional cooking may render them unpalatable. Thus it seems likely that these eggs are unlikely to receive the sorts of heat treatments which would kill potential pathogens such as *E.coli, Salmonella* spp. and *Campylobacter* spp. should they be present.

Methods

A total of 24 eggs were collected. Each egg was numbered and placed into a small commercial food bag which was tied with a twist tie and kept in a cool bag until examined. After sampling shells were returned to the same bag and returned to Southampton in the same cool bag.

Egg shells and egg contents were examined separately, the methodology being designed to minimise the risk of transfer of pathogens from the exterior of the shell to the contents. The operator wore latex gloves sterilised with alcohol and air dried between each egg to avoid cross contamination.

Sampling from the shells' exterior:

Each egg was removed from its bag and swabbed using 5ml maximal recovery diluent (MRD). The swab was rotated as the shell was swabbed to maximise recovery. Each swab was vortex mixed for 30s to remove organisms from the swab. Swabbing liquid from 8 eggs was pooled for further sampling. This mirrored the procedure for the egg contents.

Sampling from the Egg contents:

After swabbing the shell each egg was placed into 50ml of 70% ethanol for 2mins to sterilise the shell. The egg was then cracked using a sterile knife and the contents emptied into a sterile stomacher bag. The contents of 8 eggs were pooled giving a total of 4 samples. Each sample was homogenised for 2minutes using a Stomacher 400. Samples were then examined for *Campylobacter*, *Salmonella* and *E coli.*

Campylobacter Isolation

Samples for *Campylobacter* isolation were examined using a modified form of the method as described by Sahin *et al.* From each pooled, homogenised sample 10ml was added to 90ml Muller-Hinton broth and a further 10ml to 90ml Muller-Hinton broth containing Preston selective supplement. Samples were incubated for 24h and 48h at

37°C in a gas jar with CAMPY-GEN (Oxoid) to provide a microaerophilic atmosphere. After incubation 0.5ml of the selectively enriched samples was spread over the surface of dried Preston agar plates with and without supplement. These plates were incubated at 37°C and were examined for presumptive *Campylobacter* at 24h and 48h. Colonies with appropriate morphology were Gram stained, checked for motility, catalase and oxidase tests were also performed.

Gram negative slender, spirally curved rods which were motile, catalase and oxidase positive were considered to be *Campylobacter* spp.

Salmonella Isolation:

The remainder of each homogenised sample was weighed and diluted 50:50 with buffered peptone water. Samples were then incubated at 37°C for 24h. After this non-selective enrichment period a 10 ml aliquot was added to 100ml Rappaport- Vassiliadis medium and incubated at 42°C±1°C for 24h and 48h. This procedure was repeated 3 times for each batch of eggs. After incubation loopfuls of the RV medium were spread onto Brilliant Green Agar (BGA) and Xylose, Lactose Deoxycholate (XLD) agars; plates were incubated at 37°C and examined for presumptive *Salmonella* at 24 and 48h. Colonies identified as presumptive *Salmonellae* by colony morphology were Gram stained, checked for motility and inoculated into Triple Sugar Iron (TSI) medium.

Gram negative, motile rods which were produced acid & gas in the butt of a TSI slope, usually with production of H_2S were considered to be *Salmonella* spp.

Escherichia coli isolation:

A portion of each of the samples diluted for *Salmonella* isolation was transferred Chromogenic *E.coli/*coliform agar using a spiral plater. A further 10ml portion was diluted 1in 10 using maximal recovery diluent (MRD) and was plated in the same way. Plates were incubated at 37°C for 24h. After incubation approx. 20 purple colonies (presumptive *E.coli*) from each plate were pooled and sub-cultured onto Nutrient agar. After incubation (37°C for 24h) samples were Gram stained, checked for motility and IMViC tests performed.

Motile Gram negative rod shaped cells which showed the classic ++-- reaction to the IMViC tests were described as *E.coli.*

Results

All of the data collected were qualitative rather than quantitative. The presence of the named pathogens was made entirely on the basis of the tests described in the methodology. Four samples (coded by batch number) were examined and the results are presented in Table 1.

Egg Shells:

All showed very high numbers of *E.coli. Salmonella* was isolated in three of the four batches and *Campylobacter* in two. *Campylobacter* was only isolated from samples which had been isolated using media containing supplements at each stage of the process.

Table B1 Presence of named pathogens from swab samples of gulls' egg shells and egg contents

Sample code		Presence / absence of pathogens		
		Salmonella	***Escherichia coli***	***Campylobacter***
Batch 1	Shell	+ve,+ve,+ve	Present	Absent
	Contents	neg, neg, neg	Absent	Absent
Batch 2	Shell	+ve,+ve,+ve	Present	Present
	Contents	+ve,+ve, neg	Present	Present
Batch 3	Shell	+ve,+ve,+ve	Present	Present
	Contents	neg, neg, neg	Present	Absent
Batch 4	Shell	neg, neg, neg	Present	Absent
	Contents	+ve,+ve,+ve	Present	Absent

Egg Contents:
Numbers recovered from egg contents were very much lower in all cases. *E.coli* was present in all but one batch, *Salmonella* in two batches and *Campylobacter* in one batch.

Observations:
In addition to the data collected the following observations were made which may have affected the data:

1. Eggs were ~24h at ambient temperatures and a further 24h ain a domestic cool bag before microbiological sampling took place. Eggs felt cool rather than cold at sampling. No temperatures were taken.
2. Many eggs had very thin shells and were either damaged during transport or cracked when being handled during sampling.
3. Additionally some of the shells were cracked during the swabbing process
4. Some of the media used (RV/BGA/ Chromogenic agar/CAMPY-GEN) were out of date and this may have affected the data.

References

Sahin, O., P. Kobalka and Q. Zhang 2003 Detection and survival of *Campylobacter* in chicken eggs. *Journal of Applied Microbiology* **95** 1070-1079

APPENDIX C – SPECIES COMPOSITION OF THE MACROBENTHIC INVERTEBRATES IN SOUTHAMPTON WATER

Table C1. Species composition of the macrobenthic invertebrates in Southampton Water in September 2003. Taxa appear in alphabetic and taxonomic order.

	% Occurrence	Mean density (Nos.m^{-2})	SE	Mean biomass density (g.m^{-2})	SE
(a) Polychaetes					
Large *Polychaetes*					
Ampharetidae indet.	15.7	31.8	8.7	3.092	0.866
Aphroditidae indet.	2.8	3.5	2.0	0.609	0.378
Cirratulidae indet.	3.7	8.3	4.5	0.773	0.413
Cirratulus cirratus	1.9	4.7	3.3	0.447	0.333
Cirriformia tentaculata	2.8	4.7	2.9	0.289	0.220
Tharyx sp.	9.3	23.6	10.6	0.065	0.025
Eunicidae					
Marphysa sanguinea	1.9	3.5	2.6	0.585	0.434
Glyceridae					
Goniada maculata	0.9	2.4	2.4	0.065	0.065
Hesionidae indet.	0.9	1.2	1.2	0.043	0.043
Nereididae indet.	5.6	8.3	3.5	1.021	0.552
Hediste diversicolor	45.4	211.1	35.8	35.777	6.299
Neanthes virens	5.6	7.1	2.8	15.382	6.329
Nephtyidae indet.	10.2	17.7	5.7	3.853	1.394
Nephtys cirrosa	1.9	2.4	1.7	0.440	0.309
Nephtys caeca	0.9	1.2	1.2	0.120	0.120
Phyllodocidae indet.	2.8	5.9	3.9	0.107	0.086
Anaitides maculata	1.9	2.4	2.4	0.011	0.011
Eteone sp.	4.6	7.1	3.3	0.176	0.110
Sabellidae indet.	0.9	1.2	1.2	10.043	0.043
Terebellidae					
Lanice conchilega	8.3	30.7	11.7	5.419	2.260
Amphitrite sp.	2.8	3.5	2.0	0.149	0.087
Small *Polychaetes*					
Nemertea indet.	0.9	1.2	1.2	0.004	0.004
Cephalothrix rufifrons	0.9	2.4	2.4	0.008	0.008
Platyhelminthes indet.	0.9	1.2	1.2	0.004	0.004
Serpulidae indet.	0.9	3.5	2.0	0.012	0.007
Pomatoceros lamarcki	1.9	2.4	1.7	0.008	0.006
Pomatoceros triqueter	3.7	7.1	4.4	0.024	0.015
Protula tubularia	0.9	1.2	1.2	0.004	0.004
Spionidae indet.	6.5	8.3	3.5	0.028	0.012
Polydora sp.	0.9	1.2	1.2	0.004	0.004
Tubificidae indet.	18.5	12.5	33.7	0.430	0.116
Tubificoides benedeni	19.4	132.1	43.3	0.479	0.152

Table C1. continued

	% Occurrence	Mean density (Nos.m^{-2})	SE	Mean biomass density (g.m^{-2})	SE
(b) Arthropoda					
Amphipoda indet.	11.1	41.3	17.4	0.519	0.207
Corophium volutator	3.7	34.2	23.9	2.654	1.991
Cirripedia indet.	0.9	1.2	1.2	0.004	0.004
Elminius modestus	0.9	2.4	2.4	0.008	0.008
Semibalanus balanoides	0.9	1.2	1.2	0.004	0.004
Decapoda indet.	0.9	1.2	1.2	0.344	0.344
Carcinus maenas	3.7	4.7	2.3	1.280	0.976
Crangon crangon	0.9	1.2	1.2	0.344	0.344
Dipteran larva	4.6	14.2	7.2	0.045	0.022
Isopoda					
Anthura gracilis	1.9	2.4	1.7	0.129	0.102
Idotea sp.	0.9	1.2	1.2	0.011	0.011
Sphaeroma serratum	1.9	2.4	1.7	0.037	0.028
Pycnogonida indet.	0.9	1.2	1.2	0.005	0.005
(c) Molluscs					
Bivalves					
Cardiidae indet	1.9	2.4	1.7	0.013	0.009
Cerastoderma edule	28.7	108.5	29.4	50.512	14.598
Parvicardium exiguum	0.9	1.2	1.2	0.004	0.004
Corbulidae					
Corbula gibba	3.7	10.6	7.3	0.091	0.053
Lutrariidae indet.	0.9	3.5	3.5	0.050	0.050
Myacidae					
Mya arenaria	0.9	1.2	1.2	0.230	0.230
Mytilidae					
Mytilus edulis	0.9	1.2	1.2	3.160	3.160
Petricolidae					
Petricola pholadiformis	1.9	2.4	1.7	0.062	0.062
Scrobiculariidae					
Abra alba	1.9	3.5	2.0	0.505	0.355
Scrobicularia plana	14.8	30.7	7.8	9.134	2.990
Tellinidae indet.	2.8	5.9	3.5	0.955	0.570
Macoma balthica	14.8	62.5	29.0	0.663	0.233
Veneridae indet	2.8	3.5	2.0	0.705	0.428
Circomphalus casina	0.9	1.2	1.2	0.047	0.047
Ruditapes philippinarum	0.9	1.2	1.2	0.343	0.343
Venerupis senegalensis	0.9	1.2	1.2	0.034	0.034
Gastropods and Chitons					
Hydrobiidae					
Hydrobia ulvae	33.3	997.9	303.6	10.774	3.201
Littorinidae indet.	1.9	2.4	1.7	0.067	0.048
Littorina littorea	6.5	13.0	6.5	2.260	1.146
Littorina saxatilis	2.8	5.9	3.9	0.060	0.036
Nassariidae					
Hinia reticulatus	0.9	1.2	1.2	0.946	0.946
Nudibranchia indet.	0.9	1.2	1.2	0.247	0.247

Table C1. continued

	% Occurrence	Mean density (Nos.m^{-2})	SE	Mean biomass density (g.m^{-2})	SE
Polyplacophora					
Lepidochitona sp.	1.9	2.4	1.7	0.145	0.114
Trichotropidae					
Crepidula fornicate	1.9	14.2	10.1	9.464	6.661
Trochidae					
Gibbula umbilicalis	0.9	1.2	1.2	0.022	0.022
(d) Anthazoa					
Actiniaria indet.	3.7	8.3	4.5	0.495	0.392

APPENDIX D – PARAMETER VALUES USED TO APPLY MORPH TO SOUTHAMPTON WATER

Table D1. Parameter values used to apply MORPH to Southampton water.

a) Global parameters

Parameter	Value
Duration of each time step	1 h
Number of time steps	5112 = 213 days (1 Sep – 31 Mar = duration of peak winter shorebird numbers).
Day length	Varies sinusoidally between 18.11 h on 21 Jun and 9.25 h on 21 Dec. Following Stillman et al. (2000).

b) Patch parameters

	Patch								
Parameter	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Maximum area exposed (m^2)	1177485	1205242	745200	349338	423600	581800	778400	404301	757600
	Calculated using a hydrodynamic model (see text for details).								
Proportion of area exposed	Hourly values read in for each patch, based on a typical spring – neap cycle. Calculated using a hydrodynamic model (see text for details).								

c) Resource parameters

Resource	Size class (mm)	Initial numerical density on each patch (number m^{-2}) [1]									% winter mortality [2]
		1	2	3	4	5	6	7	8	9	
Crab	5 – 10	15.9	0.0	10.6	0.0	0.0	10.6	0.0	0.0	0.0	0
	15 – 20	0.0	10.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
Crustacea	0 – 5	429.7	0.0	0.0	0.0	0.0	74.3	148.5	0.0	0.0	0
	5 – 10	238.7	10.6	0.0	0.0	0.0	63.7	53.1	7.2	21.2	0
	10 – 15	159.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.6	0
	15 – 20	63.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.6	0
	20 – 25	0.0	0.0	0.0	0.0	10.6	0.0	0.0	0.0	0.0	0
	30 – 35	0.0	0.0	10.6	0.0	0.0	0.0	0.0	0.0	0.0	0
Hard bivalve	0 – 5	31.8	21.2	31.8	0.0	0.0	63.7	31.8	7.2	0.0	0
	5 – 10	0.0	0.0	148.5	74.3	10.6	84.9	42.4	10.8	0.0	0
	10 – 15	47.7	42.4	127.3	127.3	0.0	0.0	53.1	0.0	0.0	0
	15 – 20	63.6	31.8	31.8	116.7	10.6	10.6	21.2	0.0	10.6	0
	20 – 25	0.0	10.6	31.8	53.1	0.0	0.0	10.6	21.6	0.0	0
	25 – 30	0.0	0.0	21.2	21.2	0.0	0.0	21.2	3.6	0.0	0
	30 – 35	0.0	0.0	0.0	0.0	0.0	10.6	21.2	3.6	0.0	0
	35 – 40	0.0	0.0	0.0	0.0	0.0	0.0	42.4	3.6	0.0	0
	40 – 45	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.0	0
Soft bivalve	0 – 5	63.7	254.6	0.0	10.6	10.6	0.0	10.6	43.2	0.0	0
	5 – 10	63.7	42.4	0.0	21.2	21.2	0.0	0.0	14.4	0.0	0
	10 – 15	0.0	0.0	0.0	21.2	63.7	0.0	0.0	0.0	0.0	0
	15 – 20	0.0	0.0	0.0	63.7	42.4	0.0	0.0	0.0	0.0	0
	20 – 25	0.0	0.0	0.0	10.6	21.2	0.0	0.0	0.0	0.0	0
	25 – 30	31.8	0.0	0.0	10.6	0.0	0.0	0.0	0.0	0.0	0
	30 – 35	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.0	0
Hydrobia	0 – 5	1384.6	63.7	53.1	1209.6	10.6	0.0	0.0	443.2	0.0	40.1
	5 – 10	1830.3	21.2	360.8	2249.4	551.7	31.8	0.0	345.9	0.0	40.1
Annelids	0 – 5	0.0	0.0	0.0	0.0	0.0	0.0	10.6	0.0	0.0	0
	5 – 10	0.0	0.0	0.0	0.0	21.2	21.2	31.8	7.2	0.0	0
	10 – 15	0.0	31.8	0.0	0.0	53.1	31.8	0.0	28.8	21.2	0
	15 – 20	47.7	10.6	0.0	0.0	31.8	10.6	0.0	14.4	0.0	0
	20 – 25	127.4	0.0	0.0	10.6	31.8	10.6	21.2	14.4	0.0	0
	25 – 30	127.4	0.0	31.8	31.8	63.7	10.6	21.2	0.0	0.0	0
	30 – 35	31.8	21.2	21.2	10.6	31.8	0.0	10.6	3.6	42.4	0
	35 – 40	127.3	222.8	95.5	53.1	233.4	116.7	84.9	43.2	21.2	0
	40 – 45	0.0	31.8	31.8	0.0	53.1	10.6	10.6	7.2	0.0	0
	45 – 50	47.7	31.8	21.2	10.6	10.6	21.2	42.4	3.6	10.6	0
	50 – 55	0.0	10.6	0.0	21.2	53.1	42.4	21.2	0.0	53.1	0
	55 – 60	0.0	0.0	0.0	0.0	21.2	21.2	31.8	3.6	63.7	0
	60 – 65	15.9	31.8	10.6	10.6	42.4	10.6	10.6	0.0	21.2	0
	65 – 70	63.7	0.0	10.6	0.0	0.0	0.0	0.0	0.0	10.6	0
	70 – 75	31.8	31.8	0.0	21.2	10.6	0.0	0.0	0.0	0.0	0
	75 – 80	0.0	0.0	0.0	10.6	0.0	10.6	0.0	0.0	0.0	0
	80 – 85	0.0	10.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
	85 – 90	0.0	0.0	0.0	0.0	0.0	10.6	0.0	0.0	0.0	0
	90 – 95	0.0	10.6	0.0	0.0	10.6	10.6	0.0	7.2	0.0	0
	95 – 100	31.8	0.0	0.0	10.6	0.0	0.0	10.6	0.0	0.0	0
	100 – 105	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.6	0
	105 – 110	0.0	0.0	0.0	10.6	0.0	21.2	0.0	0.0	0.0	0
	130 – 135	0.0	0.0	0.0	10.6	0.0	0.0	0.0	0.0	0.0	0
	140 – 145	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
	145 – 150	15.9	0.0	10.6	0.0	0.0	10.6	0.0	0.0	0.0	0
	155 – 160	0.0	0.0	0.0	10.6	0.0	0.0	0.0	0.0	0.0	0
	180 – 185	15.9	0.0	0.0	0.0	0.0	10.6	0.0	0.0	0.0	0

1 Calculated from autumn invertebrate survey of Southampton Water (see text for details).

2 Calculated from difference between model predictions and spring invertebrate survey of Southampton Water (see text for details).

d) Component parameters

		Initial mean AFDM on each patch (g) (blank if size class not present) [1, 2]									% winter
Resource	**Size class (mm)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**change in AFDM** [3]
Crab	5 – 10	0.0051		0.0101			0.0067				0
	15 – 20		0.0815								0
Crustacea	0 – 5	0.0013					0.0014	0.0008			0
	5 – 10	0.0042	0.0291				0.0012	0.0013	0.0015	0.0014	0
	10 – 15	0.0085								0.0022	0
	15 – 20	0.0165								0.0073	0
	20 – 25					0.0082					0
	30 – 35			0.0291							0
Hard bivalve	0 – 5	0.0001	0.0002	0.0003			0.0002	0.0002	0.0003		-28
	5 – 10			0.0044	0.0067	0.0011	0.0019	0.0021	0.0014		-28
	10 – 15	0.0212	0.0212	0.0140	0.0146			0.0106			-28
	15 – 20	0.0435	0.0605	0.0417	0.0392	0.0291	0.0327	0.0470		0.0348	-28
	20 – 25		0.1158	0.1005	0.1225			0.1362	0.1012		-28
	25 – 30			0.1758	0.1671			0.1257	0.0802		-28
	30 – 35						0.3340	0.0802	0.0802		-28
	35 – 40							0.0401	0.0802		-28
	40 – 45								0.0802		-28
Soft bivalve	0 – 5	0.0003	0.0007		0.0008	0.0008		0.0001	0.0007		-28
	5 – 10	0.0019	0.0015		0.0043	0.0014			0.0028		-28
	10 – 15				0.0138	0.0121					-28
	15 – 20				0.0290	0.0254					-28
	20 – 25				0.0254	0.0445					-28
	25 – 30	0.0549			0.0827						-28
	30 – 35								0.1251		-28
Hydrobia	0 – 5	0.0004	0.0010	0.0005	0.0009	0.0007			0.0008		0
	5 – 10	0.0012	0.0012	0.0011	0.0012	0.0012	0.0012		0.0012		0
Annelids	0 – 5							0.0002			0
	5 – 10					0.0004	0.0003	0.0005	0.0005		0
	10 – 15		0.0010			0.0092	0.0059		0.0013	0.0008	0
	15 – 20	0.0017	0.0017			0.0085	0.0020		0.0016		0
	20 – 25	0.0044			0.0026	0.0028	0.0037	0.0045	0.0046		0
	25 – 30	0.0071		0.0094	0.0079	0.0048	0.0094	0.0094			0
	30 – 35	0.0038	0.0068	0.0036	0.0129	0.0065		0.0060	0.0065	0.0115	0
	35 – 40	0.0094	0.0106	0.0104	0.0119	0.0106	0.0101	0.0094	0.0117	0.0058	0
	40 – 45		0.0124	0.0122		0.0130	0.0071	0.0102	0.0136		0
	45 – 50	0.0083	0.0165	0.0154	0.0142	0.0165	0.0134	0.0165	0.0165	0.0102	0
	50 – 55		0.0213		0.0189	0.0205	0.0199	0.0209		0.0150	0
	55 – 60					0.0240	0.0149	0.0149	0.0257	0.0168	0
	60 – 65	0.0134	0.0268	0.0268	0.0248	0.0277	0.0292	0.0167		0.0207	0
	65 – 70	0.0165		0.0330						0.0206	0
	70 – 75	0.0199	0.0398		0.0398	0.0398					0
	75 – 80				0.0474		0.0474				0
	80 – 85		0.0556								0
	85 – 90						0.0373				0
	90 – 95		0.0646			0.0646	0.0433		0.0712		0
	95 – 100	0.0372			0.0743			0.0471			0
	100 – 105									0.0538	0
	105 – 110				0.0960		0.0960				0
	130 – 135				0.1483						0
	140 – 145										0
	145 – 150	0.0957		0.1915			0.1915				0
	155 – 160				0.2131						0
	180 – 185	0.1453					0.2907				0

1 Calculated from autumn AFDM of species in the Exe estuary (Durell et al. 2005b), as AFDM could not be measured for all species in Southampton Water, and tests showed that values did not differ significantly between the sites.

2 Values for a specific species and size class vary between patches due to the exact size distribution within a size class.

3 Calculated from Zwarts (1991) and Zwarts and Wanink (1993).

e) Forager parameters

Parameter	**Dunlin**	**Ringed Plover**	**Turn-stone**	**Red-shank**	**Grey Plover**	**Black-tailed Godwit**	**Oyster-catcher**	**Curlew**
Maximum number [1]	3800	130	243	415	172	79	1372	460
Day by which all birds have arrived	107	1	1	1	107	1	1	1
Proportion starting in south region [1]	0.40	0.34	0.21	0.47	0.15	0.08	0.35	0.33
Proportion starting in mid region [1]	0.56	0.66	0.79	0.31	0.85	0.08	0.58	0.55
Proportion starting in north region [1]	0.04	0.00	0.00	0.22	0.00	0.85	0.07	0.13
Arrival and target mass (g) [2]	50	64	104	147	231	207	510	797
Starvation mass (g) [3]	39	37	77	88	127	161	350	489
Energy requirements (KJ day^{-1}) [4]	150	179	247	315	428	396	733	994
Energy density of fat reserves (KJ g^{-1}) [5]	33.4	33.4	33.4	33.4	33.4	33.4	33.4	33.4
Maximum energy assimilation rate (KJ h^{-1}) [6]	16	20	28	36	50	46	88	121
Crab sizes eaten (mm) [7]			5 – 10	5 – 10			5 – 20	5 – 20
Crustacea sizes eaten (mm) [7]	0 – 10	0 – 10	0 – 35	0 – 35		0 – 35		
Hard bivalve sizes eaten (mm) [7]							15 – 45	5 – 20
Soft bivalve sizes eaten (mm) [7]	0 – 10		5 – 15	5 – 15	10 – 20	10 – 20	10 – 35	5 – 35
Hydrobia sizes eaten (mm) [7]	0 – 10	0 – 10	0 – 10	0 – 10	0 – 10			
Annelids sizes eaten (mm) [7]	10 – 60	10 – 50	10 – 60	10 – 80	15 – 185	20 – 185	45 – 185	45 – 185
Functional response	Calculated from body and prey mass (see text for details)							
Range of foraging efficiencies [8]	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125
Aggregation factor [9]	10	10	10	10	10	10	10	10
Threshold competitor density (ha^{-1}) ‘	100	100	100	100	100	100	100	100
Mobile prey interference coefficient [9]	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48
Weak kleptoparistism interference coefficient [9]	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
Strong kleptoparistism interference coefficient [9]	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Range of dominance [8]	0 – 1	0 – 1	0 – 1	0 – 1	0 – 1	0 – 1	0 – 1	0 – 1
Crab, Crustacea and Annelid assimilation efficiency [8]	0.85	0.85	0.85	0.85	0.85	0.85	0.85	0.85
Bivalve and Hydrobia assimilation efficiency [8]	0.75	0.75	0.75	0.75	0.75	0.75	0.85	0.75
Crab, Crustacea and Annelid energy density (KJ g^{-1}) [10]	23.5	23.5	23.5	23.5	23.5	23.5	23.5	23.5
Bivalve and Hydrobia energy density (KJ g^{-1}) [10]	22.0	22.0	22.0	22.0	22.0	22.0	22.0	22.0

1 Calculated from monthly populations and autumn distribution recorded in WeBS low tide counts (see text for details).

2 Dunlin, turnstone, grey plover and oystercatcher masses calculated on Southampton Water (P. Potts pers. comm.). Remaining species calculated as 94% of mass on the Wash (Johnson 1985), as dunlin, turnstone, grey plover and oystercatcher masses in Southampton Water were 94% of masses on the Wash.

3 Values used in previous studies (e.g. Stillman et al. 2005a; J. D. Goss-Custard unpubl. data).

4 Calculated from all bird equation of Nagy (1999).

5 Kersten and Piersma (1987).

6 Calculated from maximum daily energy assimilation (derived from initial body mass using Kirkwood (1983)), and assuming that birds feed for 12 hours per day.

7 Calculated from Goss-Custard et al. 2006. Missing values mean that a species is not consumed.

8 Values from previous studies (e.g. Stillman et al. 2005a). Foraging efficiency range from Goss-Custard et al. (1995a).

9 Typical values for shorebirds. Strength and type of interference based on prey characteristics. See text for details.

10 Zwarts and Wanink (1993).

APPENDIX E – BIOMASS-LENGTH RATIOS OF THREE ESTUARIES

A 2-way ANOVA General Linear Model (GLM) was used to predict ln AFDM by size and site. No significant difference between the biomass-length ratios of the three estuaries (Southampton Water, Exe and Poole Harbour) for *N. diversicolor* was found (Site $F_{2,307} = 1.52$, P>0.05, Fig. E1), and no interaction of site with length (Site*length $F_{2,307} = 1.84$, P>0.05). However, *C. edula* differed between sites (Site $F_{2,346} = 34.45$, P<0.001, Fig. E2) and showed an interaction of site with length (Site*length $F_{2,346} = 29.23$, P<0.001). Similarly, comparing just the Exe and Southampton Water the biomass-length ratios differ by site (Site $F_{1,299} = 27.36$, P<0.001 & Site*length $F_{1,299} = 24.31$, P<0.001, Fig. E3). The difference between sites in biomass-length ratio for *C. edula* may be highly significant but the magnitude of the difference is small, as seen in Figure E2 and E3. There are structural differences in the relation between the Exe Estuary data and Southampton Water (Fig. E3). The smaller body lengths from the Exe data have relatively large weights which is causing the regression to be weighted by the small values. This has also meant that logging the data has not caused full linearization. Thus the data from the Exe is supra-geometric i.e. accelerating on a log log scale, which suggests that a possible methological error has occurred with the processing of the AFDM of *C. edula* from the Exe. For example, such an error could arise if small specimens were not dried and/or burnt to a constant weight. Our experience showed that oven drying and burning in the muffle furnace often took three times as long as recommended by the Centre for Ecology and Hydrology.

By ignoring these site differences in biomass-length ratios, and using the biomass-length ratios from the Exe, in order to keep the species specific biomass-length ratios site constant, we are accepting a slow biomass-length growth of *C. edula* from the Exe with small individuals having a relatively large biomass compared to the faster growth from Southampton with small individuals having a smaller biomass.

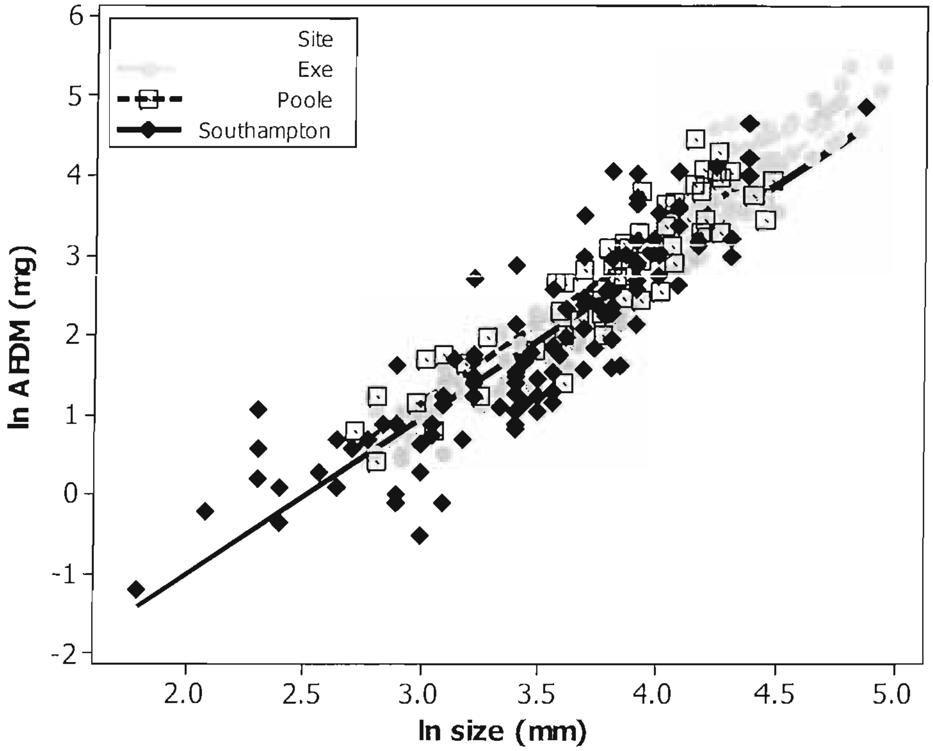


Figure E1. Scatterplot of ln (AFDM) vs. ln (size) for ***Nereis diversicolor*** taken from Southampton Water, Exe Estuary and Poole Harbour.

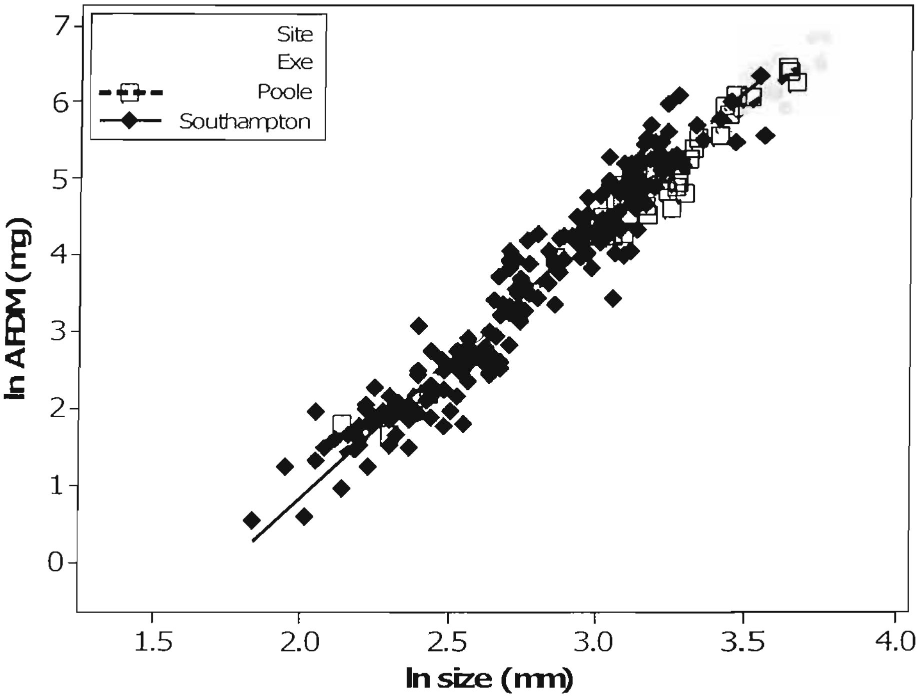


Figure E2. Scatterplot of ln (AFDM) vs. ln (size) for ***Cerastoderma edula*** taken from Southampton Water, Exe Estuary and Poole Harbour.

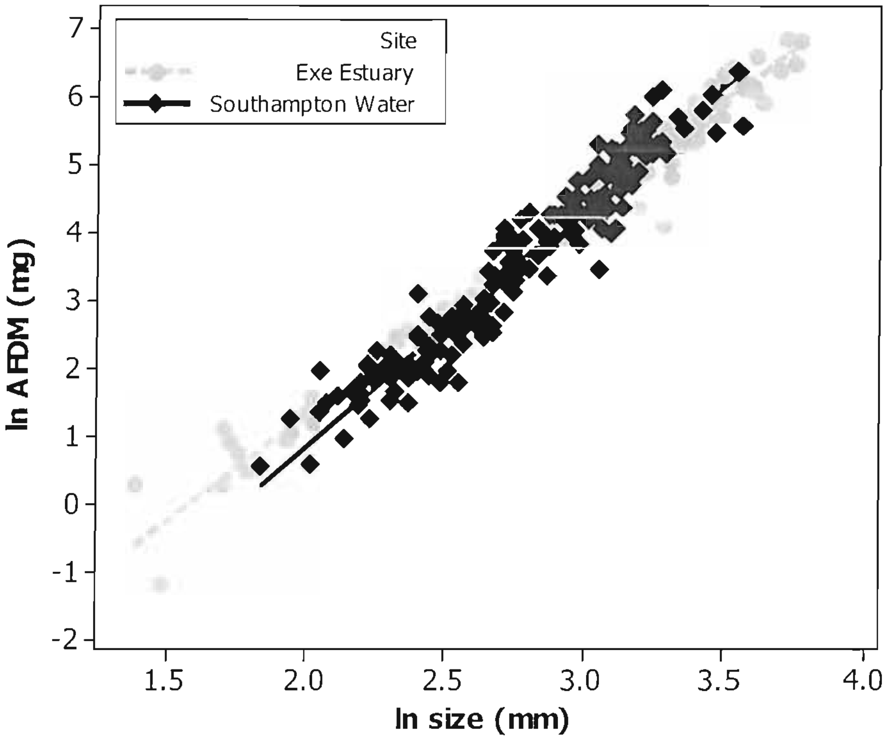


Figure E3. Scatterplot of ln (AFDM) vs. ln (size) for ***Cerastoderma edula*** taken from Southampton Water and Exe Estuary.

APPENDIX F - BENEFITS TO SHOREBIRDS FROM INVASION OF A NON-NATIVE SHELLFISH

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Benefits to shorebirds from invasion of a non-native shellfish

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SUMMARY

Introductions of non-native species are seen as major threats to ecosystem function and biodiversity. However, invasions of aquatic habitats by non-native species are known to benefit generalist consumers that exhibit dietary switches and prey upon the exotic species in addition to or in preference to native ones. There is, however, little knowledge concerning the population-level implications of such dietary changes. Here we show that the introduction of the Manila clam *Tapes philippinarum* into European coastal waters has presented the Eurasian oystercatcher *Haematopus ostralegus ostralegus* with a new food resource and resulted in a previously unknown predator-prey interaction between these species. We demonstrate, with an individuals-based simulation model (IBM), that the presence of this non-native shellfish, even at the current low density, has reduced the predicted over-winter mortality of oystercatchers at one recently invaded site. Further increases in clam population density are predicted to have even more pronounced effects on the density-dependence of oystercatcher over-winter mortality. These results suggest that if the Manila clam were to spread around European coastal waters, a process which is likely to be facilitated by global warming, this could have considerable benefits for many shellfish-eating shorebird populations.

Key words: Biological invasions, Manila clam, *Tapes philippinarum*, climate change

1. INTRODUCTION

The five most important determinants of changes in biodiversity at the global scale have been identified as changes in land use, atmospheric CO_2 concentration, nitrogen deposition and acid rain, climate change and biotic exchanges (deliberate or accidental introduction of plants and animals to an ecosystem) (Sala *et al.* 2000). Biological invasions are already a major component in global environmental change, leading to changes in economic value, biological diversity, ecosystem function and evolutionary pathways (Mooney & Cleland 2001; Leppäkoski *et al.* 2002). Most studies dealing with invasions by non-native species focus on the potential or observed detrimental effects (Mooney & Cleland 2001; Leppäkoski *et al.* 2002; Occhipinti-Ambrogi & Savini 2003). However, invasions have the potential to be beneficial in some respects. Invasions of both marine and freshwater habitats by non-native shellfish have presented diving ducks in North America and Europe with additional food resources which have been exploited due to the greater availability and energetic profitability of the non-native species (Hamilton *et al.* 1994; Richman & Lovvorn 2004; Werner *et al.* 2005; Leopold *et al.* in press). The invasion of freshwater lakes in both Europe and North America by the Zebra mussel *Dreissena polymorpha* has caused changes to the migration patterns and dramatic increases in the local abundance of diving ducks (Suter 1982a,b; Wormington & Leach 1992; Stark *et al.* 1999). Here we investigate whether the invasion of European coastal waters by the Manila clam could have beneficial population-level consequences for shellfish eating shorebirds.

Manila clams are native to the western Pacific Ocean and first spread from this area between the 1920s and 1940s when introduced to the Hawaiian Islands and the Pacific coasts of Canada and the USA (Goulletquer 1997). Manila clams have since been introduced to several European countries and have naturalised in Italy, France and Britain (Goulletquer & Heral 1997). The most spectacular invasion by Manila clams occurred in the Adriatic Sea following their introduction to Venice Lagoon in 1983 (Breber 2002). Naturally formed beds in the most favoured areas of Venice Lagoon now hold densities of > 1000 clams m^{-2} and the species has spread along the Adriatic coast at 30 km $year^{-1}$ (Breber 2002). Manila clams were deliberately introduced to Britain in the late 1980s for the purpose of aquaculture. This release was conducted in the light of studies which suggested that water temperatures would be too low to support successful larval production or recruitment (Laing & Utting 1994). However, at one site, Poole Harbour in Dorset, Manila clams have naturalised (Jensen *et al.* 2004, 2005).

The coasts of many western European countries serve as stop-over sites and wintering grounds for migratory shorebirds (Smit & Piersma 1989). Here, they rely upon adequate food resources in order to survive the winter and early spring in good enough condition to migrate in time to breed successfully (Goss-Custard 1985). The cold winter of 1962-1963 led to a prolific recruitment of cockles *Cerastoderma edule* in The Wash in England (Dare *et al.* 2004). In contrast, a series of mild winters in the late-1980s led to repeated recruitment failure of several shellfish species in the Wadden Sea and resulted in low standing stocks of prey for shorebirds (Beukema 1992). Climate change is predicted to affect the reproduction and lead to a contraction of the range of many 'northern' species of macro-invertebrates upon which shorebirds currently feed (Lawrence & Soame 2004; Kendall *et al.* 2004; Mieszkowska *et al.* 2006). Thus, any spread of 'southern' or non-native shellfish species may be of considerable benefit to shellfish eating shorebirds. Here we demonstrate that the naturalised population of Manila clams in Poole Harbour is exploited by the Eurasian oystercatcher and describe the details of this novel predator-prey interaction. We use a behaviour-based IBM of shorebird foraging (Goss-Custard & Stillman in press) to predict the way in which the density-dependence of over-winter mortality of oystercatchers may be altered by Manila clams' presence.

2. MATERIAL AND METHODS:

Field observations of oystercatchers.

Oystercatchers foraging on the intertidal mudflats of Poole Harbour (Lat 50^{0} 42' 44'' Lon 2^{0} 03' 30'' W) were observed on two consecutive days per month between August 2004 and March 2005. Observations over distances of up to 250m were made from a shore-based observation point using a telescope. Focal individuals were selected at random and observed for two consecutive 5 minute periods. Each prey item consumed was identified to species whenever possible and its size assessed on the basis of the length of the shell and/or the volume of flesh ingested.

Dietary and size-selection assessments.

Due to the distance over which observations were made it was not always possible to positively identify prey items to species level. Birds for which the majority of prey items could be clearly identified as being of one species were classified as specialising on that species of prey. Some of these birds were Manila clam specialists. Amongst the birds that could not be classified in this way, there were some individuals that consumed Manila clams occasionally as part of a mixed diet. These birds were categorised separately from those specialising on Manila clams. This allowed the number of "specialist" birds to be analysed separately from the total number of birds that included Manila clams in their diet (i.e. the sum of the two groups). The total number of birds including Manila clams in their diet and the number specialising on Manila clams in each month were converted to proportions by dividing by the total number of birds observed in each month.

The size-range of Manila clams taken by oystercatchers was assessed on the basis of only those prey items that were lifted clear of the sediment and identified as being Manila clams (i.e. ignoring the lengths of any shellfish of uncertain identity that were consumed by birds known to consume Manila clams). The size-range of Manila clams present in the mud was derived by combining monthly samples of clams taken between August 2003 and March 2004 (Humphreys *et al.* in press).

Estimating intake rates of the three principal diets.

Estimates of prey size based purely on the volume of flesh were converted to estimated shell length on the basis of prey-species specific regression equations derived from occasions on which both measures were recorded. Estimates of shell length were corrected for observer bias by a standard procedure (Goss-Custard *et al.* 1987). Using standard procedures (West *et al.* 2003) ash-free dry mass (AFDM) – length relationships were derived from samples of circa 50 individuals of each of the three principal prey species (Manila clams, cockles and sand-gapers (*Mya arenaria*)) collected in September 2002 and March 2003. These relationships were used to generate the estimated AFDM (mg) of flesh of each prey consumed, allowing for the rate of seasonal change in flesh content and the date of observation. These values were summed for each 5 minute period of observation and used to derive the mean instantaneous intake rate achieved by each focal bird (mg AFDM s^{-1}).

The intake rates achieved by birds specialising in the three principal diets were compared to establish the homogeneity of variances (Levene's test for non-homogeneity of variances – $F_{2,65} = 0.23$ $P = 0.798$). The data conform to the assumption of equal variances.

Modelling.

Individual-based models predict how animal populations will be affected by changes in their environment by modelling the responses of fitness-maximising individuals to environmental change and by calculating how their aggregate responses change the average fitness of individuals and thus demographic rates of the population (Goss-Custard & Stillman in press). Goss-Custard & Stillman (in press) provide a detailed description of the generic model. The particular model of Poole Harbour used here is described by Durell *et al.* (2006). The methods used to survey the numerical and biomass density of the intertidal macrozoobenthos throughout Poole Harbour in order to parameterise the model are described by Caldow *et al.* (2005). The stable over-winter population of oystercatchers in Poole Harbour is circa 1200 (Durell *et al.* 2006). In exploring the density dependent mortality function we used populations of between 500 and 6000 birds i.e. allowing for a 5-6 fold increase in population size. Populations of oystercatchers were varied while holding the populations of the other principal wader species in the harbour *i.e.* dunlin *Calidris alpina*, redshank *Tringa totanus*, black-tailed godwit *Limosa limosa* and curlew *Numenius arquata* at present day values. As our field observations to date have focussed on oystercatchers alone, only they were allowed to consume Manila clams in the model.

Simulations were run in which the prey resources available in the model: i) did not include Manila clams, ii) included the current population of Manila clams in each of the intertidal patches within the harbour, and iii) simulated proportionate increases to the clam density in each patch so as to achieve harbour-wide average densities of 10, 20 and 40 clams m^{-2}. In all simulations in which Manila clams were included, the clam population structure was assumed to be the same as that already present in the harbour (Humphreys *et al.* in press).

The principal output under each scenario is the percentage of the initial autumn population of oystercatchers that is predicted to die due to starvation between September and March.

3. RESULTS

Observations of oystercatcher foraging behaviour

A total of 158 oystercatchers were observed. Of these, it was possible to positively identify the majority of prey items eaten by 86 birds (manila clams (n=27), cockles (n=17), sand-gapers (n=24), mussels *Mytilus edulis* (n=3), *Macoma balthica* (n=5), worms (n=10)). Of the remaining birds (n= 72), 3 were feeding on prey so small as to be virtually invisible to the observer, 29 were feeding on larger but unidentifiable prey which were probably not bivalves, and 40 were feeding on bivalves that, due to factors including the distance of the bird, its particular method of dealing with prey, and poor visibility, could not be clearly identified. The proportion of oystercatchers that specialised on feeding on Manila clams increased significantly between late summer and the following spring (figure 1). In addition to the 27 birds that specialised on Manila clams, a further 17 birds were seen to include an occasional Manila clam in their diet. The proportion of all birds that was seen to consume Manila clams (n=44 out of 158), also increased significantly between late summer and the following spring (figure 1).

Oystercatchers consumed Manila clams within the length range 16 – 50mm. The cumulative frequency distributions of the sizes of clams consumed by oystercatchers and those available in the mud differed significantly (Kolmogorov-Smirnov test D = 0.241, n=859,77 P < 0.001) primarily because the birds ignored clams smaller than 15mm (figure 2). The average intake rate achieved by oystercatchers that specialised in the three principal diets did not differ significantly (ANOVA $F_{2,65}$ = 2.18 P = 0.1218. Manila clams: mean 2.02 mg AFDM s^{-1}, st. dev. = 0.90, n = 27, cockles: mean 1.81 mg AFDM s^{-1}, st. dev. = 0.99, n =17 and sand-gapers: mean 1.49 mg AFDM s^{-1}, st. dev. = 0.83, n = 24). The intake rate of Manila clam "specialists" in Poole Harbour compares favourably with that achieved by oystercatchers feeding on native bivalve species not only within Poole Harbour, but also at many other sites around Europe (figure 3).

Simulation modelling

The model predicts that the presence of Manila clams in Poole Harbour, even at the current mean density of *circa* 5 clams m^{-2} (Jensen *et al.* 2004), has reduced the over-winter mortality of the existing wintering population of oystercatchers (4.56% to 1.11%) and altered the shape of the density-dependent mortality function (figure 4). The model predicts that if the average clam abundance across Poole Harbour was to increase, the density-dependence of the over-winter mortality of oystercatchers would gradually diminish in strength. The density-dependence of over-winter mortality would be completely suppressed if an average density of 40 clams m^{-2} were reached, even were the local wintering population of oystercatchers to increase 5 fold (figure 4).

4. DISCUSSION

Manila clams are eaten by a variety of birds e.g. gulls (Family Laridae), crows (Family Corvidae), and scoters (Family Anatidae) (Toba *et al.* 1992). However, no instance of oystercatchers eating Manila clams has ever been recorded in the scientific literature. World-wide enquiries confirm that there is no knowledge of this predator-prey interaction. Thus, our field observations provide the first recorded instance of oystercatchers exploiting a wild population of Manila clams anywhere in the world.

Most mortality in wintering wader populations is caused by competition for limited resources leading to starvation or to risk-prone behaviour motivated by hunger (Goss-Custard 1985; Whitfield 2003) and occurs during the coldest period of the winter, usually after mid-January (Zwarts *et al.* 1996b). The proportion of oystercatchers consuming Manila clams reached 40-50% during this key stage of the winter. As only birds that were clearly seen to consume a Manila clam during a 10 minute period were included in deriving this figure, it is a very conservative estimate. Thus, this apparently anecdotal observation of a novel predator-prey interaction could have considerable biological significance. Our behaviour-based IBM of shorebird foraging supports this assertion.

Our model indicates that the invasion of Poole Harbour by Manila clams has potentially already altered the over-winter mortality of oystercatchers there. Manila clams, however, were only introduced to the site less than 20 years ago and the current average density is comparatively low (Humphreys *et al.* in press). However, the clams grow comparatively well and regularly exhibit two recruitment events per year (Humphreys *et al.* in press). Densities of 60 clams m^{-2} already occur in some locations within the harbour (Jensen *et al.* 2004). Given that a density of 1000 m^{-2} is considered moderate in the clams' native range (Ohba 1959) and that the annual variation in water temperature within Poole Harbour (3°C - 27°C) is similar to that in Southern Brittany (Golfe du Morbihan), the lagoons of the Adriatic Sea and in the Inland Sea of Japan where the Manila clam thrives at such high densities, it would be surprising if this local population does not continue to grow to attain average densities similar to those that we have modelled.

The magnitude of the effect of an alteration to the density dependence of over-winter mortality on the size of the overall population depends upon the ratio of the strengths of density dependence of mortality in winter and of reproductive output in the summer (Goss-Custard & Sutherland 1997). However, even quite small changes to over-winter mortality rates, whether density dependent or not, can lead to pronounced changes in population size, especially when the density-dependence of reproductive success is weak (Goss-Custard 1993). Given that the population of oystercatchers in Poole Harbour comprises circa 0.5% of the UK wintering population it is, however, not surprising that the invasion of Poole Harbour by Manila clams has had no discernible effect on the size of the UK wintering population of oystercatchers, which has declined since the early 1990s (Collier *et al.* 2005). In fact, numbers of many species of shorebirds have been stable or have declined on the south west coasts of Britain while increasing on the east coast (Austin & Rehfisch 2005).This pattern has been explained as a large-scale population response to warming winter climate (Austin & Rehfisch 2005). This has clearly over-ridden any local effects of clams' presence in Poole

Harbour where the size of the local wintering oystercatcher population has, in spite of the new food resources available, also not increased (Pickess & Underhill-Day 2002). Stark et al. (1999) recorded a four fold increase in the waterbird population of Lake Constance in response to the invasion of the Zebra mussel, making the site one of the most important wintering sites for waterbirds in Central Europe. It may be that the intensive winter fishery for the Manila clam in Poole Harbour which reduces the abundance, maximum age and size of Manila clams there (Humphreys *et al.* in press) has suppressed the potential benefits to oystercatchers which would otherwise have already taken place.

One of the most common reasons for the reproduction and successful invasion of non-native species in marine environments is elevated sea water temperatures in relation to regional or local conditions (Eno *et al.* 1997). Food availability and water temperature are the principal environmental variables that control the growth, reproduction and survival of Manila clams (Bodoy *et al.* 1980; Maître-Allain 1982; Melia *et al.* 2004). The optimum water temperature for growth is between 20°C and 25°C and spawning occurs when water temperatures are between 18°C and 26°C (Solidoro *et al.* 2003). The naturalisation of Manila clams in Poole Harbour, as in the lagoons of the Adriatic Sea reflects the presence of relatively warm, eutrophic waters (Jensen *et al.* 2004). Manila clams spawn more frequently and over longer periods in the southern part of their native range and within Europe (Laruelle *et al.* 1994). At present, the population of Manila clams in Poole Harbour, like those in Brittany, is subject to occasional mortality events in late winter, often associated with cold weather and negative energy budgets (Goulletquer *et al.* 1989; Humphreys *et al.* in press). Thus, in northern European waters the reproduction and survival of Manila clams are vulnerable in many locations under existing environmental conditions. However, increases in sea water temperature that have already occurred in European coastal waters and which are predicted to continue (Hulme *et al.* 2002), will favour both the reproduction and survival of Manila clams at many more sites than they currently occupy. Biological responses in the ocean to climate change will be substantially more complex than a simple, response to temperature alone (Harley *et al.* 2006) and predicting species' distributions will therefore be equally complex (Guisan & Thuiller 2005). Nonetheless, the rate at which the biogeographic limits of southern intertidal species are extending northwards and eastwards towards the colder North Sea is up to 50km per decade (Mieszkowska *et al.* 2006). Indeed, a recent survey has shown that Manila clams are now abundant on the intertidal mudflats of Southampton Water which is 50km east of Poole Harbour. This spread may not have been natural, but mediated by man. Nonetheless, given the precedents set by several southern, warm-water species, it would not be surprising if, under future climate change scenarios, the Manila clams were to (be) spread and establish populations around the increasingly warm coastal waters of north-west Europe.

The Manila clam has only recently naturalised in European waters (Goulletquer 1997; Goulletquer *et al.* 1997). Thus, it is not yet possible to be sure of the long-term consequences that its invasion may have on invaded ecosystems. When cultivated at very high densities, Manila clams are known to alter: biogeochemical cycles, the abundance of micro-plankton, zooplankton and macro-algal growth (Sorokin *et al.* 1999; Bartoli *et al.* 2001). Manila clams may also carry diseases that are transmissible to other species (Figueras *et al.* 1996), compete for resources with other species, and may provide a new food resource for generalist predators (Toba *et al.* 1992). In Venice lagoon, the Manila clam has apparently replaced *Cerastoderma glaucum* and *Tapes decussatus* (Occhipinti-Ambrogi 2000 although see Breber 2002). Surveys of the macro-invertebrate fauna on the intertidal flats of Poole harbour in the late 1980s and in 2002 reveal that the appearance of the Manila clam in Poole harbour coincided with a decline in the abundance of *Scrobicularia plana* and *Macoma balthica* (Caldow *et al.* 2005). However, the decline of these species may have been caused by tri-butyl tin pollution (Langston *et al.* 2003) and may have facilitated the naturalisation of the Manila clam. The average numerical density of bivalves as a group is more or less the same now as in the 1980s but it is *Cerastoderma edule* and *Abra tenuis* that have increased most in the intervening years rather than the Manila clam (Caldow *et al.* 2005). Thus, within Poole harbour there is no evidence yet of species replacement by the Manila clam. Within the scientific literature there is also no evidence that at the densities typical of wild populations of Manila clams, they have any negative effects on native shellfish fauna (Breber 2002; Byers 2005). However, Mieszkowska *et al.* (2006) suggested that the spread of southern warm water species may compound the retreat of northern cold water species on which shorebirds may currently depend.

The ability of birds to winter further north than they currently do under future climate change scenarios is likely to be constrained by a lack of daylight and by the lack of extensive intertidal mudflats. Thus if, in response to the warming of European coastal waters, the Manila clam spreads from its current loci, this is likely to be into locations that will hold substantial populations of over-wintering shorebirds in the future. There are several species of shorebird that winter on western European coasts and regularly prey upon bivalves *i.e.* oystercatcher, curlew *Numenius arquata*, black-tailed godwit *Limosa limosa*, bar-tailed godwit *Limosa lapponica*, knot *Calidris canutus* and grey plover *Pluvialis squatarola*. Thus, given the likely contraction of the southern range edges of many northern species of shellfish in response to climate warming (Mieszkowska *et al.* 2006), we suggest that if this non-native species were to spread, this would have the potential to be of considerable benefit to several European shorebird populations. The potential implications of our findings highlight the need for further studies to improve our understanding of the interactions between native and non-native marine species. Furthermore, given the rate of climate change and of species responses to it, there is a pressing need for studies that improve our understanding of the interactions between the drivers of biodiversity change (Sala *et al.* 2000) such as biotic exchange and climate change.

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REFERENCES

Austin, G. E. & Rehfisch, M. M. 2005 Shifting nonbreeding distributions of migratory fauna in relation to climate change. *Global Change Biology* **11**, 31-38.

Bartoli, M., Nizzoli, D., Viaroli, P., Turolla, E., Castaldelli, G., Fano, E. A. & Rossi, R. 2001 Impact of *Tapes philippinarum* farming on nutrient dynamics and benthic respiration in the Sacca di Goro. *Hydrobiologia* **455**, 203-212.

Beukema, J. J. 1992 Expected changes in the Wadden Sea benthos in a warmer world – lessons from periods with mild winters. *Neth. J. Sea Res.* **30**, 73-79.

Bodoy A., Maitre-Allain T., & Riva A.1980 Croissance comparée de la palourde européenne (*Rudiatapes decussatus*) et de la palourde japonaise (*Ruditapes philippinarum*) dans un écosystème artificial méditerranéen. *Vie Marine* **2**, 39-51.

Breber, P. 2002 Introduction and acclimatisation of the Pacific carpet clam, *Tapes philippinarum*, to Italian waters. In *Invasive Aquatic Species of Europe. Distribution, Impacts and Management.* (ed. E. Leppäkoski, S. Gollasch, & S. Olenin) pp. 120-126. Dordrecht, Netherlands: Kluwer Academic Publishers.

Byers, J. E. 2005 Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. *Ecology* **86**, 487-500.

Caldow, R. McGrorty, S., West, A., Durell, S. E. A. le V. dit., Stillman, R. & Anderson, S. 2005 Macro-invertebrate fauna in the intertidal mudflats. In *The Ecology of Poole Harbour.* (ed. J. Humphreys, & V. May) pp. 91-108. Amsterdam, Netherlands: Elsevier B.V..

Collier, M.P., Banks, A. N., Austin, G. E., Girling, T., Hearn, R. D. & Musgrove, A. J. 2005 *The Wetland Bird Survey 2003/2004: Wildfowl and Wader Counts.* Thetford, UK: BTO/WWT/RSPB/JNCC.

Dare, P. J., Bell, M. C., Walker, P. & Bannister, R. C. A. 1994 *Historical status of cockle and mussel stocks in The Wash.* Lowestoft, UK: Centre for Environment, Fisheries and Aquaculture Science.

Durell, S. E. A. le V. dit., Stillman, R. A., Caldow, R. W. G., McGrorty, S., West, A. D. & Humphreys, J. 2006 Modelling the effect of environmental change on shorebirds: a case study on Poole Harbour, U.K. *Biol. Cons.* **131**, 459-473.

Eno, N. C., Clark, R. A. & Sanderson, W. G. 1997 *Non-native Marine Species in British Waters: a Review and Directory.* Peterborough, UK: Joint Nature Conservation Committee.

Goss-Custard, J. D. 1985 Foraging behaviour of wading birds and the carrying capacity of estuaries. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (ed. R. M. Sibly & R. H. Smith) pp. 169-188. Oxford, UK: Blackwell Scientific Publications.

Goss-Custard, J. D., Cayford, J. T., Boates, J. S. & Durell, S. E. A. le V. dit 1987 Field tests of the accuracy of estimating prey size from bill length in oystercatchers *Haematopus ostralegus* eating mussels, *Mytilus edulis. Anim. Behav.* **35**, 1078-1083.

Goss-Custard, J. D. & Stillman, R. A. In press. Individual-based models and the management of shorebird populations. *Nat. Res. Model.*

Goss-Custard, J. D. & Sutherland, W. J. 1997 Individual Behaviour, Populations and Conservation. In *Behavioural Ecology. An Evolutionary Approach.* (ed. J. R. Krebs & N. B. Davies) pp. 373-395. Oxford, UK: Blackwell Science Ltd.

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

Goulletquer, P., Héral, M. Deslous-Paoli, J. M., Prou, J., Garnier, D. R. & Boromthanarat, W. 1989 Ecophysiologie et bilan énergétique de la palourde japonaise d'élevage *Ruditapes philippinarum J. Exp. Mar. Biol.* **132**, 85-108.

Goulletquer, P. 1997 *A bibliography of the Manila clam Tapes philippinarum* RIDRV-97.02/RA. La Tremblade, France: Institute française pour recherche de l'exlpoitation de la mer.

Goulletquer, P. & Héral, M. 1997 History, present conditions and future of the molluscan fisheries of North America and Europe. Marine molluscan production trends in France: from fisheries to aquaculture. *Marine Fisheries Review*, NOAA Technical Report NMFS, **129**, 137-164.

Guisan, A. & Thuiller, W. 2005 Predicting species distribution: offerinmg more than simple habitat models. *Ecol. Lett.* **8**, 993-1009.

Hamilton, D. J., Ankney, C. D. & Bailey, R. C. 1994 Predation of zebra mussels by diving ducks: an exclosure study. *Ecology*, **75(2)**, 521-531.

Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., Rodriguez, L. F., Tomanek, L. & Williams, S. L. 2006 The impacts of climate change in coastal marine systems. *Ecol. Lett.* **9**, 228-241.

Hulme, M., Turnpenny, J. & Jenkins, G. 2002 *Climate Change Scenarios for the United Kingdom: The UKCIP02 Scientific Report.* Norwich, UK: Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia.

Humphreys, J., Caldow, R. W. G., McGrorty, S., West, A. D. & Jensen, A. C. in press. Population dynamics of naturalised Manila clams *Ruditapes philippinarum* in British coastal waters. *Mar. Biol.*

Jensen, A., Humphreys, J., Caldow, R. & Cesar, C. The Manila Clam in Poole Harbour. In *The Ecology of Poole Harbour* (ed. J. Humphreys & V. May) pp. 163-173. Amsterdam, Netherlands: Elsevier B.V.

Jensen, A. C., Humphreys, J., Caldow, R. W. G., Grisley, C. & Dyrynda, P. E. J. 2004 Naturalization of the Manila clam (*Tapes philippinarum*), an alien species, and establishment of a clam fishery within Poole Harbour, Dorset. *J. Mar. Biol. Ass. U.K.* **84**, 1069-1073.

Kendall, M. A., Burrows, M. T., Southward, A. J. & Hawkins, S. J. 2004 Predicting the effects of marine climate change on the invertebrate prey of the birds of rocky shores. *Ibis* **146(Suppl. 1)**, 40-47.

Laing, I. S. D. & Utting. S. D. 1994 The physiology and biochemistry of diploid and triploid clams (*Tapes philippinarum*) larvae and juveniles. *J. Exp. Mar. Biol. Ecol.* **184**, 159-169.

Langston, W.J., Chesman, B.S., Burt, G.R., Hawkins, S.J., Readman, J. & Worsfold, P. 2003 *Site Characterisation of the South West European Marine Sites. Poole Harbour SPA. Marine Biological Association Occasional Publication No 12.* Plymouth, UK: Marine Biological Association.

Laruelle, F., Guillou, J. & Paulet, Y. M. 1994 Reproductive pattern of the clams, *Ruditapes decussatus* and *R. philippinarum* on intertidal flats in Brittany. *J. Mar. Biol. Assoc. UK* **74**, 351-366.

Lawrence, A. J. & Soame, J. M. 2004 The effects of climate change on the reproduction of coastal invertebrates. *Ibis* **146(Suppl. 1)**, 29-39.

Leopold, M. F., Spannenburg, P. C., Verdaat, H. J. P. & Kats, R. K. H. In press. Identification and size estimation of *Spisula subtruncata* and *Ensis americanus* from shell fragments in stomachs and faeces of common eiders *Somateria mollissima* and common scoters *Melanitta nigra*. *Atlantic Seabirds.*

Leppäkoski, E. Gollasch. S. & Olenin. S. *Invasive Aquatic Species of Europe. Distribution, Impacts and Management.* Dordrecht. Netherlands: Kluwer Academic Publishers.

Maître-Allain T. 1982 Influence du milieu sur la croissance de deux palourdes. *Ruditapes decussatus* et *Ruditapes philippinarum*. dans l'étang de Thau (Hérault). *Vie Marine* **4**. 37-50.

Melià P.. De Leo G. A. & Gatto M. 2004 Density and temperature-dependence of vital rates in the Manila clam *Tapes philippinarum*: a stochastic demographic model. *Mar Ecol Prog Ser* **272**. 153-164.

Mieszkowska, N.. Kendall. M. A.. Hawkins. S. J., Leaper, R., Williamson, P.. Hardman-Mountford. N. J. & Southward. A. J. 2006 Changes in the range of some common rocky shore species in Britain – a response to climate change? *Hydrobiologia*, **555**, 241-251.

Mooney, H. A. & Cleland, E. E. 2001 The evolutionary impact of invasive species. *Proc. Natl. Acad. Sci.* **98**, 5446-5451.

Occhipinti-Ambrogi, A. 2000 Biotic invasions in a Mediterranean Lagoon. *Biol. Invas.* **2**, 165-176.

Occipinti-Ambrogi, A. & Savini, D. 2003 Biological invasions as a component of global change in stressed marine environments. *Mar. Poll. Bull.* **46**, 542-551.

Ohba, S. 1959 Ecological Studies in the Natural Population of a Clam, *Tapes japonica*, with Special Reference to Seasonal Variations in the Size and Structure of the Population and to Individual Growth. *Biol. J. Okayama Univ.* **5,** 13-43.

Pickess, B. P. & Underhill-Day, J. C. 2002 *Important Birds of Poole Harbour*. Wareham, UK: Poole Harbour Study Group.

Richman, S. E. & Lovvorn, J. R. 2004 Relative foraging value to lesser scaup ducks of native and exotic clams from San Francisco Bay. *Ecol. Appl.* **14**, 1217-1231.

Sala, O. E., and 18 others 2000 Global Biodiversity Scenarios for the Year 2100. *Science* **287**, 1770-1774.

Smit, C. & Piersma, T. 1989 Numbers, mid-winter distribution and migration of wader populations using the East Atlantic flyway. In *Flyways and Reserve Networks for Waterbirds. IWRB Special Publication No 9* (ed. H. Boyd & J.-Y. Pirot) pp. 24-63. Slimbridge UK: International Wildfowl and Wetlands Research Bureau.

Solidoro, C., Melaku Canu, D. & Rossi, R. 2003 Ecological and economic considerations on fishing and rearing of *Tapes philippinarum* in the lagoon of Venice. *Ecol Model* **170**, 303-318.

Sorokin, I.I., Giovanardi, O., Pranovi, F. & Sorokin, P.I. 1999 Need for restricting bivalve culture in the southern basin of the Lagoon of Venice. *Hydrobiologia* **400**, 141-148.

Stark, H., Bauer, H.-G., Suter, W. & Jacoby, H. 1999 Internationale Wasservogelzählung am Bodensee. Ergebnisse aus den Zählperioden 1961/62 bis 1996/97. Dynamik der

Zugrast- und Überwinterungbestände und der Einfluß von Umweltbedingungen. In *Die Vögel des Bodenseegebietes.* (eds. G. Heine, H. Jacoby, H. Leuzinger & H. Stark), pp 64-122.

Suter W. 1982a Der Einfluss von Wasservögeln auf Populationen der Wandermuschel (*Dreissena polymorpha* Pall.) am Untersee-Ende/Hochrhein (Bodensee). *Schweizerische Zeitschrift für Hydrologie*, **44**, 149-161.

Suter, W. 1982b Die Bedeutung vom Untersee-Ende/Hochrhein (Bodensee) als wichtiges Überwinterungs-gewässer für Tauchenten (*Aythya, Bucephala*) und Bläßhuhn (*Fulica atra*). *Ornithologischer Beobachter*, **79**, 73-96.

Toba, D. R., Thompson, D. S., Chew, K. K., Anderson, G. J. & Miller, M. B. 1992 *Guide to Manila Clam Culture in Washington.* Seattle: Washington Sea Grant Publication, University of Washington.

Werner, S., Mörtl, M., Bauer, H.-G. & Rothhaupt, K.-O. 2005 Strong impact of wintering waterbirds on zebra mussel (*Dreissena polymorpha*) populations at lake Constance, Germany. *Freshwater Biol.*, **50**, 1412-1426.

West, A. D., Goss-Custard, J. D., McGrorty, S, Stillman, R. A. & 5 others. 2003 The Burry shellfishery and oystercatchers: using a behaviour-based model to advise shellfishery management policy. *Mar. Ecol. Prog. Ser.* **248**, 279-292.

Whitfield, D. P. 2003 Predation by Eurasian sparrowhawks produces density-dependent mortality of wintering redshanks. *J. Anim. Ecol.* **72**, 27-35.

Wormington, A. & Leach, J. H. 1992 Concentrations of migrant diving ducks at Point Pelee, Ontario, in response to invasion of zebra mussels, *Dreissena polymorpha. Can. F. Nat.* **106**, 376-380.

Zwarts, L., Ens, B. J., Goss-Custard, J. D., Hulscher, J. B. & Durell, S. E. A. le V. dit. 1996a Causes of variation in prey profitability and its consequences for the intake rate of the oystercatcher *Haematopus ostralegus. Ardea* **84A,** 229-268.

Zwarts, L., Hulscher, J. B., Koopman, K., Piersma, T. & Zegers, P. M. 1996b Seasonal and annual variation in body weight, nutrient stores and mortality of oystercatchers *Haematopus ostralegus*. *Ardea*, **84A**, 327-356.

FIGURE LEGENDS

Figure 1. Seasonal variation in the proportion of oystercatchers which specialised on feeding on Manila clams (open circles) and of those which ever included Manila clams in their diet (filled squares). The total numbers of birds observed in consecutive months are: 7, 12, 19, 23, 21, 23, 24, 29 ($\Sigma = 158$). The lines depict the binary logistic regression equations between date and the proportions (p) of birds: specialising on Manila clams (dashed line – $\log (p/(1-p)) = -3.339 + 0.373 *$ months after August, $G = 10.92$, $n = 158$, d.f. = 1, $P = 0.001$), and those including Manila clams in their diet (solid line – $\log (p/(1-p)) = -2.882 + 0.419 *$ months after August, $G = 19.41$, $n = 158$, d.f. = 1, $P < 0.001$).

Figure 2 Frequency distribution of the shell lengths (mm) of Manila clams in the sediment (solid line) ($n = 859$) and consumed by oystercatchers (dashed line) ($n = 77$). Both frequency distributions have been expressed as percentages of the sample size to facilitate comparison.

Figure 3 An overview of published studies of the intake rates (mg AFDM sec^{-1}) of free-living, over-wintering European oystercatchers consuming native bivalve species: *Mytilus edulis* (black), *Cerastoderma edule* (open), *Scrobicularia plana* (dark grey) and *Macoma balthica* (pale grey). Frequencies refer to the number of independent values of intake rate presented in the source paper (Zwarts *et al.* 1996a). The arrow denotes the value of the mean intake rate achieved by birds specialising on Manila clams (n=27) in this study (2.02 mg AFDM sec^{-1} (95% CI 1.673 – 2.367 mg AFDM sec^{-1})).

Figure 4 Variation in the form of the density-dependent mortality function of oystercatchers given various population densities of Manila clams (0 clams m^{-2} – filled circles, 5 clams m^{-2} – open circles, 10 clams m^{-2} – filled squares, 20 clams m^{-2} – open squares, 40 clams m^{-2} – filled triangles). Each data point depicts the mean predicted over-winter mortality arising from 10 replicate simulations of each scenario. The variation between replicate simulations was so small that the 95% confidence intervals cannot be presented given the size of the symbols.

Figure 1

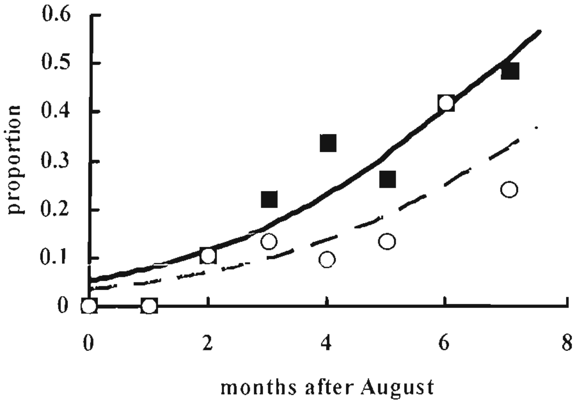


Figure 2

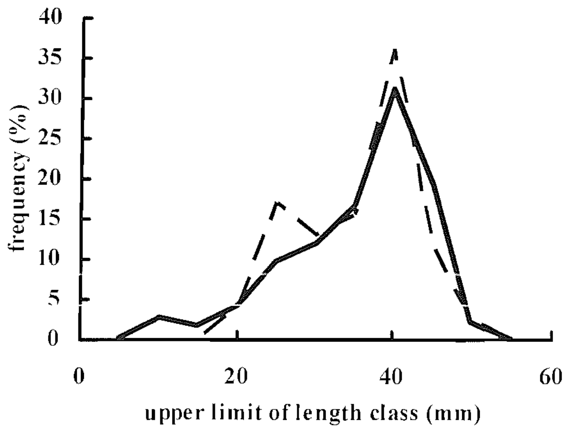

40
35
30
25
20
15
10
5
0
frequency (%)
0
20
40
60
upper limit of length class (mm)

Figure 3

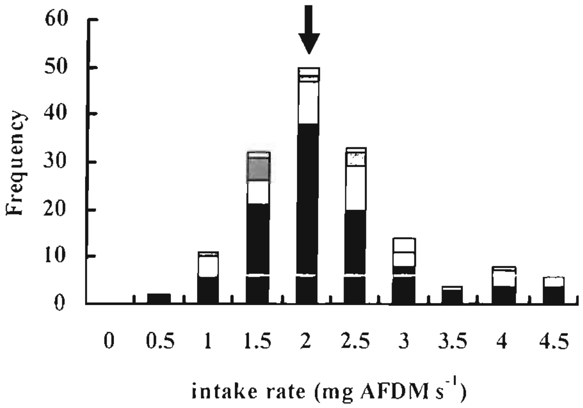
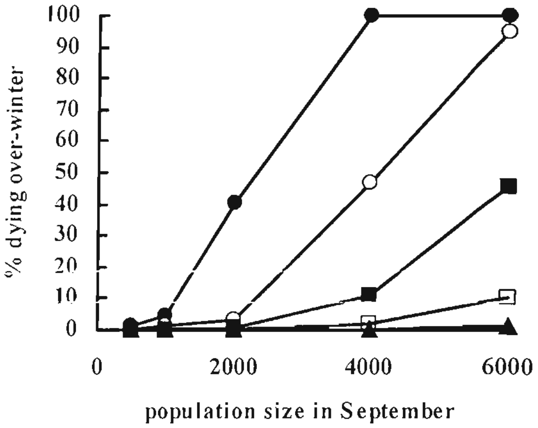

60
50
40
30
20
10
0
Frequency
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
intake rate (mg AFDM s^{-1})

Figure 4



% dying over-winter
100
90
80
70
60
50
40
30
20
10
0
0
2000
4000
6000
population size in September

REFERENCES

Ainley, D.G., Lewis, T.J., 1974. The history of Farallon Island marine bird populations. Condor 76 (4), 432-446.

Anderson, D.W., Keith, J.O., 1980. The human influence on seabird nesting success: conservation implications. Biol. Conserv. 18, 65-80.

Ar, A., Paganelli, C.V., Reeves, R.B., Greene, D.G., Rahn, H., 1974. The avian egg: water vapour conductance, shell thickness, and functional pore area. Condor 76, 153–158.

Aspinall, S.J., Venner J.P.F., 1991. A survey of breeding Black-headed Gulls and egg-collecting at Needs Ore Point, Hampshire in 1990. JNCC Report No. 11. Lyndhurst.

Aspinall, S.J., Taverner, J.H., Wiseman, E.J., 1993. History of Black-headed Gull colonies in Hampshire and neighbouring counties. British Birds 86, 103-114.

Associated British Ports 2000a. The Port of Southampton (Dibden Terminal) Harbour Revision Order: Environmental Statement and Plan.

Associated British Ports 2000b. Harbour Revision Order Application: Technical Statement – Inter-tidal and sub-tidal ecology impact assessment TS/E4.

Atkinson, P.W., 2003. Can we create or restore intertidal habitats for shorebirds? Wader Study Group Bull 100, 67-72.

Azouzi. L., Bourget, E., Borcard, D., 2002. Spatial variation in the intertidal bivalve Macoma balthica: biotic variables in relation to density and abiotic factors. Mar. Ecol. Prog. Ser. 234, 159–170.

Balph, M.H., 1977. Winter social behaviour of dark-eyed juncos: communication, social organization and ecological implications. Anim. Behav. 25, 859-884.

Beale, C.M., Monaghan, P., 2004. Human disturbance: people as predation free predators? J. Appl. Ecol. 41, 335-343.

Bekhuis, J., Meininger, P.L., Rudenko, A., 1997. Mediterranean Gull. In: Hagemeijer, W.J.M. and Blair, M.J. (eds.) The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. T. and A.D. Poyser, London.

Bertness, M.D., Grosholz, E., 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: the cost and benefits of an aggregated distribution. Oecologia 67, 192–204.

Beukema, J.J., Flach, E.C., 1995. Factors controlling the upper and lower limits of the intertidal distribution of two *Corophium* species in the Wadden Sea. Mar. Ecol. Prog. Ser. 125, 117–126.

Blumstein, D.T., Frenández-Juricic, E., Zollner, P.A., Garity, S.C., 2005. Inter-specific variation in avian responses to human disturbance. J. Appl. Ecol. 49, 943-953.

Bolduc, F.B., Guillemette, M., 2003. Human disturbance and nesting success of Common Eiders: interaction between visitors and gulls. Biol. Conserv. 110, 77-83.

Bolton, M., Houston, D., Monaghan, P., 1992. Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. J. Anim. Ecol. 61, 521-532.

Bolton, M., Monaghan, P., Houston, D.C., 1993. Proximate determination of clutch size in the Lesser Black-backed Gull: the role of food supply and body condition. Can. J. Zool. 71, 273-279.

Boutin, S., 1990. Food supplementation experiments with terrestrial vertebrates: Patterns, problems and the future. Can. J. Zool. 68, 203-220.

Boyden, C.R., Little, C., 1973. Faunal distributions in soft sediments of the Severn estuary. Est. Coast. Mar. Sci. 1, 203–223.

Bray, M.J., Hooke, J.M., Carter, D.J., 2000. Sea-level rise in the Solent region. in: Collins. M., Ansell, K. (Eds.), Solent Science – A Review. Elsevier, London, pp. 101-102.

Brown, K.M., Morris, R.D., 1994. The influence of investigator disturbance on the breeding success of Ring-billed Gulls (*Larus delawarensis*). Colonial Waterbirds 17, 7-17.

Brown, K.M., Morris, R.D., 1996. From tragedy to triumph: renesting in Ring-billed Gulls. The Auk 113 (1), 23-31.

Burfield, I., van Bommel, F., 2004. Birds in Europe: population estimates, trends and conservation status. Birdlife International, Cambridge.

Burger, J., 1981. Effects of human disturbance on colonial species, particularly gulls. Colonial Waterbirds 4, 28-36.

Burger, J., 1982. An overview of proximate factors affecting reproductive success in colonial birds: concluding remarks and summary of panel discussion. Colonial Waterbirds 5, 58-65.

Burger, J., Gochfeld, M., 1994. Predation and effects of humans on island-nesting seabirds, in: Nettleship, D.N., Burger, J., Gochfeld, M. (Eds.), Seabirds on Islands: Threats, Case Studies, and Action Plans. Birdlife International, Cambridge, UK, pp. 39-67.

Burges, D., 2000. Ornithology of the Solent, in: Collins, M., Ansell, K. (Eds.), Solent Science – A Review. Elsevier, London, pp. 261-270.

Caccamise, D.F., Morrison, D.W., 1988. Avian communal roosting: implications of "diurnal activity centres". Am. Nat. 128, 191-198.

Cadiou, B., Monnat, J.Y., 1996. Parental attendance and squatting in the kittiwake *Rissa tridactyla* during the rearing period. Bird study 43, 164-171.

Caldow, R.W.G., Beadman, H.A., McGrorty, S., Stillman, R.A., GossCustard, J.D., Durell, S.E.A. Le V. dit, West, A.D., Kaiser, M.J., Mould, K., Wilson, A., 2004. A behavior-based modelling approach to reducing shorebird–shellfish conflicts. Ecol. Appl. 14, 1411–1427.

Caldow, R.W.G, McGrorty, S., West, A.D., Durell, S.E.A. le V. dit, Stillman, R.A., Anderson, S., 2005. Macro-invertebrate Fauna in the Intertidal Mudflats, in: Humphreys, J., May, V. (Eds.), The Ecology of Poole Harbour. Elsevier, London, pp. 91-108.

Caldow, R.W.G., Stillman, R.A., Durell, S.E.A. le V.dit., West, A.D., McGrorty, S., Goss-Custard, J.D., Wood, P.J., Humphreys, J., in press. Benefits to shorebirds from invasion of a non-native shellfish. Proc. R. Soc. B.

Carey, C., 1996. Female reproductive energetics, in: Carey, C. (Eds.), Avian Energetics and Nutritional Ecology, Chapman and Hall, pp. 324-374.

Carey,C., 1986. Tolerance of variation in eggshell conductance, water loss, and water content by Red-winged Blackbird embryos. Physiol. Zool. 59, 109-122.

Carney, J.M., Sydeman, W.J., 1999. A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22, 68-79.

Chapin, F.S., Reynolds, H.L., D'Antonio, C., Eckhart, V., 1996. The functional role of species in terrestrial ecosystems, in: Walker, B. (Eds.), Global change in terrestrial ecosystems, Cambridge University Press, Cambridge, pp. 403-428,

Chapin, F.S., Sala, O.E., Burke, I.C., Grime, J.P., Hooper, D.U., Lauenroth, W.K., Lombard, A., Mooney, H.A., Mosier, A.R., Naeem, S., Pacala, S.W., Roy, J., Steffen, W.L., Tilman, D., 1998. Ecosystem consequences of changing biodiversity: experimental evidence and a research agenda for the future. Bioscience. 48, 45-52.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18: 117-143.

Clarke, K.R., Warwick, R.M., 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth.

Clode, D., MacDonald, D.W., 2002. Invasive predators and the conservation of island birds: the case of American Mink *Mustela vison* and terns *Sterna* spp. In the Western Isles, Scotland. Bird Study 49, 118-123.

Colenutt, A.J., 2005. Notes on Lymington and Keyhaven Saltmarshes and Inter-tidal Mudflats for the Western Solent Coastal Defence Strategy Study. New Forest District Council.

Collier, M.P., Banks, A.N., Austin, G.E., Girling, T., Hearn, R.D., Musgrove, A.J., 2005. The Wetland Bird Survey 3003/04: Wildfowl and wader counts. BTO/WWT/RSPB/JNCC, Thetford.

Connell, J.H.1978. Diversity in tropical rain forests and coral reefs. Science. 199:1302-1310.

Cooke, F., Rockwell, R.F., Lank, D.B., 1995. The snow geese of La Pérouse Bay. Oxford University Press.

Coulson, J.C., White, E., 1958. The effect of age on the breeding biology of the Kittiwake *Rissa tridactyla*. Ibis 100, 40-51.

Coulson, J.C., Johnson, M.P., 1993. The attendance and absence of adult kittiwakes *Rissa tridactyla* from the nest-site during the chick stage. Ibis 135, 372-378.

Craik, J.C.A., 1995. Effects of North American mink on the breeding success of terns and smaller gulls in west Scotland. Seabird 17, 3-11.

Craik, J.C.A., 1997. Long-term effects of North American Mink Mustela vison on seabirds in western Scotland. Bird Study 44, 303-309.

Craik, J.C.A., Campbell, B., 2000. Bruce Campbell's islands revisited: changes in the seabirds of Loch Sunart after a centaury. Atlantic Seabirds 2, 181-194.

Cramp, S., 1983. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palaearctic. Oxford University Press, Oxford.

Cramp, S., Bourne, W.R.P., Saunders, D., 1974. The Seabirds of Britain and Ireland. Collins, London.

Crawford, R.J.M., Shelton, P.A., 1981. Population trends for some southern African seabirds related to fish availability, in: Cooper, J. (Eds.), 1979. Proceedings of the symposium on birds of the sea and shore. African seabird group, Cape Town, pp, 15-41.

Cresswell, W., 1994. Flocking is an effective anti-predator strategy in redshank, *Tring tetanus*. Anim. Behav. 47(2), 433-442.

Croxall, J.P., Rothery, P., Crisp, A., 1992. The effect of maternal age and experience on egg-size and hatching success in wandering Albatrosses *Diomedea exulans*. Ibis 134, 219-228.

Davidson, N.C., Laffoley, D.d'A., Doody, J.P., Way, 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.

Davis, T.J., 1994. The Ramsar Convention Manual. A guide to the Convention of Wetlands of International Importance especially as waterfowl habitat. Ramsar Convention Bureau, Gland, Switzerland.

de Forest, L.N., Gaston, A.J., 1996. The effect of age on timing of breeding and reproductive success in Thick-billed Murre. Ecology 77, 1501-1511.

de Juana, E., 1984. The status and conservation of seabirds in the Spanish Mediterranean. In: Croxall, J.P., Evans, P,G.H., Schreiber, R.W. (Eds.), Status and Conservation of the World's Seabirds. International Council for Birds Preservation, Cambridge, England, pp. 347-370.

Dernie, K.M., Kaiser, M.J., Richardson, E.A., Warwick, R.M., 2003. Recovery of soft sediment communities and habitats following physical disturbance. J. Exp. Mar. Biol. Ecol. 285–286, 415–434.

Doncaster, C.P., Davey, A.J.H., 2007. Analysis of variance and covariance: how to choose and construct models for the life sciences. Cambridge University Press, Cambridge.

Doncaster, C.P., Davey, A.J.H., 2007. Analysis of variance and covariance: how to choose and construct models for the life sciences. Cambridge University Press, Cambridge.

Drewitt, A., 2001. Orthithology. Dibden Terminal public enquiry proof of evidence for English Nature, EN/4/1.

Duhem, C., Bourgeois, K., Vidal, E., Legrand, J., 2002. Food resources accessibility parameters of Yellow-legged Gulls *Larus michahellis*. Revue D'Ecologie – La Terre & La Vie 57, 343-453.

Dunstone, N.. 1993. The Mink. T. and A.D. Poyser, London.

Durell, S.E.A. Le V. dit, Stillman. R.A., Triplet, P., Aulert, C., dit Bio, D.O., Bouchet. A., Duhamel, S.. Mayot. S., Goss-Custard, J.D., 2005a. Modelling the efficacy of proposed mitigation areas for shorebirds: a case study on the Seine estuary. France. Biol. Conserv. 123, 67–77.

Durell, S. E. A. le V. dit, McGrorty, S, West, A. D., Clarke, R. T., Goss-Custard. J. D. & Stillman. R. A. 2005b. A strategy for baseline monitoring of estuary Special Protection Areas. Biol. Conserv. 121, 289-301.

Durell, S.E.A. Le V. dit, Stillman, R.A., Caldow, R.W.G., McGrorty, S., West, A.D., Humphreys J., 2006. Modelling the effect of environmental change on shorebirds: A case study on Poole Harbour, UK. Biol. Conserv. 131, 459-473.

Dyer, K. R., 1973. Estuaries: A Physical Introduction. Wiley, London, pp. 140.

Ehrlich, P.A., Wilson, E.O., 1991. Biodiversity studies: science and policy. Science. 253, 758-762.

Ehrlich, P.R., Mooney, H.A., 1983. Extinction, substitution, and ecosystem services. BioScience 33, 248-254.

Eiserer, L.A., 1984. Communal roosting in birds. Bird Behav. 5, 61-80.

Eisner, T., 1989. Prospecting for nature's chemical riches. Issues Sci.Technol. 6, 31–34.

Ephron, B., Tibshirani, R.J., 1993. An Introduction to the Bootstrap. Chapman and Hall, London.

Erwin, R.M., 1980. Breeding habitat use by colonially nesting waterbirds in two mid-Atlantic U.S. regions under different regimes of human disturbance. Biol. Conserv. 18, 39-51.

Feare, C.J., 1976a. The exploitation of sooty tern eggs in the Seychelles. Biol. Conserv. 10, 169-181.

Feare, C.J., 1976b. The breeding of the Sooty Tern *Sterna fuscata* in the Seychelles and the effects of experimental removal of its eggs. J. Zool. 179, 317-360.

Feare, C.J., Gill, E.L., Carty, P., Carty, H.E., Ayrton, V.J., 1997. Habitat use by Seychelles Sooty Terns *Sterna fuscata* and implications for colony management. Biol. Conserv. 81, 69-76.

Fetterolf, P.M., 1983. Effect of investigator activity on Ring-billed Gull behaviour and reproductive performance. Wilson Bull. 95, 23-41.

Finney, S.K., Pearce-Higgins, J.W., Yalden, D.W., 2005. The effect of recreational disturbance on an upland breeding bird, the golden plover *Pluvialis apricaria*. Biol. Conserv. 121, 53-63.

Furness, R.W., 1982. Competition between fisheries and seabird communities. In Blaxter, J.H.S., Russell, F.S., Yonge, M. (Eds.). Advances in marine biology. Vol. 20. Academic Press, New York. Pp. 225-307.

Fyhn, M., Gabrielsen, G.W., Nordoy, E.S., Moe, B., Langseth, I., Bech, C., 2001. Individual variation in field metabolic rate of Kittiwakes (*Rissa tridactyla*) during the chick-rearing period. Physiol. Biochem. Zool. 74, 343-355.

Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B., Page, G., 2002. Global climate change and sea level rise: Potential losses of intertidal habitat for shorebirds. Waterbirds 25 (2), 173-183.

Ghalambor, C.K., Martin, T.E., 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292, 494-497.

Gibbons, D.W., Reid, J.B., Chapman, R.A., 1993. The New Atlas of Breeding Birds in Britain and Ireland: 1998-1991. T. and A.D. Poyser, London.

Gill, J.A., Sutherland, W.J., Watkinson, A.R., 1996. A method to quantify the effects of human disturbance on animal populations. J. Appl. Ecol. 33, 786-792.

Gill, J.A., Watkinson, A.R., Sutherland, W.J., 1997. Causes of the redistribution of Pink-footed Geese *Anser brachyrhynchus* in Britain. Ibis 139:497–503.

González, J.A., 1999. Effects of harvesting of waterbirds and their eggs by native people in the Northeastern Peruvian Amazon. Waterbirds, 22 (2), 217-224.

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., 1996. The oystercatcher: from individuals to populations. Oxford University Press, Oxford.

Goss-Custard, J.D., Moser, M.E., 1988. Rates of change in the numbers of dunlin Calidris alpina wintering in British estuaries in relation to the spread of Spartina anglica. J. Appl. Ecol. 25, 95-109.

Goss-Custard, J.D., Sutherland, W.J., 1997. Individual behaviour, populations and conservation. In: Krebs, J.R., Davies, N.B. (Eds.), Behavioural Ecology: An Evolutionary Approach. Blackwell Science, Oxford, pp. 373–395.

Goss-Custard, J.D., Jones, R.E., Newberry, P.E., 1977. The ecology of the Wash I. Distribution and diet of wading birds (Charadrii). J. Appl. Ecol. 14, 681-780.

Goss-Custard, J.D., Durell, S.E.A. Le V. dit., 1984. Parkstone Bay: Birds Feeding on the Mudflats. Nature Conservancy Council.

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. J. Appl. Ecol. 28, 1004-1026.

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, 56–66.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., West, A.D., 1995b. Deriving population parameters from individual variations in foraging behaviour: II. Model tests and population parameters. J. Anim. Ecol. 64, 277-289.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell, S.E.A. le V. dit., Sutherland, W.J., 1995c. Deriving population parameters from individual variations in foraging behaviour: I. Empirical game theory distribution model of oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis*. J. Anim. Ecol. 64, 265-276.

Goss-Custard, J.D., Stillman, R.A., West, A.D., McGrorty, S., Durell, S.E.A. Le V. dit, Caldow, R.W.G., 2000. The role of behavioural models in predicting the ecological impact of harvesting. In: Gosling, L.Morris, Sutherland, W.J. (Eds.), Behaviour and Conservation. Cambridge University Press, Cambridge, pp. 65–82.

Goss-Custard, J.D., West, A.D., Yates, M.G., Caldow, R.W.G., Stillman, R.A., Bardsley, L., Castilla, J., Castro, M., Dierschke, V., Durell, S.E.A. le V. dit, Eichhorn, G., Ens, B.J., Exo, K.-M., Fernando, P.U.U., Ferns, P.N., Hockey, P.A.R., Gill, J.A., Johnstone, I., Kalejta-Summers, B., Masero, J.A., Moreira, F., Nagarajan, R. V., Owens, I.P.F., Pacheco, C., Perez-Hurtado, A., Rogers, D., Scheiffarth, G., Sitters, H., Sutherland, W.J., Triplet, P., Worrall, D.H., Zharikov, Y., Zwarts, L. & Pettifor, R.A., 2006. Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. Biol. Rev. 81, 1-29.

Götmark, F., 1992. The effects of investigator disturbance on nesting birds. In Power, D.M. (ed.) Current Ornithology, Plenum Press, New York.

Graveland, J., Berends, A.E., 1997. Timing of the calcium uptake and effect of calcium deficiency on behaviour and egg-laying in captive Great Tits, *Parus major*. Physiol. Zool. 70, 74-84.

Gray, J.S., 1974. Animal–sediment relationships. Oceanogr. Mar. Biol., Annu. Rev. 12, 223–262.

Green, C.D., 1975. Sediments of the Tay estuary. III. Sedimentological and faunal relationships on the southern shore at the entrance to the Tay. Proc. R. Soc. Edinburgh 75, 91–112.

Gregory, R.D., Wilkinson, N.I., Noble, D.G., Robinson, J.A., Brown, A.F., Hughes, J., Procter, D., Gibbons, D.W., Galbraith, C.A., 2002. The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002-2007. British Birds 95, 410-448.

Grell, M. B., 1998. Fuglenes Danmark. Gads Forlag, København.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Model. 198, 115-126.

Guthová, Z., 1993. Variations in reproduction parameters of Black-headed Gulls (*Larus ridibundus*) living in different conditions in the Czech and Slovak Republics. Enviro. Conserv. 29, 347-351.

Gutzwiller, K.J., Riffell, S.K., Anderson, S.H., 2002. Repeated human intrusion and the potential for nest predation by gray jays. J. Wildl. Manage. 66(2), 372-380.

Hallsworth, C. R., Knox, R. WO'B., 1999. BGS Rock Classification Scheme. Volume 3. Classification of sediments and sedimentary rocks. British Geological Survey Research Report, 99-03.

Hammond, N., Pearson, B., 1994. Waders. Hamlyn Bird Behaviour Guides. Hamlyn.

Hand, J.L., 1980. Human disturbance in Western Gull *Larus occidentalis livens* colonies and possible amplification by intraspecific predation. Biol. Conserv. 18, 59-63.

Harrison, C.J.O. and Castell, P. 2002. *Birds nests, eggs and nestlings of Britain and Europe.* Harper Collins, London.

Haynes, A.M., 1987. Human exploitation of seabirds in Jamaica. Biol. Conserv. 41 (2), 99-124.

Hayward, P. J., Ryland, J. S., 2000. Handbook of the Marine Fauna of North-West Europe. Oxford University Press, Oxford.

Heaney, N., Monaghan, P., 1995. A within-clutch trade-off between egg production and rearing in birds. Proc. R. Soc. Lond. B 261, 361-365.

Heldbjerg, H., 2001. The recent decline in the population of Blavk-headed Gulls *Larus ridibundus* in Denmark and its plausible causes. Dansk Orn. Foren. Tidsskr. 95, 19-27.

Hill, D.A., Treweek, J., Yates, T. and Pienkowski, M. 1996. *Actions for Biodiversity in the UK: Approaches in UK to Implementing the Convention on Biological Diversity, Ecological Issue No. 6.* British Ecological Society, London.

Hill, D.A., Hockin, D., Price, D., Tucker, G., Morris, R., Treweek, J., 1997. Bird disturbance: improving the quality and utility of disturbance research. J. Appl. Ecol. 34, 275-288.

Hipfner, J.M., Gaston, A.J., 1999. The relationship between egg size and posthatching development in the Thick-billed Murre. Ecology 80 (4). 1289-1297.

Hipfner, J.M., Gaston, A.J., Herzberg, G.R., Brosnan, J.T., Storey, A.E., 2003. Egg composition in relation to female age and relaying: Constraints on egg production in Thick-billed Murres (*Uria lomvia*). The Auk 120 (3). 645-657.

Houston, D.C., Jones, P.J., Sibley, R.M., 1983. The effect of female body condition on egg laying in Lesser black-backed Gulls *Larus fuscus*. J. Zool. 200. 509-520.

Houston, D.C., Donnan, D., Jones, P., Hamilton, I., Osbourne, D., 1995. Changes in the muscle condition of female Zebra Finches *Poephila guttata* during egg laying and the role of protein storage in bird skeletal muscle. Ibis 137, 322-328.

Hoyt, D. F., 1979. Practical methods of estimating volume and fresh weight of birds eggs. The Auk 96, 73-77.

Hunt, G.L., 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology 53, 1051-1061.

Ickes, S.K., Belant, J.L., Dolbeer, R.A., 1998. Nest disturbance techniques to control nesting gulls. Wildl. Soc. Bull. 26 (2), 269-273.

Jensen, A.C., Humphreys, J., Caldow, R.W.G., Grisley, C., Dyrynda, P.E.J., 2004 Naturalization of the Manila clam (*Tapes philippinarum*), an alien species, and establishment of a clam fishery within Poole Harbour, Dorset. J. Mar. Biol. Ass. U.K. 84, 1069-1073.

Jensen. A., Humphreys, J., Caldow, R., Cesar, C., 2005. The Manila Clam in Poole Harbour. In Humphreys, J., May, V. (Eds.) The Ecology of Poole Harbour, pp. 163-173. Amsterdam, Netherlands: Elsevier.

Johnson, C., 1985. Patterns of seasonal weight variation in waders on the Wash. Ringing and Migration 6, 19-32.

Junoy, J., Vieitez, J.M., 1990. Macrozoobenthic community structure in the Ria de Foz, an intertidal estuary (Galicia, Northwest Spain). Mar. Biol. 107, 329–339.

Keller, V., 1989. Variations in the response of Great Crested Grebes *Podiceps cristatus* to human disturbance – a sign of adaptation? Biol. Conserv. 34, 31-45.

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.

Kilpi, M., Hillström, L., Lindström, K., 1996. Egg-size variation and reproductive success in the Herring Gull *Larus argentatus*: adaptive or constrained size of the last egg. Ibis 138, 212-217.

Kirkman, F.B. 1937. Bird Behaviour: A contribution based chiefly on a study of the Black-headed Gull. Nelson, T., and sons, Ltd. / Jack, T. C., and Jack, E. C., Ltd. London/Edinburgh.

Kirkwood, J.K., 1983. A limit to metabolizable energy-intake in mammals and birds. Comp. Biochem. Physiol. A 75, 1-3.

Klomp, H., 1970. The determination of clutch size in birds, a review. Ardea 58, 1-125.

Kondoh, M., 2001. Unifying the relationships of species richness to productivity and disturbance. Proc. R. Soc. Lond. B 268, 269-271.

Krause, J., Ruxton, G.D., 2002. Living in Groups. Oxford University Press, Oxford.

Kruuk, H., 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus*). Behav. Suppl. 11, 1-130.

Krzanowski, W.J., 1988. Priciples of Multivariate Analysis: A User's Prespective. Carendon Press, Oxford.

Kullberg, C., Jakobsson, S., Kaby, U., Lind, J., 2005. Impaired flight ability prior to egg-laying: a cost of being a capital breeder. Funct. Ecol. 19, 98-101.

Kury, C.R., Gochfield, M., 1975. Human interference and gull predation in cormorant colonies. Biol. Conserv. 8, 23-34.

Laffoley, D., 2000. Viewpoint: Conservation, policy and management of maritime biodiversity, in: Collins, M., Ansell, K. (Eds.), Solent Science – A Review. Elsevier, London, pp. 225-230.

Lamont, B.B., 1995. Testing the effect of ecosystem composition/structure on its functioning. Oikos 74, 283-295.

Leakey, R.E., 1996. The sixth extinction: biodiversity and its survival. Wiedenfeld and Nicolson.

Lloyd, C.S., 1979. Factors affecting breeding of razorbills *Alca torda* on Skokholm. Ibis 121, 165-176.

Lloyd, C.S., Bibby, C.J., Everett, M.J., 1975. Breeding terns in Britain and Ireland in 1969-74. British Birds 68, 221-237.

Lloyd, C.S., Tasker, M.L. and Partridge, K. 1991. The status of seabirds in Britain and Ireland. T. and A.D. Poyser, London.

Longbottom, M.R., 1970. The distribution of *Arenicola marina* with particular reference to the effect of particle size and organic matter of the sediments. J. Exp. Mar. Biol. Ecol. 5, 138-157.

Lundberg, C.A., Väisänen, R.A., 1979. Selective correlation of egg size with chick mortality in the Black-headed Gull (*Larus ridibundus*). Condor 81, 146-156.

Lundy, H., 1969. A review of the effects of temperature, turning and gaseous environment in the incubator on the hatchability of the hen's egg, in: Carter, T.C., Freeman, B.M. (Eds.) The fertility and hatchability of the hen's, Oliver and Boyd, Edinburgh, pp 143-176.

Mänd, R., Tilgar, V., 2003. Does supplementary calcium reduce the cost of reproduction in the Pied Flycatcher *Ficedula hypoleuca*? Ibis 145, 67-77.

Margalef, R., 1958. Information theory in ecology. Gen. Syst. 3, 26-71.

Martin, T.E., 1987. Food as a limit on breeding birds: a life history perspective. Annu. Rev. Ecol. Syst. 18, 453-487.

Massey, B., Francher, J.M., 1989. Renesting by California Least Terns. J. Field Ornithol. 60, 350-357.

Mavor, R.A., Parsons, M., Heubeck, M. and Schmitt, S. 2006. *Seabird numbers and breeding success in Britain and Ireland, 2005.* Joint Nature Conservation Committee, Peterborough.

McClusky, D.S., 1981. The Estuarine Ecosystem. Blackie, Glasgow and London.

McGrorty, S., 1973. A guide to the sampling of intertidal flat macroinvertebrate faunas. Institute of Terrestrial Ecology, Norwich.

McNamara, J.N., Houston, A.I., 1996. State-dependent life histories. Nature 380, 215-221.

Meathrel. C.E., Ryder, J.P., 1987. Intraclutch variation in the size, mass and composition of Ring-billed Gulls eggs. Condor 89, 364-368.

Meathrel, C.E., Ryder, J.P., Termaat, B.M., 1987. Size and composition of Herring Gull eggs: relationship to position in the laying sequence and the body condition of females. Colon. Waterbirds 10, 55-63.

Meininger, P.L., Bekhuis, J.P., 1990. The Mediterranean Gull *Larus melanocephalus* as a breeding bird in the Netherlands and Europe. Limosa 63, 121-134.

Mitchell, I.P., Newton, S.F., Ratcliffe, N. and Dunn, T.E. 2004. Seabird populations of Britain and Ireland. T. and A.D. Poyser, London.

Møller, A.P., 1978. Mågernes Larinae yngleudbredelse, bestandsstørrelse og – ændringer i Danmark, med supplerende oplysninger om forholdene i det øvrige Europa. Dansk Orn. Foren. Tidsskr. 72, 15-39 (in Danish).

Monaghan, P., Bolton, M., Houston, D.C., 1995. Egg production constraints and the evolution of avian clutch size. Proc. R. Soc. Lond. B 259, 189-191.

Monaghan, P., Nager, R.G., 1997. Why don't birds lay more eggs? Trends Ecol. Evol. 12 (7), 270-274.

Monaghan, P., Nager, R.G., Houston, D.C., 1998. The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents. Proc. R. Soc. Lond. B 265, 1731-1735.

Moreno, J., Osorno, J.L., 2003. Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? Ecol. Lett. 6, 803-806.

Moxom, D.J., Burden, R.F., 2004. The recent history of monitoring and management of Little Tern *Sterna albifrons* and Common Tern *Sterna hirundo* on Chesil Bank, Dorset, 1974-1999. Dorset Proceedings 126, 63-84.

Musgrove, A.J., Pollitt, M.S., Hall, C., Hearn, R.D., Holloway, S.J., Marshall, P.E., Robinson, J.A., Cranswick, P.A., 2001. The Wetland Bird Survey 1999-2000: Wildfowl and wader counts. BTO/WWT/RSPB/JNCC, Slimbridge.

Nager, R. G., Monaghan, P., Houston, D.C., 2000. Within-clutch trade-offs between the number and quality of eggs: experimental manipulations in gulls. Ecology 81, 1339-1350.

Nager, R. G., Monaghan, P., Houston, D.C., 2001. The cost of egg production: increased egg production reduces future fitness in gulls. J. Avian. Biol. 32:159-166.

Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of freeranging mammals, reptiles and birds. Annu. Rev. Nutr. 19, 247–77.

Nilsson, J.A., Svensson, E., 1993. The frequency and timing of laying gaps. Ornis scandinavica 24, 122-126.

Nisbet, I.C.T., Drury, W.H., 1972. Post-fledging survival in Herring Gulls in relation to brood-size and hatching date. Bird-Banding 43 (3), 161-240.

Oppliger, A., Christe, P., Richner, H., 1996. Clutch size and malaria resistance. Nature 381, 565.

Oro, D., Pradel, R., Lebreton, J.-D., 1999. Food availability and nest predation influence life history traits in Audouin's Gull, *Larus audouinii*. Oecologia 118, 438-445.

Ortiz, N.E, Smith, G.R., 1993. Landfill sites, botulism and gulls. Epidemiol. Infect. 112, 385-391.

Packard, M.J., Packard, G.C., 1993. Water-loss from eggs of domestic fowl and calcium status of hatchlings. J. Comp. Physiol. 163, 327-331.

Parry, D.M., Kendall, M.A., Pilgrim, D.A., Jones, M.B., 2003. Identification of patch structure within marine benthic landscapes using a remotely operated vehicle. J. Exp. Mar. Biol. Ecol. 285–286, 497–511.

Parsons, J., 1975. Seasonal variation in the breeding success of the Herring Gull: an experiment approach to pre-fledging success. J. Anim. Ecol. 44, 553-573.

Parsons, J., 1976. Factors determining the number and size of eggs laid by the Herring Gull. Condor 78, 481-492.

Parsons, K. C., Chao, J., 1983. Nest cover and chick survival in Herring Gulls (*Larus argentatus*). Colonial Waterbirds 6, 553-573.

Parsons, M.S., Fosters. A. P., 1996. Coastal invertebrate fauna, in: Barne, J. et al. (Eds.), British Coasts and Seas. Region 9: southern England. Hayling Isalnd to Lyme Regis. Joint Nature Conservation Committee. Peterborough, UK, pp. 249.

Patterson. I.J., 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. Ibis 107 (4). 433-459.

Perring. F.H., Walters. S.M., 1976. Atlas of the British flora. Botanical Society of the British Isles.

Perrins. C.M., 1970. The timing of birds' breeding seasons. Ibis 112, 242-255.

Peterson. C.H., 1991. Intertidal zonation of marine invertebrates. Am. Sci. 79, 236–249.

Peterson. C.H., Black. R., 1987. Resource depletion by active suspension-feeders on tidal flats: influence of local density and tidal elevation. Limnol. Oceanogr. 32,143–166.

Pickess, B.P., Underhill-Day, J.C., 2002. Important Birds of Poole Harbour. Poole Harbour Study Group, Wareham.

Pienkowski, M.W., 1982. Diet and energy intake of grey and ringed plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. J. Zool. (Lond.) 197, 511-549.

Pienkowski, M.W., Ferns, P.N., Davidson, N.C., Worrall, D.H., 1984. Balancing the budget: measuring the energy intake and requirements of shorebirds in the field. Pp. 29-56, in P. R. Evans, J. D. Goss-Custard and W. G. Hale, eds. Coastal waders and waterfowl in winter. Cambridge University Press, Cambridge.

Pollitt, M.S., Hall, C., Holloway, S.J., Hearn, R.D., Marshall, P.E., Musgrove, A.J., Robinson, J.A., Cranswick, P.A., 2003. The Wetland Bird Survey 2000-01: Wildfowl and Wader counts. BTO/WWT/RSPB/JNCC, Slimbridge.

Poole, A., 1985. Courtship feeding and Osprey reproduction. Auk 102, 479-492.

Prévot-Julliard, A.C., Julliard, R.P.R., Grosbois, V., Lebreton, J.D., 2001. Hatching date influences age at first reproduction in the Black-headed Gull. Oecologia 127, 62-68.

Proulx, M., Mazmuder, A., 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79, 2581-2592.

Pullin, A.S., 2002. Conservation biology. Cambridge University Press, Cambridge.

Quinn, J.L., Cresswell, W., 2004. Predator hunting and prey vulnerability. J. Anim. Ecol. 73, 143–154.

Rae, S., 1999. The effects of predation by mink on ground-nesting birds in the Outer Hebrides. Outer Hebrides (the Western Isles) Bird Report 1999, 105-113.

Rahn, H., Ar, A., 1974. The avian egg: incubation time and water loss. Condor 76, 147-152.

Ratcliffe, N., 2003. Little terns in Britain and Ireland: estimation and diagnosis of population trends, in: Schmitt, S. (Eds.) Abstracts Proc. 2003 Little Tern Symp. Royal Society for the Protection of Birds, Sandy.

Reid, J.M., Monaghan, P., Ruxton, G.D., 2000. The consequences of clutch size for incubation conditions and hatching success in Starlings. Funct. Ecol. 14(5), 560-565.

Reid, W.V., 1987. Constraints on clutch size in the glaucous-winged gull. Stud. Avian Biol. 10, 8-25.

Reid-Henry, D., Harrison, C. 1988. The History of the Birds of Britain. Collins/Witherby, London.

Ricklefs, R.E., 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9, 1-48.

Riffell, S.K., Gutzwiller, K.J., Anderson, S.H., 1996. Does repeated human intrusion cause cumulative declined in avian richness and abundance? Ecol. Appl. 6(2), 492-505.

Robbins, C.T., 1981. Estimation of the relative protein costs of reproduction in birds. Condor 83, 177-179.

Roberts, H.C., Ralph, C.J., 1975. Effects of human disturbance on the breeding success of gulls. Condor 75, 495-499.

Ruiz, X., Jover, L., Pedrocchi, V., 1998. Audouin's Gull intraspecific variability in yolk and albumen egg contents: why is yolk size constant? Biol. Cons. Fauna 102, 327-334.

Ruiz, X., Jover, L., Pedrocchi, V., Oro, D., González-Solis, J., 2000. How costly is clutch formation in the Audouin's Gull *Larus audoninii*? J. Avian Biol. 31, 567-575.

Safina, C., Burger, J., 1983. Effects of human disturbance on reproductive success in the Black Skimmer. Condor 85, 164-171.

Salzer, D.W., Larkin,G.J., 1990. Impact of courtship feeding on clutch and third-egg size in glaucous –winged gulls. Anim. Behav. 39, 1149-1162.

Shannon, C.E., Weaver, W., 1949. The mathematical theory of communication. The University of Illinois Press, Urbana, pp. 117.

Shannon, L.J., Crawford, R.J.M., 1999. Management of the African penguins *Spheniscus demersus* – Insights from modelling. Mar. Ornithol. 27, 119-128.

Sharrock, J.T.R., 1976. The Atlas of Breeding Birds in Britain and Ireland. T. and A.D. Poyser, Berkhamsted.

Simpson, D., 2001. Whatever happened to the Ravenglass gullery? British Wildlife 12, 153-162.

Smith, A.J., 1974. Changes in the average weight and shell thickness of eggs produced by hens exposed to high environmental temperatures – A review. Trop. Anim. Health. Prod. 6(4), 237-244.

Snyder, G.K., Birchard, G.F., 1982. Water loss and survival in embryos of the domestic chicken. J. Exp. Zool. 219, 115-117.

Southern, W.E., Southern, L.K., 1982. Intensification of adult Ring-billed Gull aggression during reproduction and its possible consequences. Colonial Waterbirds 5, 2-10.

Spear, L., Nur, N., 1994. Brood size, hatching order and hatching date: Effects on four life-history stages from hatching to recruitment in western Gulls. J. Anim. Eco. 63, 283-298.

Stillman, R.A., Goss-Custard, J.D., Clarke, R.T., Durell, S.E.A. le V dit., 1996. Shape of the interference function in a foraging vertebrate. J Anim Ecol 65:813–824.

Stillman, R.A., Goss-Custard, J.D., Caldow, R.W.G., 1997. Modelling interference from basic foraging behaviour. J Anim Ecol 66, 692–703.

Stillman, R.A., Goss-Custard, J.D., West, A.D., Durell, S.E.A. le V. dit., Caldow, R.W.G., McGrorty, S., Clarke, R.T., 2000. Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. J. Appl. Ecol. 37, 564-588.

Stillman, R.A., Goss-Custard, J.D., West, A.D., McGrorty, S., Durell, S.E.A. le V. dit., Caldow, R.W.G., Norris, K.J., Johnstone, I.G., Ens, B. J., Van der Meer, J., Triplet, P., 2001. Predicting shorebird mortality and population size under different regimes of shellfishery management. J. Appl. Ecol. 38, 857-868.

Stillman, R.A., Poole, A.E., Goss-Custard, J.D., Caldow, R.W.G., Yates, M.G., Triplet, P., 2002. Predicting the strength of interference more quickly using behaviour-based models. J. Appl. Ecol. 71, 532–541.

Stillman, R.A., West, A.D., Goss-Custard, J.D., Caldow, R.W.G., McGrorty, S., Durell, S.E.A. le V. dit., Yates, M.G., Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P.J., Mander, M., 2003. An individual behaviour-based model can predict shorebird mortality using routinely collected shellfishery data. J. Appl. Ecol. 40, 1090-1101.

Stillman, R.A., West, A.D., Goss-Custard, J.D., McGrorty, S., Frost, N.J., Morrisey, D.J., Kenny, A.J., Drewitt, A., 2005a. Predicting site quality for shorebird communities: a case study on the Humber estuary, UK. Marine Ecology Progress Series 305, 213–217.

Stillman, R.A., Caldow, R.W.G., Durell, S.E.A. Le V. dit, West, A.D, McGrorty, S., Goss-Custard, J.D, Pe´rez-Hurtado, A., Castro, M., Estrella, S., Masero, J.A., Rodrı´guez-Pascual, F.H., Triplet, P., Loquet, N., Desprez, M., Fritz, H., Clausen, P., Ebbinge, B., Norris, K., Mattison, E., 2005b. Maintaining Migratory Coastal Bird Diversity: Management through Individual-based Predictive Population Modelling, European Commission.

Storr, G. M., Johnstone, R.E., Griffin, P., 1986. Birds of the Houtman Abrolhos, Western Australia. Records of the Western Australian Museum, Supplement 24, 1-42.

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

Tapper, S.C., 1992. Game Heritage: An Ecological Review From Shooting and Gamekeeping Records. The Game Conservancy, Fordingbridge.

Taverner, J.H., 1966. The Needs Ore gullery and ternery. Hampshire bird Report for 1965, 32-45.

Taverner, J.H., 1972. Mediterranean Gulls in Hampshire 1970-71. British Birds 65, 185-186.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145-148.

Thompson, K.R., Brindley, E., Heubeck, M., 1996. Seabird numbers and breeding success in Britain and Ireland, 1995. Joint Nature Conservation Committee, Peterborough.

Thrush, S.F., Hewitt, J.E., Pridmore, R.D., 1989. Patterns in the spatial arrangements of polychaetes and bivalves in intertidal sandflats. Mar. Biol. 102, 529–535.

Triplet. P., Stillman. R.A., Goss-Custard, J.D., 1999. Prey abundance and the strength of interference in a foraging shorebird. J Anim Ecol 68, 254–265.

Tubbs, C.R., 1990. The Solent: an estuarine system in flux. Wader Study Group Bulletin 60, 21-23.

Tubbs, C.R., 1999. The ecology, conservation and history of the Solent. Chichester, Packard Publishing.

Turner, S.J., Thrush, S.F., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., MaSkery, M., 1995. Are soft sediment communities stable? An example from a windy harbour. Mar. Ecol. Prog. Ser. 120, 219–230.

Underwood, A.J., Chapman, M.G., 1996. Scales of spatial distribution of intertidal invertebrates. Oecologia 107, 212-224.

Upton, A. J., Pickerell, G., Heubeck, M., 2000. Seabird numbers and breeding success in Britain and Ireland, 1999. Joint Nature Conservation Committee, Peterborough.

Veasey. J.S., Houston. D.C., Metcalfe, N.B., 2000. Flight muscle atrophy and predation risk in birds. Funct. Ecol. 14, 115–121.

Veasey. J.S., Houston. D.C., Metcalfe, N.B., 2001. A hidden cost of reproduction: the trade-off between clutch size and escape take-off speed in female zebra finches. J. Anim. Ecol. 70. 20–24.

Velegrakis. A., 2000. Geology, geomorphology and sediments of the Solent system, in: Collins. M., Ansell, K. (Eds.), Solent Science – A Review. Elsevier, London, pp. 21-43.

Vermeer. K., Morgan. K.H., Smith, G.E.J., York, B.A., 1991. Effects of egging on the reproduction success of Glaucous-winged gulls. Waterbirds 14 (2), 158-165.

Visser, M.E., Lessells, C.M., 2001. The costs of egg production and incubation in great tits (*Parus major*). Proc. R. Soc. Lond. B 268:1271-1277.

Walsberg, G.E., Schmidt, C.A., 1992. Effects of variable humidity on embryonic development and hatching success of Mourning Doves. The Auk 109 (2), 309-314.

Walsh, P.M., Halley, D.J., Harris, M.P., del Nevo, A., Sim, I.M.W., Tasker, M.L., 1995. Seabird monitoring handbook for Britain and Ireland. Joint Conservation Committee, the Royal Society for the Protection of Birds, the Institute of Terrestrial Ecology, and the Seabird Group.

Wanless, S., Harris, M.P., Calladine, J., Rothery, P., 1996. Modelling responses of herring gull and lesser black-backed gull populations to reduction of reproductive output: implications for control measures. J. Appl. Ecol. 33, 1420-1432.

Ward, D., 1992. The role of satisficing in foraging theory. Oikos 63:312–317.

Ward, P., Zahavi, A., 1973. The importance of certain assemblages of birds as 'information-centres' for food-finding. Ibis 115, 517-534.

Warwick, R.M., Goss-Custard, J.D., Kirby, R., George, C.L., Pope, N.D., Rowden, A.A., 1991. Static and dynamic environmental factors determining the community structure of estuarine macronethos in SW Britain: why is the Severn estuary different? J. Appl. Ecol. 28, 329–345.

Warwick, R.M., Ashman, C.M., Brown, A.R., Clarke, K.R., Dowell, B., Hart, B., Lewis, R.E., Shillabeer, N., Somerfield, P.J., Tapp, J.F., 2002. Inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional events. Mar. Ecol. Prog. Ser. 234, 1–13.

Webb, D.R., 1987. Thermal tolerance of avian embryos: a review. Condor 89, 874-898.

Webber, N B., 1980. Hydrography and water circulation in the Solent, in: The Solent Estuarine System: An Assessment of the Present Knowledge. N.E.R.C. Publications, Series C, No 22, 6-19.

Weidmann, U., 1956. Observations and experiments on egg-laying in the Black-headed Gull (*Larus ridibundus* L.). Bri. J. Anim. Behav. 4, 150-161.

Weimerskirch, H., Shaffer, S.A., Mabille, G., Martin, J., Boutard, O., Rouanet, J.L., 2002. Heart rate and energy expenditure of incubating wandering albatrosses: basal levels, natural variation, and the effect of human disturbance. J. Exp. Biol. 205, 475-483.

West, A.D., Goss-Custard, J.D., Stillman, R.A., Caldow, R.W.G., Durell, S.E.A. le V. dit., McGrorty, S., 2002. Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model. Biol. Conserv. 106, 319-328.

West, A.D., Goss-Custard, J.D., McGrorty, S., Stillman, R.A., Durell, S.E.A. le V. dit., Stewart, B., Walker, P., Palmer, D.W., Coates, P., 2003. The Burry shellfishery and oystercatchers: using a behaviour-based model to advise on shellfishery management policy. Mar. Ecol. Prog. Ser. 248, 279-292.

West, A.D., Goss-Custard, J.D., Durell, S.E.A. Le V. dit, Stillman, R.A., 2005. Maintaining estuary quality for shorebirds: towards simple guidelines. Biol. Conserv. 123, 211–224.

West, A.D., McGrorty, S., 2003. Modelling oystercatchers and their food on the Dee estuary, Traeth Lafan and Burry Inlet SPAs to inform target setting and site management. Coutryside Council for Wales.

Whitfield, D.P., 1985. Raptor predation on wintering waders in southeast Scotland. Ibis 127, 544–548.

Whitfield, D.P., 2003. Predation by Eurasian sparrowhawks produces density dependent mortality of wintering redshanks. J. Anim. Ecol. 72, 27–35.

Wilson, R.P., Culik, B., 1995. Penguins disturbed by tourists. Nature 376, 30-32.

Wissman, M.A., 1996. Artifical incubation. Proc. Avicult. Program 29-42.

Woehler, E.J., Penney, R.L., Creet, S.M., Burton, R.H., 1994. Impacts of human visitors on breeding success as long-term population trends in Adélie penguins at Casey, Antarctica. Polar Biol. 14, 269-274.

Wolff, W.J., 1973. The estuary as habitat. An analysis of data on the sift-bottom macrofauna of the estuarine areas of the rivers Rhine, Meuse and Scheldt. Zool. Verh. 126, 1-242.

Woodin, S.A., 1974. Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. Ecol. Monogr. 44, 171–187.

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.J., 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. J. Appl. Ecol. 30, 599–614.

Yates, M.G., Stillman, R.A., Goss-Custard, J.D., 2000. Contrasting interference functions and foraging dispersion in two species of shorebird (Charadrii). J. Anim. Ecol. 69, 314–322.

Ydenberg, R.C., Prins, H.H.T., 1984. Why do birds roost communally in winter? In: Coastal waders and wildfowl in winter (Eds.) Evans, P.R., Goss-Custard, J.D., Hale, W.G. pp-123-139. Cambridge University Press, Cambridge.

Yorio, P., Garcia Borboroglu, P., 2002. Breeding biology of Kelp Gulls (*Larus dominicanus*) at Golfo San Jorge, Patagonia, Argentina. Emu 102 (3), 257-263.

Zador, S. G., Piatt, J.F., Punt, A.E., 2005. Balancing predation and egg harvest in a colonial seabird: A simulation model. Ecol. Model. 195 (3-4), 318-216.

Zwarts, L., 1991. Seasonal variation in body weight of the bivalves *Macoma* balthica, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden Sea. Neth J Sea Res 28, 231–245.

Zwarts, L., Wanink, J.H., 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth J Sea Res 31, 441–476.