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COAST BIRD DIVERSITY

Maintaining Migratory Coastal Bird Diversity: management through individual-based predictive population modelling

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SUMMARY

The overall aim of this project was to provide for policy-makers and their scientific advisors a suite of field-tested predictive population models with which they can devise local and Europe-wide management plans for maintaining the biodiversity of migratory (wintering/on passage) coastal birds (waders and wildfowl) that feed on inter-tidal and, often, supra-tidal (supplementary) habitats. The original project objective was to achieve this by adapting, simplifying and parameterising two existing individual-based population models so that they could be applied rapidly to a variety of species whenever policy decisions were required and at any geographic scale. Both predicted the body condition and mortality rate over the non-breeding season of classes of individuals within the population. Both models assumed that, when responding to management-induced changes in their feeding environment, individual birds chose the options that maximize their intake rate. Both were individual-based, in the sense that they tracked the location, foraging decisions and ultimate fate of each individual within the population, and predicted population level responses to environmental change (e.g. mortality rate) from the behaviour and fates of individuals (e.g. the proportion of individuals which die). One model, the *single-site wader model*, was a single-site (e.g. estuary) model for the non-breeding season which had been developed, parameterized and extensively (and successfully) tested for one common European wader species. The other, the *multi-site goose model*, was a multi-site, Europe-wide model which had been parameterized and tested, in a preliminary fashion, for one common wildfowl species. The aim of the project was to build, test and define the utility of the models for a much wider range of species in order to rapidly provide, at whatever geographic scale required, bird population predictions for a range of policy options. The original objective of adapting two existing models was extended during the project, and instead a completely new model was developed capable of making predictions for both waders and geese, at either the single or multi-site scale. The new model can be applied to a much wider range of systems and issues than could either of the initial models. The new model is based on the same principles as the existing models and is also individual-based. It builds on the strengths of the existing models, and adds improvements where the previous models were limited.

Three key scientific advances were made during the project.

- *Development of a general individual-based modelling framework*. The development of the new individual-based model has been one of the major scientific advances made during the project. The new model has the following advantages over the initial models. (i) It is much more flexible than the original models and so can be applied to a wider range of environmental issues. (ii) Using a single model for both geese and waders highlighted the similarities between these systems, rather than differences. (iii) The new model has been developed in a more general way than the previous models and so it not simply restricted to waders and geese, increasing the potential application of the model in the future.

- *Development of a general equation to predict the feeding rate of waders*. The project showed that the a simple equation could be used to predict the feeding rate of wading birds feeding on a range of prey species. Feeding rate is one of the most important parameters in the model. All that needs to be known is the mass of the wading bird species, and the mass and abundance of the prey. This breakthrough meant that wader models could be developed much more quickly and for a wider range of species than would have been possible if feeding rate needed to be measured for each new wader and prey species.

- *Rapid application of models to real-world issues*. If individual-based models are to be valuable tools for advising policy, they must be developed within a relatively short time span (e.g. a few years) and produce realistic predictions. Three site-specific multi-species wader models (Bahia de Cadiz, Spain, Baie de Somme, France and Exe Estuary, England) and a multi-site brent goose model (throughout western Europe) were successfully parameterised using data collected or collated during the four years of the project. The models successfully predicted much of the observed behaviour (e.g. amount of time spent feeding, rate of consuming food) and ecology (e.g. distribution between habitats) of the birds in the real systems. They were also used to answer a wide range of key site or system specific policy issues (e.g. hunting, disturbance, habitat loss of saltpans, fish farms, intertidal vegetation and sandflats). The successful parameterisation, testing and application of the wader and goose models is one of the key scientific advances made during the project, because it shows the potential of the approach to address European coastal issues.

The site and system-specific wader and goose models predicted the effect of a wide range of environmental issues (e.g. disturbance from people, hunting, habitat loss, sedimentation, encroachment of saltmarsh vegetation onto mudflats) on the survival and body condition of birds. These specific predictions are detailed in the report. In addition, the following more general policy recommendations can be derived from the results of the project.

- *Monitor bird food reserves as well as bird numbers*. Estuary managers are often required to monitor the quality of a site for important bird species or to assess how potential changes to a site may influence site quality. The conservation importance of an estuary is often measured in terms of bird numbers using the estuary, but monitoring numbers is not necessarily a reliable way of assessing changes in site quality. In particular, this is because the numbers of birds using a site depend not only on the conditions at the site, but also the conditions at other sites both within the non-breeding and breeding seasons. Changes in the food supply can be used in combination with bird numbers to determine whether any decline in bird numbers is likely to reflect a problem on the site itself. Decreasing bird numbers in combination with a decrease in the amount of food would indicate that the problem was within the site, whereas decreasing bird numbers without a decrease in the food supply would indicate either that the problem was not limited food within the site, or that the decrease in bird numbers was due to factors outside of the site. A policy derived from these predictions would be to establish a monitoring programme to record the abundance of food on sites at the start of winter as well as continuing the usual procedure of monitoring bird numbers.

- *Monitor the use of marginal habitats and feeding times*. The models developed during this project all predicted that birds fed in the most profitable and safest places and times when feeding conditions were good and survival rates high, behaviour which mimicked that of real birds. In contrast, birds were predicted to feed more in marginal habitats or at more risky times when feeding conditions were poorer, again behaviour which mimicked that of real birds. A possible policy would be to establish a monitoring programme to detect such changes in the behaviour of bird populations as an early warning that survival rates are likely to be falling. This approach would pick up possible detrimental changes on a site before increases in mortality rate could be detected through traditional approaches based on bird ringing programmes, increasing the chance that management can be implemented to improve conditions before bird survival declines greatly.

- *Maintain a network of sites*. The multi-site models predicted that birds emigrated from a site when the feeding conditions declined on the site. The consequences for the population depended on whether emigrating birds were able to find and survive on an alternative site. Birds could not survive if they did not have the energy reserves to successfully fly between the two sites (i.e. alternative sites must be relatively close together). A simple policy derived from this prediction is that wherever possible a network of high-quality sites should be maintained. This maximises the chance that emigrating birds are able to find and survive on an alternative site, if conditions deteriorate on their initial site.

- *Include terrestrial habitats in conservation areas*. Birds were predicted to use terrestrial habitats when feeding conditions declined on their intertidal habitats, a pattern also observed in real birds. For example, brent geese in northern Europe fed on grass when intertidal *Zostera* and algae biomass declined during winter. Waders consumed more earthworms from terrestrial fields when intertidal food was depleted in late winter. These terrestrial habitats are often critical to the survival of waders and geese, even though they are often considered as marginal habitats. These habitats are often excluded from the designation of Special Protection Areas, but this means that vital habitat is not being protected and as a result may be lost to building developments, or suffer high disturbance levels. A simple policy derived from these predictions is that wherever possible conservation areas should include the terrestrial habitats around estuaries as well as the intertidal habitats of the estuary itself. This would ensure that the full range of habitats required by birds are protected.

The model developed in this contract provides a means for predicting the effects of environmental issues on the survival and body condition of wading birds and wildfowl. As such, it is a tool which can be used by decision-makers concerned with the management of the coastal zone throughout Europe, whether they represent governments, fisheries organisations or nature conservation bodies. The model also provides the basis for further research into the interaction between coastal birds and their environment, and could be expanded in a number of directions, including application to the breeding season and to species other than waders and geese.

1 INTRODUCTION

1.1 Summary

This chapter describes the policy background to the Coast Bird Diversity project, the project's objectives and the link between these objectives and the chapters in this report. The overall objective of the Coast Bird Diversity project was to develop the scientific and technological basis and tools for understanding and predicting quantitatively, in the context of sustainable development, the effects on coastal bird diversity of habitat loss and the many other human activities carried out on the coast. It achieved this through the development of a suite of individual-based models parameterised and tested for wader species in sites in Spain, France and the UK, and for the brent goose throughout north-western European from Denmark to southern France. These models are individual-based, in the sense that they track the location, foraging decisions and ultimate fate of each individual within the population, and predict population level responses to environmental change (e.g. mortality rate) from the behaviour and fates of individuals (e.g. the proportion of individuals which die). The original project objective was to develop these models by adapting two existing models, the single-site wader and multi-site goose models. During the course of the project, it was decided to make a major extension to this objective, by creating a completely new model and applying this model to all species and sites included in the project. The new model has been developed in a much more general way than the previous models, allowing it to be applied to a much wider range of species and issues, both within the current project and beyond.

1.2 Policy background

European coastal areas (estuaries, bays and extensive flats) provide vital feeding areas for migratory shorebirds (waders and wildfowl), particularly outside the breeding season while they are on passage and/or wintering. Most of the birds can only feed on their macro-invertebrate and plant food supplies when these are exposed on the intertidal flats over low tide. These species contribute importantly to the biodiversity of the coastal zone. But as many human activities which are potentially damaging to bird populations are carried out on the coast (e.g. reclamation, salt production, resource harvesting, recreation) policy decisions are frequently required, at geographic scales ranging from local to European, on how best to maintain biodiversity and to reconcile its protection with economic development. Before this project, these decisions were not based on quantitative population predictions from models that simulate the effect on a range of species, and thus biodiversity, of alternative management and policy options. The Coastal Bird Diversity project has filled this gap by developing individual-based population models for a wide range of bird species that can be applied rapidly whenever predictions are required, whether at one or more local sites or to guide a regional or Europe-wide policy.

The objective of the project was to develop the scientific and technological basis and tools for understanding and predicting quantitatively, in the context of sustainable development, the effects on coastal bird diversity of habitat loss and the many other human activities carried out on the coast. The migratory species involved are subject to multilateral national, European and international treaties and conventions which have been introduced to protect these populations and their most important sites. The human activities concerned occur throughout Europe and there is often the possibility of implementing mitigating measures to prevent biodiversity loss. The project aimed to provide policy makers with quantitative predictions as to the possible negative effects on bird diversity of a wide range of potentially conflicting human activities. Simultaneously, it aimed to provide quantitative predictions as to the possible positive, or counter-acting, effects of mitigating measures on biodiversity. It therefore provides the means by which informed decisions can be taken on how best to reconcile human activities and economic development with the conservation of biodiversity.

Since the objective of non-breeding wader and wildfowl conservation policy is to at least maintain present bird numbers, the best measure of the effect of a human activity on birds is the predicted change in population size. Population size is a function of the interaction between (i) the mortality and reproductive rates in the breeding range and (ii) the mortality rate in the non-breeding range, including the migratory routes. The models developed in this project predict the effect of any activity on the two quantities that are believed to determine individual fitness in these birds outside the breeding season. The first is the size of the fat reserve which is needed by the birds to fuel migration and, in spring, also to breed successfully after they have reached the breeding grounds. The second is the chance of dying during the non-breeding season. If it can be shown that the feeding conditions following a proposed change in land-use, policy or management regime would allow the present-day rates of fat storage and overwinter survival to continue, there would be no reason to be concerned for the birds. If, on the other hand, body condition and survival were predicted to decline, population size would be expected to decrease, by an amount that depends on (i) the strength of any compensatory density-dependent reproduction on the breeding grounds (Goss-Custard & Durell 1990) and (ii) the availability of alternative wintering or passage sites (Pettifor *et al*. 2000).

1.3 Project background – existing models

The overall aim of the project was to provide for policy-makers and their scientific advisors a suite of field-tested predictive population models with which they can devise local and Europe-wide management plans for maintaining the biodiversity of migratory (wintering/on passage) coastal birds (waders and wildfowl) that feed on inter-tidal and, often, supra-tidal (supplementary) habitats. The original project objectives were to achieve this by adapting, simplifying and parameterising two existing individual-based population models so that they can be applied rapidly to a variety of species whenever policy decisions are required and at any geographic scale. Both predicted the body condition and mortality rate over the non-breeding season of classes of individuals within the population. Both models assumed that, when responding to management-induced changes in their feeding environment, individual birds choose the options that maximize their intake rate. One model, the *single-site wader model*, was a single-site (e.g. estuary) model for the non-breeding season which had been developed, parameterized and extensively (and successfully) tested for one common European wader species (Stillman *et al*. 2000, 2001, 2003). The other, the *multi-site goose model*, was a multi-site, Europe-wide model which had been parameterized and tested, in a preliminary fashion, for one common wildfowl species (Pettifor *et al*. 2000). The aim of the project was to build, test and define the utility of the models for a much wider range of species in order to rapidly provide, at whatever geographic scale required, bird population predictions for a range of policy options. Both models were individual-based, in the sense that they tracked the location, foraging decisions and ultimate fate of each individual within the population, and predicted population level responses to environmental change (e.g. mortality rate) from the behaviour and fates of individuals (e.g. the proportion of individuals which die).

1.4 Original project objectives

The overall scientific and technological objectives of the project, as described in the original documentation for the project, were

- To adapt, simplify and parameterize two existing individual-based population models, the single-site wader model and multi-site goose model, so that they could be applied rapidly whenever policy decisions are required and at any geographic scale. The single-site wader model had been extensively tested for one common wader species. The multi-site goose model had been parameterized and tested, in a preliminary fashion, for one common wildfowl species.

- To provide policy guidelines for occasions when the models cannot be applied to the particular case because of shortage of time, resources or expertise.

Achieving these objectives required five detailed scientific objectives.

1) To parameterize the single-site (no emigration) model for the common European wader species through a combination of literature search and new fieldwork on key function parameters.

2) To test the utility and to maximize the speed with which the simplified single-site model could be applied to solve policy dilemmas in a particular system by parameterising the model for three exemplary systems in Spain, France and England which, between them, are subject to diverse activity (salt production, fish-farming, shellfishing, bait-digging, hunting, cycling, disturbance, shore-level rise, habitat loss). The aim was to demonstrate that population predictions for a wide range of policy options are obtainable within an environmental impact investigation of typical duration (e.g. two to three years).

3) To parameterize the multi-site, year-round model for one exemplary herbivorous wildfowl species, the brent goose, which is currently the focus of much debate as to how best to limit its conflict with various human activities, including agriculture, while protecting its most important sites.

4) To explore how predictions are affected by the assumption in single-site models that hard-pressed, or ‘stressed’, birds do not emigrate to another site (e.g. estuary) in search of better feeding conditions. This will allow a judgement to be made as to the circumstances in which the models provided for policy-makers should be multi-site or single-site.

5) To explore how population predictions are affected by the rate-maximizing assumption that is made in the present models, when state-dependent decisions may be more biologically realistic.

The project’s objectives were achieved through the eight Work packages.

WP1 *Simplified single-site wader model*. The objective of this Work package was to collect new field data on the rate at which wading birds consume food at different food densities, and to adapt the single-site wader model to use these data during simulations.

WP2 *Modelling the Spanish study site*. The objective of this Work package was to parameterise and test the single-site wader model for the Bahia de Cadiz, Spain.

WP3 *Modelling the French study site*. The objective of this work package was to parameterise and test the single-site wader model for the Baie de Somme, France.

WP4 *Modelling the UK study site*. The objective of this work package was to parameterise and test the single-site wader model for the Exe estuary, UK.

WP5 *Multi-site model for wildfowl*. The objective of this work package was to parameterise and test the multi-site goose model for brent geese in Europe.

WP6 *Comparison of single-site and multi-site models*. The objective of this work package was to compare single-site and multi-site models for two wading bird species.

WP7 *Comparison of state-dependent and rate-maximising models*. The objective of this work package was to determine how the decision rules birds use to select prey (either state-dependent or rate-maximising) affect the predictions of the single-site wader model in two sites.

WP8 *Model evaluation, delivery and utility*. The objective of this work package was to develop a general framework for the application of individual-based models or their predictions to European Coastal issues.

1.5 Addition to the project's objectives

One of the two main scientific and technological objectives of the project was to derive predictions from two existing models, the single-site wader model and the multi-site goose model. These models existed before the project and so only minor modifications were required to enable the models to be applied to each of the systems to be addressed in the project. During the course of the project it became clear that, even though one model was based on wader biology and the other on goose biology, they in fact shared many characteristics (e.g. the decision rules birds used to decide which food and patches to feed on). Realising that the models were more similar than appreciated at the start of the project, it was decided that a more profitable way of progressing would be to develop a new model capable of making predictions for both waders and geese, at either the single or multi-site scale. The existing models were also primarily concerned with mortality caused by starvation, where a more flexible approach would be to incorporate any possible source of mortality (e.g. hunting, predation). It was therefore decided, even though it meant a substantial addition to the project's objectives, that a new model would be developed. Figure 1.1 highlights how the two models available at the start of the project have now been superseded by a new more general and flexible model. The new model has been called MORPH to indicate that it can take on many forms and be applied to a much wider range of systems and issues than could either of the initial models. The new model is based on the same principles as the existing models and is also individual-based. It builds on the strengths of the existing models, and adds improvements where the previous models were limited.

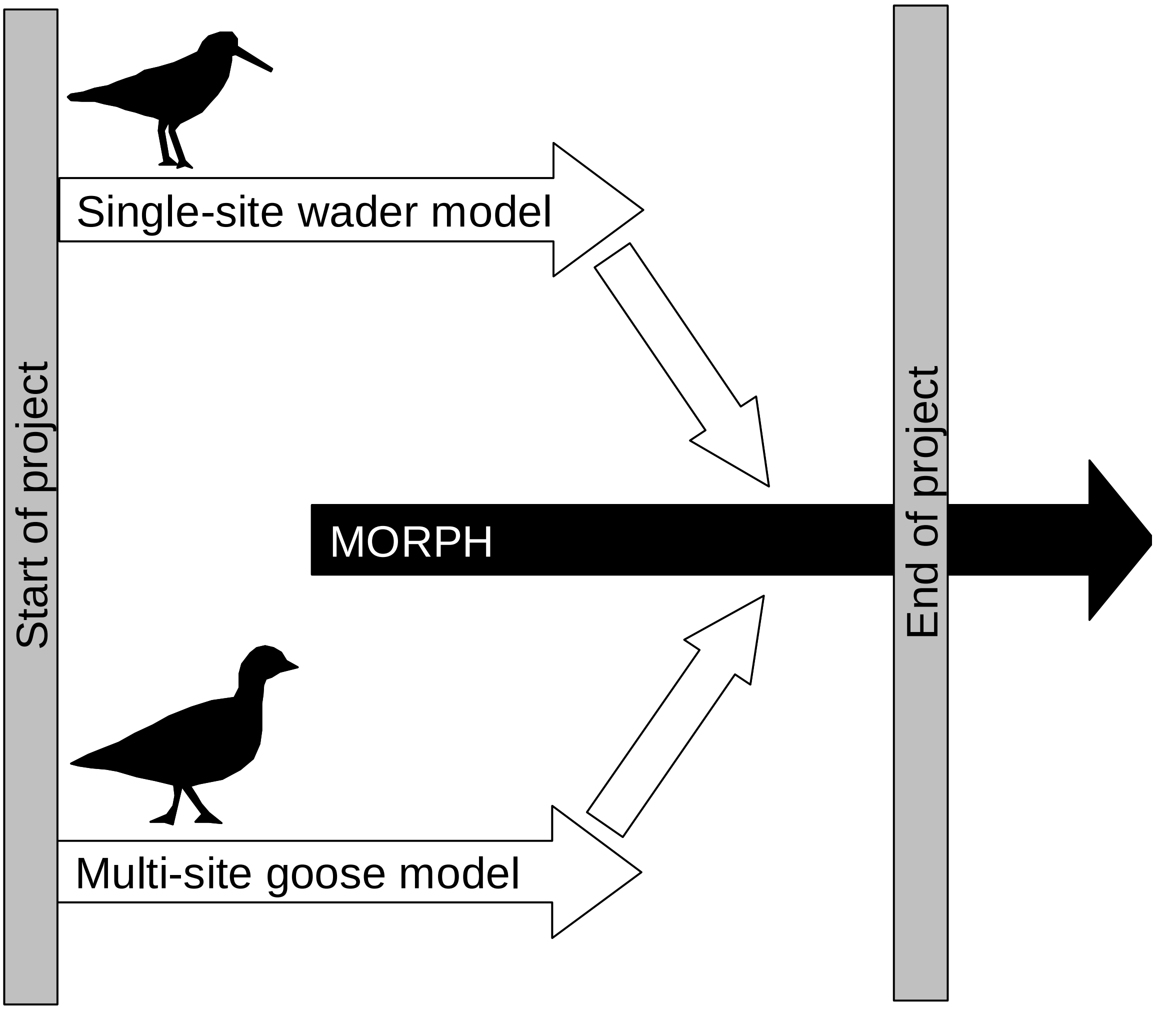

Figure 1.1 Model development strategy during the project. The single-site wader model and multi-site goose model existed at the start of the project. The original project objective was to derive predictions from these two models. During the project, the modelling strategy was improved and a single model, MORPH, was developed that can make predictions for waders or geese at single- or multi-site scales. This model will be used for all models developed during the project.

1.6 Structure of the report

This section describes the structure of the report and how each of the project's objectives and work packages relate to the chapters of the report (Table 1.1). Chapter 2 describes the new individual-based model developed during the project. It addresses objective OB1 and work package WP1. Chapters 3 and 4 describe new work conducted to understand the underlying biology of waders, later used to parameterise the wader models. Chapter 3 describes new research to provide a general mathematical description of the functional response of waders (i.e. the relationship between the rate at which waders consume food and the amount of food available). This general relationship is used to predict the rate at which birds consume food in each of the wader models. This chapter addresses objective OB1 and work package WP1. Chapter 4 describes new research to understand the decision rules waders use when faced with a range of different size classes of food. It investigates the possible trade-offs birds face between consuming large food, which yields a large reward in terms of energy, but may have more risks (e.g. more parasites) than small food items. This chapter addresses objective OB5 and work package WP7. Chapters 5 to 10 present the models developed during the project. They each address specific objectives and work packages, but additionally all address work package WP8 by showing how the general modelling framework developed during the project can be applied to a wide range of European coastal issues. Chapter 5 describes a simple model which is used to determine the consequences of the different decision rules identified in Chapter 4 for the survival rates of a wading bird. This chapter addresses objective OB5 and work package WP7. Chapters 6, 7 and 8 describe single-site wader models developed for sites in Spain, France and the UK respectively. These chapters address objectives OB2 and OB5, and work packages WP2, WP3 and WP4. Chapters 9 and 10 describe the multi-site wader and goose models respectively. The multi-site wader model is developed in a general way to explore how predictions are affected by the assumption in single-site models that hard-pressed, or 'stressed', birds do not emigrate to another site in search of better feeding conditions. The multi-site goose model is parameterised using detailed information on the biology on brent geese and their food supplies. These chapters address objectives OB3 and OB4, and work packages WP5 and WP6. Chapter 11 summaries the main conclusions of the project. This chapter addresses work package 8 by summarising how the modelling framework developed during the project can be applied to a wide range of European coastal issues. The Technological Implementation Plan (TIP) is contained in the Appendix.

Table 1.1 The relationship between the project’s objectives and work packages and the chapters in this report. The project’s Technological Implementation Plan (TIP) is contained in the Appendix

	Objectives					Work packages							
Chapter	OB1	OB2	OB3	OB4	OB5	WP1	WP2	WP3	WP4	WP5	WP6	WP7	WP8
2	*					*							
3	*					*							
4					*							*	
5					*							*	*
6		*					*						*
7		*						*					*
8		*							*				*
9				*							*		*
10			*							*			*
11													*

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2 THE MODEL

Richard A. Stillman

2.1 Introduction

This chapter describes the individual-based model, MORPH, used to make predictions for each of the systems included in the project. This model has been developed during the project, and replaces the single-site wader and multi-site goose models, which existed at the start of the project, and which were originally planned to be used during the project. These models have been tested on a wide range of sites and used to predict the consequences of several environmental factors, including disturbance (West *et al.* 2002), shellfishing (Stillman *et* al. 2000, 2001, 2003; West *et al.* 2003; Caldow *et al.* 2004; Goss-Custard *et al.* 2004), habitat loss (Durell *et al.* 2005) and site quality (West *et al.* 2005). The development of the new model is an addition to the original project objectives. The new model is based on the same fundamental principle as the previous models – that individuals behave in ways that maximise their own chances of survival and reproduction. It also tracks the location, behaviour and ultimate fate of each individual in the population, and incorporates variation in the foraging abilities of different individuals. However, the new model is much more flexible than either of the original models, and hence can be used to address a much wider range of environmental issues both within the project and beyond. For example, the previous wader and goose models contained wader- or goose-specific assumptions, and assumptions applicable to coastal areas but not others (e.g. the tidal cycle). The new model removes these limitations and contains virtually no species or system-specific assumptions. However, once parameterised, it can still be applied to specific species or systems.

The purpose of the chapter is to describe the general aspects of the model, applicable to any system. System-specific details are described in later chapters. The model is described using a standard protocol, designed by Grimm & Railsback (2005). The general protocol ensures that individual-based models are fully described in a way that is clearly understandable and would enable the models to be recreated by others. Clear communication of individual-based models has often been a problem in the past, which has limited the widespread use of some models (Grimm & Railsback 2005). The protocol has been used to avoid this problem. Model description is divided into the following sections: Purpose, Structure, Processes, Concepts, Initialisation, Input and Submodels. A general overview of the main elements of the model is initially presented (Purpose, Structure, Processes and Concepts), followed by a more detailed mathematical description (Initialisation, Input and Submodels). A number of technical modelling terms are used in this description, as these are required to describe the model unambiguously. However, each of these terms is defined when first used.

2.2 Purpose

The overall purpose of the model is to predict how environmental change (e.g. habitat loss, changes in human disturbance, climate change, mitigation measures in compensation for developments and changes in population size itself) affects the survival rate and body condition in animal populations. The model does this by predicting how individual animals respond to environmental change by altering their feeding location, consuming different food or adjusting the amount of time spent feeding. The central assumption of the model is that animals behave in ways that maximise their chances of survival. The model does not itself predict reproductive rate but its survival and body condition predictions can be input into other models that do make this prediction.

The model has been designed to be very flexible (hence the name MORPH), so that it can produce both general predictions (when parameterised in a very simple way), and predictions for specific systems (when parameterised using detailed system-specific data). The model can read in equations as parameters, and so can potentially represent a very wide ranges of species or systems.

2.3 Structure

The model itself contains only very general aspects of behaviour and ecology, applicable to a wide range of systems. The basic assumptions of the model are as follows.

- Time progresses in discrete, fixed duration, time steps.
- Space is divided into a number of uniform habitat patches, with fixed location and area.
- Habitat patches contain a number of resources which can be consumed by foragers.
- Resources contain components which are assimilated into foragers when resources are consumed.
- Foragers remain at the same location during a time step, either on a patch or travelling between patches, but move between time steps.
- Foragers alter their location and the food they consume in order to maximise their chances of survival.

The model defines the following five entities (*objects within the model*).

- *Global environment* - State variables (*values used to describe the global environment*) which apply throughout the modelled system.
- *Patches* - Locations with local, patch variables (*values used to describe patches*), containing resources and foragers. Foragers may experience travel costs when moving between patches.
- *Resources* - The food consumed by foragers. Foragers can simultaneously consume one or more resources from a patch. Such collections of resources are termed *diets*.
- *Components* - Elements within resources which foragers assimilate into their bodies.
- *Foragers* - Animals which move within the system attempting to maximise their survival and body condition. One or more *forager types / species* may be present within the modelled system.

Table 2.1 lists the state variables (*values used to describe a model entity*) of each entity. The global state variables are the major driving variables in the model system. Patch variables may depend on these global variables. Patches contain one or more resources, which in turn contain one or more components. Foragers have a range of possible diets, which are simply a collection of resources. Foragers consume diets, from which they assimilate components. Components can either have positive, neutral or negative effects on foragers. Foragers are not forced to consume diets, but instead may occupy a patch and not feed.

Table 2.1 State variables used to describe model entities.

Entity	**State variable**	**State variable description**
Global	• Global variables	Zero or more environmental variables which apply throughout the modelled system
Patches	• Location	Central coordinates
	• Size	Surface area / volume of patch
	• Patch variables	Zero of more patch-specific environmental variables
Resources	• Density on patch	Density of each resource on each patch
Components	• Density in resource	Density of each component within each resource on each patch
Foragers	• Forager type / species	Forager type / species to which forager belongs
	• Forager constants	Zero or more forager-specific constants which remain constant throughout a simulations
	• Forager variables	Zero or more forager-specific variables which can change throughout a simulation
	• Location	Coordinates of foragers location
	• Patch	Patch number being occupied by forager during current time step
	• Diet	Diet number being consumed by forager during current time step (zero if no diet is being consumed)
	• Proportion of time moving	Proportion of time moving between patches during current time step
	• Proportion of time feeding	Proportion of time feeding during current time step
	• Diet consumption rate	Rate at which diet is being consumed during current time step and averaged over previous and predicted for future time steps
	• Component consumption rate	Rate at which a component is being consumed during current time step and averaged over previous and predicted for future time steps
	• Component assimilation rate	Rate at which a component is assimilated into the body during current time step and averaged over previous and predicted for future time steps
	• Component metabolic rate	Rate at which a component is metabolised / excreted from the body during current time step and averaged over previous and predicted for future time steps
	• Component reserve size	Amount of a component within the body's reserves during current time step

2.4 Processes

The model defines the following processes (*the transfer of information or model entities between (other) model entities*).

- *Change in resource density*. Changes in the density of a resource on a patch caused by consumption by the foragers and / or other factors.

- *Change in component density*. Changes in the density of a component in a resource.

- *Forager immigration*. The movement of foragers into the system.

- *Forager decision making*. The optimal patch and diet selection of foragers and decisions to emigrate from the system.

- *Forager emigration*. The movement of foragers away from the system.

- *Forager movement between patches*. Movement of foragers between patches. Movement may have associated costs and may take more than one time step.

- *Forager diet consumption*. The transfer of resource components into foragers when diets are consumed.

- *Forager physiology*. Change in the size of a forager's component reserve due to the balance of consumption and metabolism.

- *Forager mortality*. Death of foragers.

2.5 Concepts

The following concepts (*basic characteristics common to all individual-based models*) are represented in the model.

2.5.1 EMERGENCE

The following phenomena emerge from the interaction between individual forager traits and global and patch variables, resource and component densities, and forager constants and variables.

- *Resource depletion*. The amount of each resource consumed by foragers from each patch during each time step.

- *Forager distribution and diet selection*. The location of each forager and its diet during each time step.

- *Proportion of time foragers spend feeding*. Proportion of each time step each forager spends feeding.

- *Forager component reserve size*. The amount of each component within each forager's reserves during each time step.

- *Forager mortality and emigration*. The number of foragers remaining in the system after a given number of time steps.

2.5.2 ADAPTATION

Foragers adaptive traits (*behaviour through which foragers maximise their fitness (i.e. survival and reproduction)*) are their location and diet selection. During each time step, foragers select the patch / diet combination which maximises their perceived fitness, or emigrate from the entire system if this has a higher perceived fitness than any patch / diet combination.

2.5.3 FITNESS

A number of *fitness components* are assumed to affect the survival of animals and hence their overall fitness. Fitness components may have negative or positive affects on survival. Each fitness component has associated submodels (see below) to calculate the true probability of surviving the fitness component during a time step. The combined true survival probability for all fitness components is the product of the survival probabilities associated with each fitness component (see below). Each fitness component has a *fitness measure*, calculated using a submodel (see below), which animals use to assess the fitness consequences of different decisions. The combined fitness measure is the product of the fitness measures associated with each fitness component (see below). The forager selects the patch and diet combination (including no diet) which maximises its combined fitness measure, or emigrates from the system if this has a greater fitness measure than any of the possible patch and diet combinations. Once the forager has selected a patch and diet, the consequences of this decision are determined by true probability of survival. Both true survival probability and fitness measure submodels can depend on any combination of global, patch, resource, component or forager state variables.

2.5.4 PREDICTION

Foragers remember their foraging success during a given number of previous time steps. This memory is used to calculate average state variables over previous time steps (see Table 2.1 for a list of these variables). Foragers can also predict their future foraging success, over a given number of time steps, taking into account the time taken to move from their current location to a target patch. In making these predictions, the model assumes that foragers do not know the future values of any state variables, resource or component densities or the location of other animals. Instead, state variables, resource and component densities and the location of other foragers are all assumed to remain the same as in the current time step.

2.5.5 INTERACTION

Foragers interact within patches through the consumption of a shared resource (depletion competition). The number and / or density of other foragers within a patch can also effect any of a forager’s state variables, and fitness measures and true survival probabilities. These effects can be either positive or negative, depending on the submodels used. Increased competitor numbers or density can either increase consumption rate (facilitation) or decrease consumption rate (interference competition), again depending on the submodels used. Foragers can only interact within patches. The actual mechanisms of interactions within patches are not incorporated explicitly.

2.5.6 SENSING

The amount of knowledge foragers have can be varied. This can range from perfect knowledge of the complete system during the current time step, through complete knowledge of local patches, to no knowledge at all. Similarly, the amount of knowledge a forager has of its own state, both during the current time step and previous and future time steps, can be varied. Foragers base their decisions on the fitness measures associated with different patches and diets (or no diet). The fitness measure may or may not be related to the true probability. Foragers will tend to avoid patches and diets with low fitness measures. Depending on the relationship between the true survival probabilities and fitness measures, this can mean that foragers avoid safe patches and diets (i.e. high true survival probability) because these are perceived as dangerous (i.e. low fitness measure), or select dangerous patches or diets because these are perceived as safe. The model does not explicitly represent any sensing mechanisms.

2.5.7 STOCHASTICITY

The amount of stochasticity (*random variation in model predictions*) can be varied. Any state variables, except for patch size and location, and forager type / species can be stochastic. The probability of a forager (or the individuals within the forager (see below)) dying during a time step is a stochastic event unless the probability is zero or one.

2.5.8 COLLECTIVES

Collectives (*groups or aggregations of foragers*) are included in the model. These are represented by the number and / or density of foragers on each patch, and arise from the patch and diet selection of foragers. Collectives are not represented as social groups, instead each individual behaves independently albeit with its behaviour influenced the number and / or density of competitors on different patches. Super-individuals can be incorporated, with each forager (super-individual) representing more than one individual. The number of individuals within a forager is set at the start of a simulation, but can decrease through time as some individuals within the forager die. In contrast, all individuals within a forager simultaneous immigrate to or emigrate from the system.

2.5.9 SCHEDULING

Time is represented using discrete time steps which are of constant duration. Figure 2.1 shows the sequence of events during each time step. Global events are processed first, followed by patch events and then forager events. Finally, results are displayed and saved. The order in which foragers are processed can either be random or based on the value of a specified forager constant. Once the order of foragers has been determined, foragers are updated one at a time during each time step (*asynchronous scheduling*). This means that all forager events (immigration, patch and diet selection, movement and emigration, diet consumption, resource depletion and forager mortality) are applied to one forager before the next forager is processed.

2.5.10 OBSERVATION

The results used to test the model depend on the particular system for which it is parameterised. All state variables can be displayed and saved during each time step.

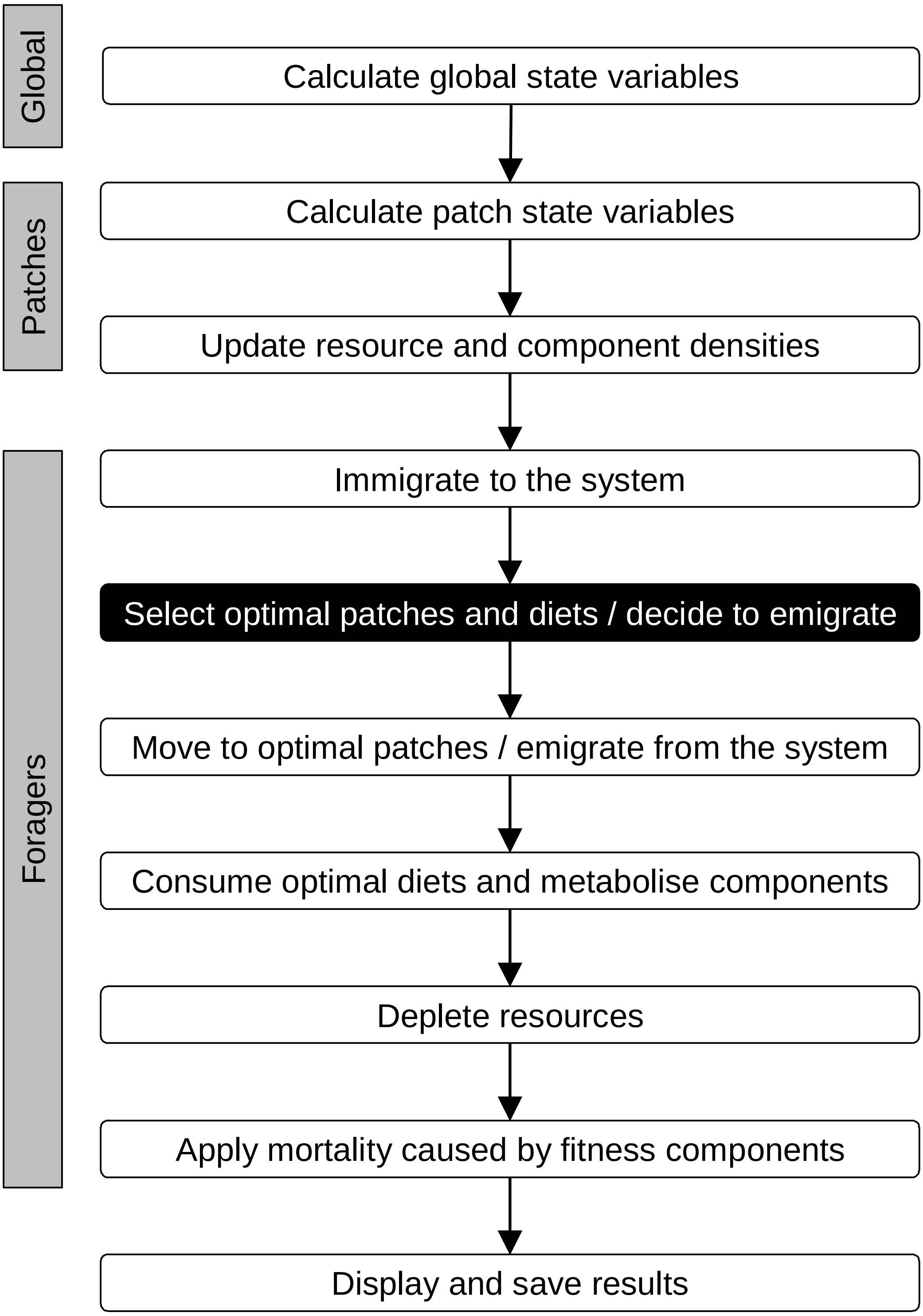

Figure 2.1 The sequence of events during each time step. The grey bars show the entity in which each event occurs. The black box indicates where foragers adaptive traits are executed to determine which patch and diet to feed on or whether to emigrate from the system. Forager events are either processed asynchronously. Foragers are only processed once they immigrate to the system, and are no longer processed after they emigrate or all their individuals have died. Patch and diet selection does not occur while foragers are moving. Components are metabolised while a forager is moving, unless moving is instantaneous.

2.6 Initialisation

The initial values of state variables are either read from a parameter file, created using random numbers, or calculated from state variables defined earlier in the parameter file. The sequence of random numbers is itself randomised at the start of each simulation so that replicate simulations using the same set of parameters will produce slightly different predictions. All global and patch variables are initialised at the start of the simulation. Forager state variables are initialised once the forager has immigrated into the system, and so foragers immigrating at different times may have different initial state variables.

2.7 Input

The particular data used to parameterise the model will depend on the particular system to which it is applied. However, Table 2.2 lists the basic set of parameters, which would be required for any system. Parameters can either be single values, values for each time step read in from a file, or an equation (submodel) to calculate values during each time step.

Table 2.2 Basic set of parameter values / submodels required by the model.

Entity	**Parameter**
Global environment	• Number and names of global variables • Value / submodel for each global variable
Patches	• Number and names of patches • Size of each patch • Location of each patch • Value / submodel for each patch variable on each patch
Resources	• Number and names of resources • Initial density of each resource on each patch • Submodel for change in density (excluding consumption by foragers) of each resource on each patch
Components	• Number and names of components • Value / submodel for density of each component in each resource on each patch
Diets	• Number and names of diets • Number and names of resources in each diet
Foragers	• Number and names of forager types / species, and type / species of each forager • Number and names of forager constants • Value of each forager constant for each forager • Number and names of forager variables • Value / submodel for each forager variable • Value / submodel for time to move between patches • Number and names of diets consumed by forager type / species • Rule to determine whether patches can be located • Rule to determine whether fitness measure can be assessed on a patch • Value / submodel for diet consumption rate • Value / submodel for maximum diet consumption rate • Value / submodel for assimilation efficiency of each component in each diet • Value / submodel for rate of metabolising each component • Value / submodel for target reserve size for each component • Number of fitness components • Value / submodel for fitness measure for each fitness component • Value / submodel for true survival probability for each fitness component • Value / submodel for expected fitness measure on patches on which fitness measure cannot be assessed • Value / submodel for expected fitness measure of emigrating

2.8 Submodels

Many of the model's submodels will be read in as equations from the parameter files. In these cases the particular submodels will depend on the specific system to which the model is being applied. These are termed parameter submodels in the follow sections. However, a number of submodels are incorporated into the model itself. The following sections describe the submodels used to represent each of the models processes.

2.8.1 CHANGE IN RESOURCE DENSITY

Resource densities change on patches due to (i) *non-depletion change* and (ii) *depletion* when foragers consume diets on a patch.

Non-depletion change is calculated at the start of each time step, exception the first time step, using a parameter submodel which determines how resource density is updated at the start of each time step.

$$R = f\left(p_1, p_2 .. p_n\right) R_{previous} \tag{2.1}$$

where R = new resource density at start of current time step, $R_{previous}$ = old resource density at end of previous time step, $f\left(p_1, p_2 .. p_n\right)$ = a submodel containing n parameters. The submodel's parameters may be any number of global or patch state variables.

After the resource density has been calculated at the start of each time step, the density of each diet is updated. Diets are simply a collection of resources, and so the density of a diet is simply the sum of all of the resources it contains.

$$R_{diet} = \sum_{r=1}^{N} R_r \tag{2.2}$$

where R_{diet} = diet resource density, r = resource number, N = number of resources in diet and R_r = density of resource r.

Depletion is incorporated by reducing the amount of a resource in a patch by the amount consumed by foragers. Foragers consume diets, rather than separate resources and so the model needs to calculate the amount of each resource consumed in the diet. The model assumes that resources are consumed in proportion to their relative density within a diet. The amount of a resource is consumed within a diet is therefore given by.

$$E = E_{diet} \frac{R}{R_{diet}} \tag{2.3}$$

where E = amount of resource consumed (eaten), E_{diet} = amount of diet consumed, R = density of resource and R_{diet} = density of diet. The density of the resource on the patch is updated by assuming that depletion occurs uniformly throughout the patch.

$$R = R_{previous} - \frac{E}{A} \tag{2.4}$$

where R = new density of resource, $R_{previous}$ = previous density of resource before depletion, A = size (area / volume) of patch and E = amount of resource eaten.

Depletion either occurs continually during a time step (as foragers are processed asynchronously). Diet densities are updated every time depletion occurs.

2.8.2 CHANGE IN COMPONENT DENSITY

Component density within each resource on each patch is either read in as a single value which applies throughout the simulation or read in as a parameter submodel to calculate values during each time step. Component density submodels can depend on global or patch state variables.

The density of a component within a diet is a weighted mean of the component density within each of the resources contained in the diet.

$$C_{diet} = \frac{\sum_{r=1}^{N} C_r R_r}{\sum_{r=1}^{N} R_r} \tag{2.5}$$

where C_{diet} = density of component in diet, r = resource number, N = number of resources in diet, C_r = density of component in resource r and R_r = density of resource r.

2.8.3 FORAGER IMMIGRATION

The probability of immigrating to the system for each forager type / species is read in as a single value which applies throughout the simulation or read in as a parameter submodel to calculate values during each time step.

2.8.4 FORAGER DECISION MAKING

Foragers in the model make three types of decisions.

- Patch choice
- Diet choice
- Emigration from the system

The model uses the same submodel to determine how foragers make these decisions. The model's basic assumption is that foragers behave in order to maximise their fitness, which in turn is assumed to be measured as the probability of survival. Reproductive components of fitness are not considered directly as these are outside of the scope of the model. Model foragers test the fitness consequences of moving to different patches, consuming different diets, consuming no diet or emigrating from the system. The list of possible diets depends on the diets consumed by the forager type / species to which the forager belongs. Foragers select the combination which maximises their combined fitness measure.

Foragers do not necessarily have perfect knowledge of their survival probability when moving to different patches or consuming different diets. This uncertainty operates at two levels.

- Ability to assess fitness measures
- Accuracy of fitness measures (i.e. their relation to the true survival probability)

Ability to assess fitness measures. Figure 2.2 shows how the ability to assess the fitness measures associated with different decisions is incorporated. Foragers are assumed to be able to assess fitness measures associated with consuming different diets on their current patch. Other patches fall into one of three different categories. (1) Foragers may know the location of a different patch and be able to assess fitness measures on the patch. They can assess the survival consequences of moving to this patch consuming any diet, and know the values of all of the patch's state variables during the current time step. (2) Foragers may know the location of a patch, but not be able to assess the fitness measures associated with different diets. They cannot assess the survival consequences of consuming different diets, and are unaware of any of the patches state variables. However, they do have an expected fitness measure on this patch ($F_{expected}$), which is used to compare this patch with others. (3) Patches may be of unknown location, and so cannot be considered as potential locations to move to. Emigration from the system also has an expected fitness measure, which is used to determine whether emigration is the decision which maximises survival ($F_{emigrate}$).

Accuracy of perceived survival. For patches on which survival consequences can be detected, the following process is used to assess fitness measures, which may be unrelated to the true survival probability. Survival is assumed to be affected by a number of fitness components. Each fitness component has an associated submodel to predict the fitness measure given the foragers state (including average state over previous time steps) and any combination of global or patch state variables. The combined fitness measure is found from the product of the fitness measures associated with each fitness component.

$$F_{assessed} = \prod_{c=1}^{N} f_c \tag{2.6}$$

where $F_{assessed}$ = combined fitness measure for all fitness components; c = fitness component number, N = number of fitness components, f_c = fitness measure for fitness component c. $F_{assessed}$ is calculated for all possible combinations of patches and diets, including the option to occupy a patch but not feed. The forager selects the patch and diet combination which maximises either $F_{assessed}$ or $F_{expected}$ (depending on whether fitness can be assessed on the patch), or emigrates if $F_{emigrate}$ exceeds any of these values. In the event that more than one decision maximises survival, the forager takes a random option, but weighed by patch area, or remains in the system if $F_{emigrate}$ equals the probability associated with remaining in the system.

Once the forager has selected a patch and diet, it is allowed to move and consume its selected diet (see below). The consequences of this decision are then determined by true probability of survival.

$$S_{true} = \prod_{c=1}^{N} s_c \tag{2.7}$$

where S_{true} = true probability of surviving all fitness measures; c = fitness component number, N = number of fitness components, s_c = true probability of surviving fitness component c. The assessed fitness measure may or may not be related to the true probability. Foragers will tend to avoid patches and diets with low fitness measures. Depending on the relationship between these and the true survival probabilities, this can mean that foragers avoid safe patches and diets (i.e. high true survival probability) because these are assessed as dangerous (i.e. low fitness measures), or select dangerous patches or diets because these are perceived as safe.

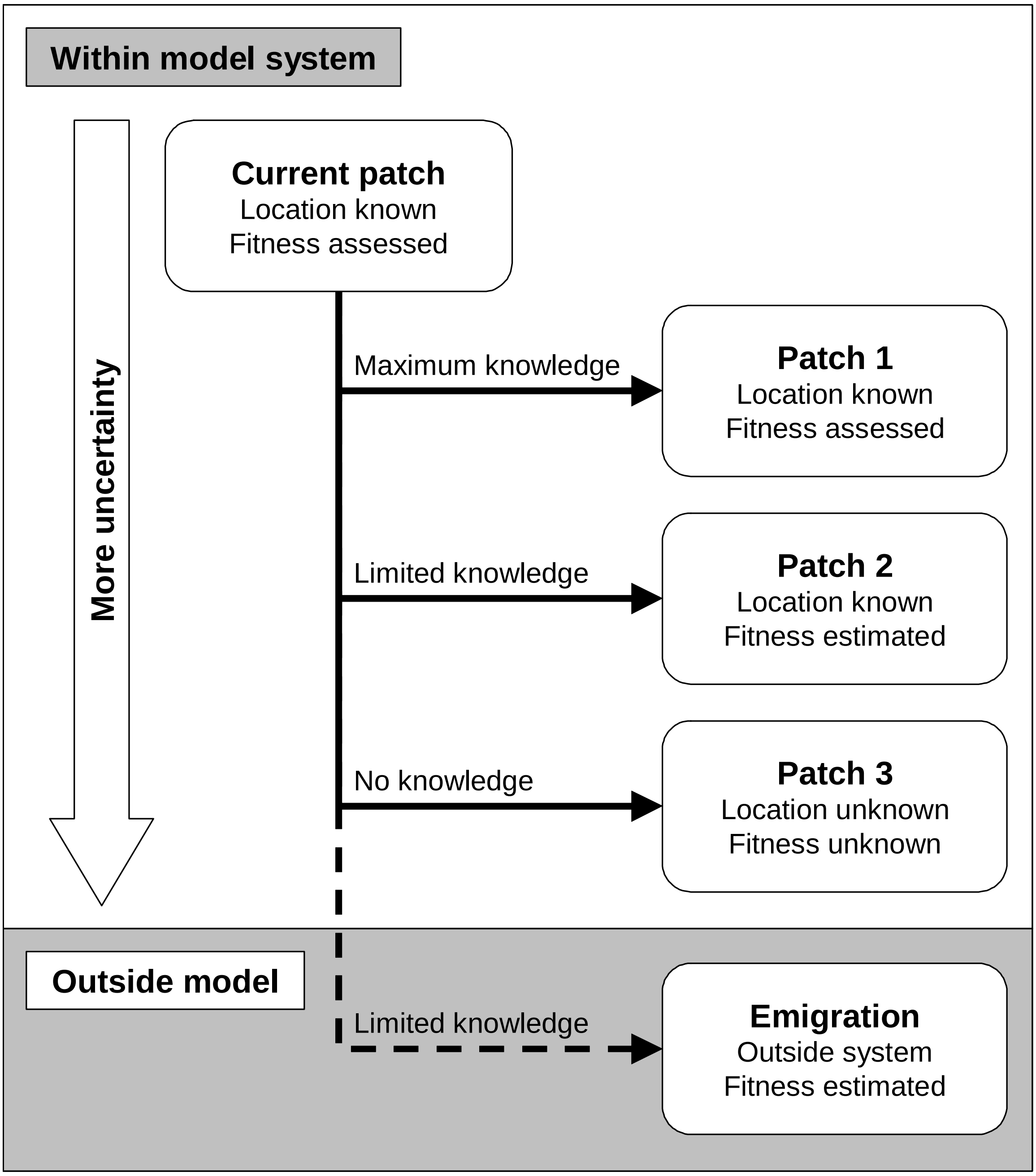

Figure 2.2 How uncertainty is incorporated into the model. Foragers are assumed to be able to assess the fitness measure associated with consuming different diets on their current patch. Other patches fall into one of three different categories. (1) Foragers may know the location of a different patch and be able to assess fitness measures on the patch (e.g. Patch 1). (2) Foragers may know the location of a patch, but not be able to assess the fitness measures associated with different diets (e.g. Patch 2). In this case the estimated fitness measure on the patch is used. (3) Patches may be of unknown location (e.g. Patch 3). Emigration from the system also has an expected fitness measure. Although, the figure shows increasing uncertainty associated with increasing distance between patches, this does not have to be the case.

2.8.5 FORAGER EMIGRATION AND MOVEMENT BETWEEN PATCHES

Foragers move when they emigrate from the system or change patches. Emigration is assumed to be instantaneous, with foragers leaving the system during the same time step in which they decide to emigrate. Movement between patches may or may not be instantaneous. When movement is instantaneous, foragers move to a target patch as soon as they decide to move and then spend the whole of a time step on the target patch. Otherwise, movement may take one or more time steps. If movement takes one or more time steps, foragers are assumed to reach a patch at the start of a time step. This means that they are able to respond to the local conditions on the patch (i.e. decide which diet to select or move to another patch), as these may not have been fully known when the forager initially decided to move to the patch. The time to travel between patches is calculated from a parameter submodel.

$$T_{move} = f\left(p_1, p_2 .. p_n\right) \tag{2.8}$$

where T_{move} = time to move between patches and $f\left(p_1, p_2 .. p_n\right)$ = a submodel containing n parameters. The submodel can depend on any global variables, the relative location of patches and any forager constants or variables.

For simplicity, the movement submodel assumes that movement always takes a whole number of time steps. The submodel checks that the relative values of movement time and time step length always result in movement time exactly equalling a whole number of time steps.

$$N_{timestep} = \frac{T_{move}}{T_{timestep}} \tag{2.9}$$

where $N_{timestep}$ = movement time in time steps, T_{move} = time to move between patches and $t_{timestep}$ = duration of one time step.

While moving, forager's metabolise their component stores at a rate determined by the moving metabolic rate. The change in component reserve size while moving is.

$$C_{final} = C_{initial} - N_{timestep} T_{timestep} M_{moving} \tag{2.10}$$

where C_{final} = final component reserve size after moving, $C_{initial}$ = initial component reserve size and M_{moving} = rate of metabolising / excreting component while moving.

For simplicity, it is assumed that foragers cannot make any decisions while moving between patches, but can die while moving.

2.8.6 FORAGER DIET CONSUMPTION AND PHYSIOLOGY

A submodel parameter is read in to calculate the diet consumption rate of foragers of each forager type / species. The efficiency of assimilating each component from the resources in the diet to the body (i.e. the proportion of the component in the diet that is transferred to the body) is also read in as a submodel parameter. Both submodels can depend on any forager constant or variable, patch state variable or global variable. The rate of assimilating a component is calculated from.

$$I_{assim} = aC_{diet}I_{diet} \tag{2.11}$$

where I_{assim} = rate of assimilating component, a = efficiency of assimilating the component, C_{diet} = density of component in the diet and I_{diet} = rate of consuming the diet.

The amount of the component assimilated during a time step also depends on the proportion of time spent feeding during the time step. The proportion of time spent feeding can be limited in two ways.

- Regulation of diet consumption rate
- Regulation of component reserve size

Regulation of diet consumption rate. A submodel is used to calculate the maximum diet consumption rate ($I_{\max}$) during a time step. The maximum proportion of time that can be spent feeding ($P_{\max}$) is calculated from.

$$\begin{aligned} P_{\max} &= \frac{I_{\max}}{I_{diet}} \qquad \text{if } I_{diet} > I_{max} \\ P_{\max} &= 1 \qquad \text{if } I_{diet} \le I_{max} \end{aligned} \tag{2.12}$$

Regulation of component reserve size. If the forager were to feed for P_{max} of the time step, its component reserve size at the end of the time step would be.

$$C_{final} = C_{initial} + T_{timestep}\left(P_{\max}I_{assim} - P_{\max}M_{feeding} - (1 - P_{\max})M_{resting}\right) \tag{2.13}$$

where C_{final} = final component reserve size at end of time step, $C_{initial}$ = initial component reserve size at start of time step, $M_{feeding}$ = rate of metabolising / excreting component while feeding and $M_{resting}$ = rate of metabolising / excreting component while resting. The model uses a parameter submodel to calculate the target component reserve size (C_{target}) during any time step. The required proportion of time needed to exactly match this target, or approach it as closely as possible is found by setting C_{final} to C_{target}, and P_{max} to P_{target} and rearranging the previous equation.

$$\begin{aligned} P_{target} &= \frac{C_{target} - C_{initial} + T_{timestep}M_{resting}}{T_{timestep}\left(I_{assim} - M_{feeding} + M_{resting}\right)} \quad \text{if } \frac{C_{target} - C_{initial} + T_{timestep}M_{resting}}{T_{timestep}\left(I_{assim} - M_{feeding} + M_{resting}\right)} \le 1 \\ P_{target} &= 1 \quad \text{if } \frac{C_{target} - C_{initial} + T_{timestep}M_{resting}}{T_{timestep}\left(I_{assim} - M_{feeding} + M_{resting}\right)} > 1 \end{aligned} \tag{2.14}$$

where P_{target} = proportion of time that forager needs to feed for to match its target or approach it as closely as possible.

The actual proportion of time spent feeding depends on the value of P_{max} and the values of P_{target} for each component in the diet. The model attempts to exceed or match the target reserve size for each component, with the constraint the proportion of time feeding cannot exceed P_{max}. It does this by comparing the maximum value of P_{target} with P_{max}.

$$P_{feed} = \max(P_{target}) \quad \text{if } \max(P_{target}) \leq P_{\max}$$
$$P_{feed} = P_{\max} \quad \text{if } \max(P_{target}) > P_{\max} \qquad (2.15)$$

where P_{feed} = proportion of time feeding during time step. The component store size at the end of the time step is then found from.

$$C_{final} = C_{initial} + T_{timestep}\left(P_{feed} I_{assim} - P_{feed} M_{feeding} - (1 - P_{feed}) M_{resting}\right) \qquad (2.16)$$

2.8.7 FORAGER MORTALITY

A submodel parameter is read to calculate the probability of surviving each fitness component based on a forager's state, and any combination of global or patch variables. A uniform random number generator is used to determine whether each of a forager's individuals is killed by any of the fitness components. In the event of two or more fitness components killing an individual, one is selected at random. When all the individuals in a forager are killed, the forager is removed from the simulation.

2.8.8 PREY INTAKE RATE OF WADERS

Each of the preceding submodels are used for all models developed in the project. This section describes the submodel used to calculate prey intake rate in the wader-specific models developed during the project. A different submodel is used to calculate the intake rate of geese.

Wader intake rate depends on the density of prey and competitors. Intake rate in the absence of competitors is initially calculated from the following equation.

$$IFIR = f\,\frac{IFIR_{\max} B}{B_{50} + B} \qquad (2.17)$$

where $IFIR$ = Interference-free intake rate (mg s^{-1}), f = foraging efficiency of focal individual, B = patch biomass density of prey within the size range consumed (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 of each individual within the population was drawn from a normal distribution. A literature review was used to estimate the values $IFIR_{max}$ and B_{50} (Chapter 3). $IFIR_{max}$ was related to shorebird body mass and prey mass by the following equation.

$$\log_e(IFIR_{\max}) = -2.802 + 0.245\log_e(M_{spec}) + 0.365\log_e(rM_{prey}) \qquad (2.18)$$

where M_{spec} = average body mass (g) of the shorebird species in September, M_{prey} = mean ash-free dry mass (mg) of prey within the size range consumed and r = ratio of size of prey consumed to size in patch. A literature review showed that birds select the larger-sized prey within the size range consumed, giving a value of r of 1.05. $IFIR_{max}$ was greater in larger birds and when larger prey were consumed. B_{50} was unrelated to either bird or prey mass, with a mean value of 0.761 g ash-free dry mass m^{-2}.

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

$$IR = IFIR\left(\frac{gD+1}{D_0+1}\right)^{-(m_{\max}-(m_{\max}-m_{\min})d)} \qquad \text{if } D \geq D_0 \tag{2.19}$$

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

where IR = intake rate (mg s^{-1}), D = conspecific competitor density in patch (ha^{-1}), D_o = conspecific competitor density above which interference reduces intake rate, g = aggregation factor, d = dominance of focal 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 = 0). D_o was set to 100 birds ha^{-1} for all systems in which interference was assumed to occur, as this is the approximate threshold in a number of systems in which interference occurs through either kleptoparasitism (Stillman et al. 1996, Triplet et al. 1999) or a reduction in prey availability due to prey avoidance behaviour (prey depression (e.g. Yates et al. 1999)). The aggregation factor accounts for the fact that birds will usually be aggregated in a patch, rather than being spread uniformly. The default aggregation factor was assumed to be 10, the value measured for cockle-feeding oystercatchers on the Burry Inlet, UK (West et al. 2003), but species-specific values were used when available. The values of m_{max} and m_{min} for each species were predicted from previous studies on a range of species, the foraging behaviour of individual species and the mobility and predator escape responses of different prey. Interference was assumed to be absent (m_{max} = 0, m_{min} = 0) in small prey (e.g. *Hydrobia*), which are consumed quickly, minimising interference through prey stealing (Stillman et al. 1997), and cannot rapidly escape as birds approach, eliminating interference through prey depression. Interference within species consuming mobile prey (e.g. Annelids and *Corophium*), which can often rapidly escape into the sediment as birds approach, was assumed to occur through prey depression. Interference in these systems was assumed to be independent of dominance (m_{max} = 0.48, m_{min} = 0.48) with the same strength as that observed between *Corophium*-feeding redshank (Yates et al. 1999), the only system in which the strength of interference through prey depression has been measured. For non-mobile, larger prey (e.g. *Cerastoderma* and *Macoma*), interference was assumed to occur through prey stealing and hence to depend on dominance, being absent for the most dominant birds (m_{max} = 0) and strongest for the least dominant. The strength of interference was assumed to depend on prey size and hence the time taken for a bird to consume a single prey item (handling time). For all species except *Cerastoderma*-feeding oystercatchers, relatively small prey are consumed, and handling time is short (< 10 s). The strength of interference in these systems (m_{max} = 0, m_{min} = 0.08) was that predicted for short handling times by an interference model (Stillman et al. 2002). The strength of interference between *Cerastoderma*-feeding oystercatchers (m_{max} = 0, m_{min} = 0.5) was that observed for low *Cerastoderma* densities in the Baie de Somme, France (Triplet et al. 1999).

2.9 Summary

This chapter describes the general features of the new individual-based model (MORPH) developed during the project. Extensions to the model used to model specific systems are described in later chapters. The original intension of the project was to derive predictions from two existing models, the single site wader model and the multi-site goose model. The new model is much more flexible than either of its predecessors and is capable of making predictions for both waders and geese, single and multi-sites. Its development is therefore a substantial addition to the original project objectives.

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3 UNDERLYING BIOLOGY: WADER FUNCTIONAL RESPONSE

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3.1 Summary

This chapter describes the work performed under work package 1 of the project. The aim of this work package was to determine whether a simple equation could be used to predict the relationship between food intake rate and food density (i.e. the functional response) for a wide range of wading bird species. A review of 30 functional responses of waders eating macro-invertebrates in the wild showed that intake rate varied independently of prey density over a wide range of prey densities and that the asymptote was usually reached at very low prey densities (<150/m2). A multivariate analysis of 468 additional 'spot' estimates of intake rates from 26 wader species of 11 genera identified ten variables, representing characteristics of the prey and wader, that accounted for 81% of the variance in the logarithm-transformed measurements of intake rate. A reduced set of four variables accounted for almost as much (77.3%), the variables being bird size, prey size, whether the bird was an oystercatcher *Haematopus ostralegus* eating mussels *Mytilus edulis* and whether it was breeding. A multivariate analysis of 23 estimates of the gradient suggested that they were more steep when prey were small but less steep when the birds were large, especially in oystercatchers. The resulting equation could be used to predict the gradient, but its predictive power has yet to be tested. This results of this work package are used to predict the intake rate of waders in each of the single-site wader models.

3.2 Introduction

This chapter describes the work performed under work package 1 of the project. The aim of this work package was to determine whether a simple equation could be used to predict the relationship between food intake rate and food density (i.e. the functional response) for a wide range of wading bird species. The functional response must be known to model and predict how the fitness of foragers is affected by food abundance, but is usually difficult and time-consuming to determine in the field. Despite its importance for forager-food interactions, remarkably few functional responses have been described for foragers in the wild, even in such well-studied animals as birds. This chapter has also been written up as a submitted paper, where full details of the work can be found.

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The functional responses of free-living waders feeding on macro-invertebrates, usually in the intertidal zone but sometimes in fields, follows the general form of the Holling (1959) type II ('disc equation') theoretical model of a decelerating rise in intake rate to an asymptote (Goss-Custard 1977a,b; Hulscher 1982; Sutherland 1982a,b; Barnard & Thompson 1985; Ens *et al.* 1996; Gill, Norris & Sutherland 2001; Goss-Custard *et al.* 2001; Hiddink 2003; Smart & Gill 2003). But despite this apparent convergence between theoretical expectation and empirical evidence, an increasing number of studies suggest that the assumptions of the disc equation often do not hold in waders (e.g. Wanink & Zwarts 1985), or in other groups of birds (e.g. Caldow & Furness 2001) or in predators in general (Jeschke, Kopp & Tollrian 2002). The disc equation assumes that, over a short time-base, the maximum number of prey consumed per unit time is the reciprocal of time spent attacking and handling prey. Early studies on waders (Goss-Custard 1977a; Hulscher 1982; Wanink & Zwarts 1985) and passerines (Green 1978) showed that this was not the case, and that the asymptote occurred well below the level at which all the time was spent attacking and handling prey, as has now been confirmed for a wide range of predators (Jeschke *et al.* 2002). At the asymptote, waders were spending significant amounts of time searching for and not attacking prey, either successfully or unsuccessfully, or handling captures.

This mismatch between theory and data is unfortunate because measuring the asymptotic intake rate would be easy if all one had to do was (i) to measure the reciprocal of the handling time, which estimates the feeding rate (*i.e.* number of prey consumed per unit time) and then (ii) multiply it by the mean mass of the prey being consumed to determine the intake rate. In the absence of a tested process model upon which to base predictions, this work package instead derived simple empirical equations that allow the functional response to be predicted from a small number of very easily measured variables.

3.3 Methods

3.3.1 FUNCTIONAL RESPONSES

Thirty estimates of the asymptote and 23 of the gradient of a functional response could be obtained. In most cases, the methods used are described in published papers. The data were taken either from papers or provided by the authors of papers. Some data came from unpublished fieldwork carried out on the Exe estuary over the winters 1998-99 to 2000-01 to increase the number and variety of responses available. Birds were observed throughout the tidal exposure period either from the shore or from a hide in a flat-bottomed boat stranded on the flats as the tide receded. Digital video recorded the feeding activities of individual birds feeding within 100m; each study plot was therefore approximately 1 ha. Data for one bird species/prey species in one site were obtained over a period of 2-5 tidal cycles. Fifteen sediment samples (surface area 0.00785m2) were taken at random to a depth of 30cm and sieved through a 1mm mesh to extract the macro-fauna. Individual prey animals were stored in a separate polythene bag and returned to the laboratory and frozen, prior to their length and ash-free dry mass (AFDM) being measured using procedures described in Goss-Custard *et al.* (2002).

The mean AFDM of the prey consumed by birds was estimated in one of three ways. 1) For oystercatchers opening and leaving emptied clams *Scrobicularia plana* shells on the mud surface, samples of opened shells were collected. 2) For birds eating the ragworm *Nereis diversicolor*, samples of droppings were collected to estimate worm length from the length of the mandibles, as described in Durell, Goss-Custard & Perez-Hurtado (1996). 3) Where neither of these two methods could be used, prey size was estimated as 1.05 times the mean AFDM of the prey in the sediment that were within the birds' size range based on an extensive literature review (J. D. Goss-Custard, unpublished information). The mean AFDM of the prey consumed was obtained by converting the lengths of each animal to its AFDM, these being obtained from allometric equations of AFDM against body length. The videos of feeding birds were used to measure the number of prey consumed per minute and, in some cases, the handling time of the prey and the delay imposed on searching by making a failed peck or probe, using the procedure in Goss-Custard & Rothery (1976). The product of feeding rate (number of prey consumed per s) and the mean AFDM of the prey consumed estimated the gross intake rate, defined as mg AFDM s^{-1}.

The shape of the type II functional response is captured by the asymptotic hyperbolic function:

$$I = \frac{aD}{b + D} \tag{3.1}$$

where a = asymptote (i.e. maximum intake rate at high prey densities) and D = the numerical density of the prey. The coefficient b is the prey density at which intake rate has risen to half its asymptotic level. To estimate the two coefficients, a and b, this equation was applied to the data on intake rate and the numerical density of the prey that lay within the size range normally consumed by the bird.

3.3.2 INTAKE RATES

Details of location, prey species and methods are given in the source papers. Some unpublished and published data were provided as the intake rate of dry mass or of gross or net energy (kJ). These were converted to mg AFDM s^{-1} using the author's own values for assimilation efficiency and energy density of the prey, if stated. In the few cases where these values were unavailable, typical values of assimilation efficiency were taken from the literature; 0.65 for large and heavily-armoured crustaceans (e.g. crabs and large prawns), 0.75 for polychaetes likely to be coated in mud, 0.85 for small crustaceans (e.g. *Corophium*), 0.75 for molluscs in the shell and 0.85 for bivalve flesh removed from the shell. Energy densities came from Zwarts & Wanink (1993).

3.3.2.1 Main data set

Following Zwarts *et al.* (1996), 153 estimates from European oystercatchers eating the heavily armoured prey cockles *Cerastoderma edule* and mussels were analysed separately. The remaining data, including those from oystercatchers eating prey other than cockles and mussels, are called the 'main data set'.

A number of bird and prey variables were used as possible predictor variables of intake rate. Although in many cases only one prey species was consumed, birds sometimes took a mixture of prey. Usually, however, most of the consumption came from a single species: one prey species contributed >90% of the consumption in 84% of the estimates of intake rate. The characteristics of the majority prey species were used independent variables in the analysis. The following variables were used:

- *Prey size*: Generally waders attain higher intake rates when eating large prey than when eating small ones (e.g. Ens *et al.*1996; Zwarts *et al.* 1996; Goss-Custard *et al.* 2001). Prey size was measured as the mean AFDM of the consumed prey, including both the majority and minority species, and was either measured directly from the prey size frequency distribution or by dividing intake rate by feeding rate.

- *Bird size*: Large waders usually have higher intake rates than small ones because their larger gape allows them to swallow larger-sized prey. Additionally, large body size might also enable birds to search faster and detect prey over a greater distance, further increasing intake rate. Bird size was measured at their 'basal' body mass in early autumn, after their return from the breeding grounds and before increasing their body reserves. Data were obtained mainly from Cramp and Simmons (1983) but sometimes from the source papers.

- *Prey characteristics*: Different prey species have different modes of living, which might affect their vulnerability to waders. For each estimate of intake rate, and using a dummy 0/1 variable, the majority prey species was scored as having (1) or not having (0) the following characteristics,: (i) taxon – *i.e.* polychaete worm or mollusc or crustacean or insect larva (or pupa) or earthworm Lumbricidae or brine shrimp *Artemia* spp.; (ii) surface-living or burrowing and (ii) whether it is an active prey able to retreat into a burrow to avoid bird predators (e.g. *Nereis diversicolor*). Thus, if the majority prey species was *N. diversicolor*, the scores would be: polychaete (1), mollusc (0), crustacean (0), insect (0), earthworm (0), *Artemia* (0), surface-living (0), active (1).

- *Bird characteristics*: Oystercatchers were disproportionately represented so a dummy 0/1 variable was used to identify this species in case it had a singular and over-influential effect on the results. Dummy 0/1 variables distinguished (i) visual (1) from tactile (0) foragers, (ii) the 'stand-and-wait' plover search strategy (1) from the more continuously searching 'sandpiper' (0) strategy, (iii) breeding birds (1), with eggs or young, from non-breeders, and (iv) adults (1) from sub-adults(0): as there were many missing values for bird age, its effect was only explored after the various models had already been selected. Interference competition is widespread in waders (Stillman *et al.* 2002) but its possible influence on intake rate could not be considered as bird density and/or the occurrence of aggressive interactions was usually unreported. However, most of the data were collected over low tide when birds would have been able to spread out, keeping interference to a minimum.

- *Latitude*: Latitude might have an effect because of a global trend for prey diversity to be higher near the equator (Piersma *et al.* 1993), or because temperature influences prey activity. It was represented as minutes north or south of the equator.

Multiple regression was used to identify the correlates of intake rate. Transforming intake rates, prey mass and bird body mass to logarithms satisfactorily stabilised the variance. The interaction term between the $\log_e$ bird mass and $\log_e$ prey mass was also included. All the other predictor variables were dummy 0/1 variables except for latitude, which was untransformed. MINITAB 13 was used to first identify the best-fitting model in which all variables had a significance level of <5%.

3.3.2.2 European oystercatchers eating mussels and cockles

This multiple regression analysis included the mean AFDM of the consumed prey ($\log_e$) along with 0/1 dummy variables representing whether birds (a) fed by sight (1) or by touch (0); (b) opened shells by hammering (1) or stabbing (0); (c) were breeding or not (1) or not (0), and (d) were in captivity (1) or free-living (0) and whether the prey was a cockle (1) or mussel (0). In addition, the time taken by the birds to handle a typical-sized cockle (25mm) and mussel (45mm) was included because thick shells, and the associated long handling times, could reduce intake rate. This was done by expressing the observed handling time as a ratio against the typical value for a cockle or mussel of these lengths, obtained from the equations given in Zwarts *et al.* (1996). The typical values were: (a) 20.2s and 28.3s for 25mm cockles opened by stabbing and hammering respectively, and (b) 59.7s, 103.2s and 105.5s for 45mm mussels opened by stabbing, dorsal hammering and ventral hammering respectively. Where no data on handling times were available, the ratio was assumed to be 1.

3.4 Results

3.4.1 FUNCTIONAL RESPONSES

In most functional responses, intake rates varied independently of prey density over a wide range but were often highly variable at a particular density (Figure 3.1). A multiple regression analysis of intake rate against mean prey mass and numerical prey density showed that much of this variation reflected differences between sites in the mean AFDM of the prey. Prey density was either untransformed or the square root or cube root taken to capture its possible non-linear effect on intake rate. In 16 of the 23 cases with sufficient data for analysis, prey mass had a highly significant positive effect on intake rate, much more often than did prey density (6).

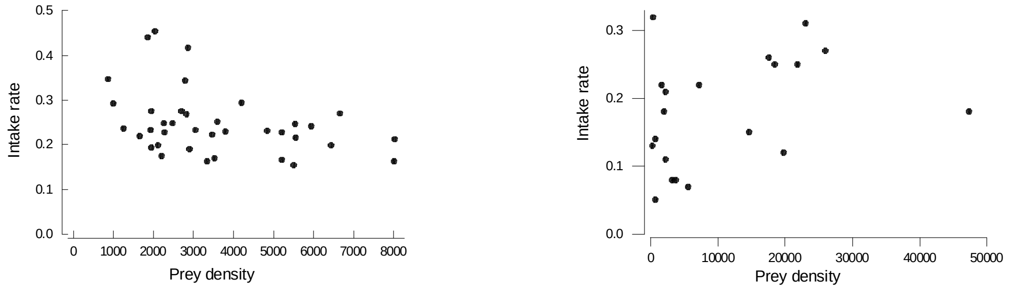
In estimating the coefficients of the functional response, the data were therefore divided into sub-sets according to prey size because, where prey size varies greatly between sites, biassed estimates of the asymptote can arise. For example, if some sites have low densities of small prey (and thus low intake rates) while others have high densities of large prey (and thus high intake rates), the fitted functional response gives a very high estimate of the asymptote. Sub-setting the data by prey size enabled both coefficients of the asymptotic hyperbolic functions to be estimated in 23 cases. In the remaining 7, there were no data at low prey densities so the gradient could not be estimated. However, prey densities were generally so high in these cases that it can be safely assumed that intake rates had reached the asymptote (Figure 3.1), so the mean intake rate was used as the estimate of the asymptote.

The asymptote, a, varied between 0.183 and 3.117 mg AFDM s^{-1}. The prey density at which intake rate reached 50% of its asymptotic value, b, also varied, but in most cases had very low values; *i.e.* gradients were generally steep. In 21 of 23 estimates, intake rate reached half its asymptotic value before prey density had reached only 65 m^{-2}, which is very low compared with the very high prey densities recorded in most studies (Figure 3.1).

Figure 3.1 Functional responses of waders eating macro-invertebrates: intake rate (mg AFDM s^{-1}) against numerical density of the prey (number m^2). In oystercatchers eating mussels or cockles, the method of feeding is given; *stabbing* between the shell valves or *hammering* into shells on the *dorsal* or *ventral* sides. Species are shown in ascending order of body size.

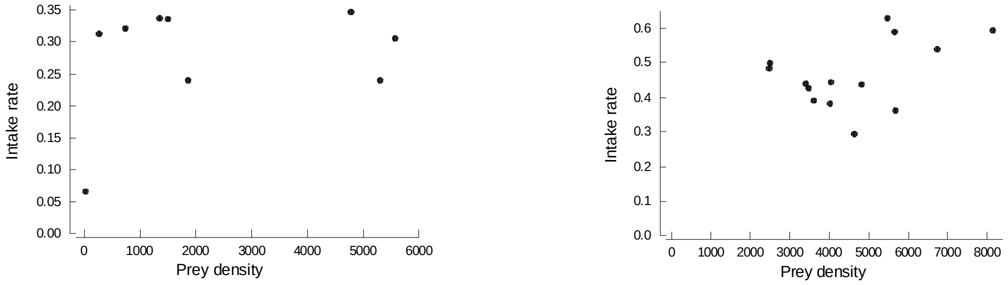
(a) Curlew sandpiper
- *Ceratonereis*

(b) Knot
– *Cerastoderma*



(c) Redshank
– Corophium (SW England)

(d) Redshank
– *Corophium* (Ythan estuary)



(e) Redshank
– *Nereis*

(f) Grey plover
– *Ceratonereis*

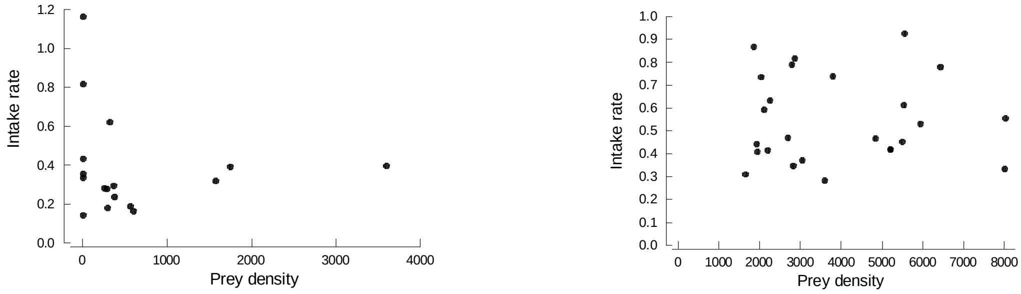
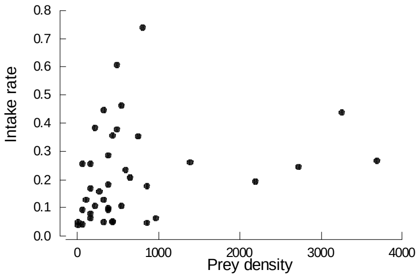
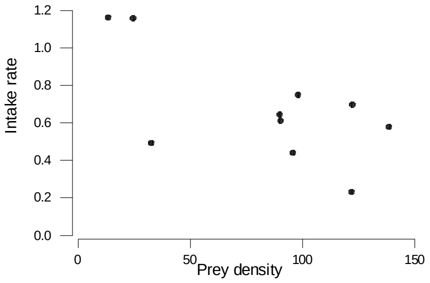


Figure 3.1 (continued) Functional responses of waders eating macro-invertebrates: intake rate (mg AFDM s-1) against numerical density of the prey (number m2). In oystercatchers eating mussels or cockles, the method of feeding is given; stabbing between the shell valves or hammering into shells on the dorsal or ventral sides. Species are shown in ascending order of body size.

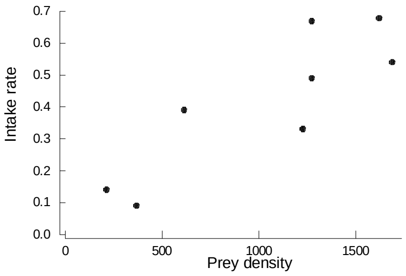
(g) Black-tailed godwit
– bivalves (SE England)



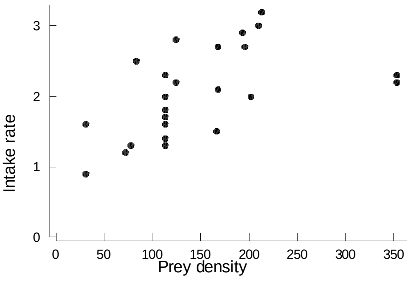
(h) Black-tailed godwit
– Scrobicularia (Exe estuary)



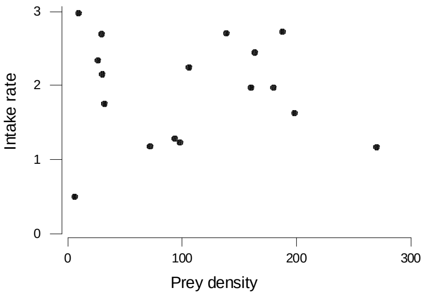
(i) Black-tailed godwit
– *Lumbricidae*



(j) Oystercatcher
– *Macoma*



(k) Oystercatcher
– *Scobicularia*



(l) Oystercatcher
– *Nereis*

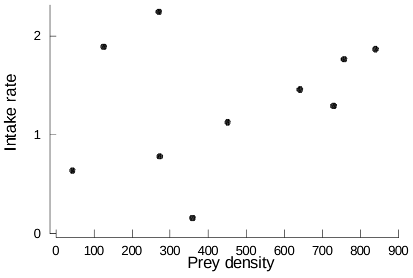
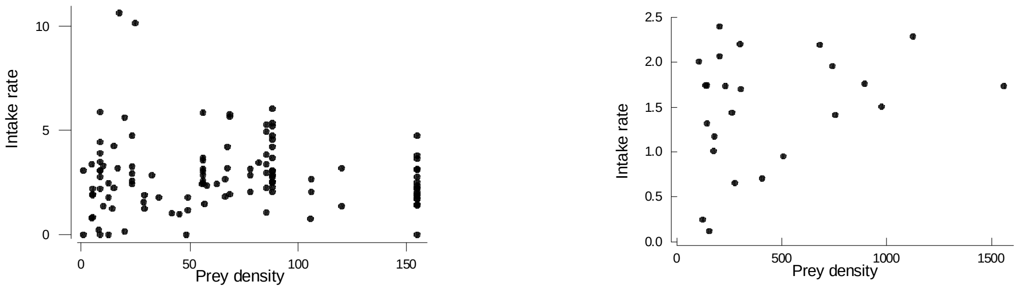
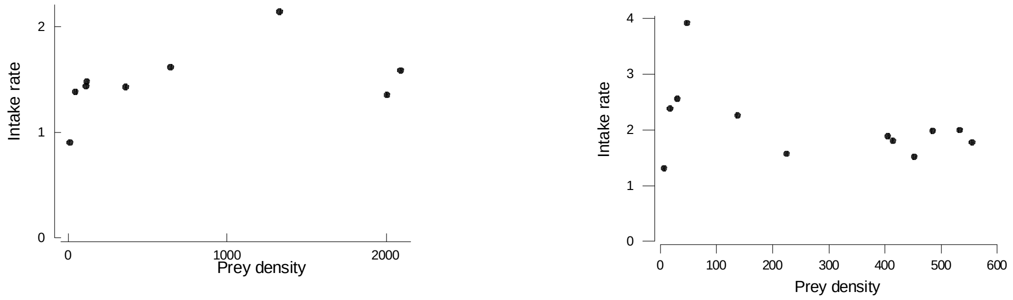


Figure 3.1 (continued) Functional responses of waders eating macro-invertebrates: intake rate (mg AFDM s^{-1}) against numerical density of the prey (number m^2). In oystercatchers eating mussels or cockles, the method of feeding is given; *stabbing* between the shell valves or *hammering* into shells on the *dorsal* or *ventral* sides. Species are shown in ascending order of body size.



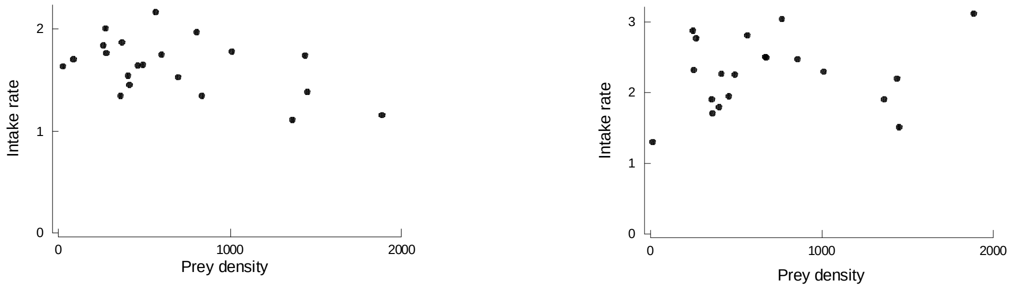
(m) Oystercatcher (Stabbers)
– *Cerastoderma* (Wadden Sea)

(n) Oystercatcher (Hammerers)
– *Cerastoderma* (Burry Inlet)



(o) Oystercatcher (Stabbers)
– *Cerastoderma* (baie de Somme)

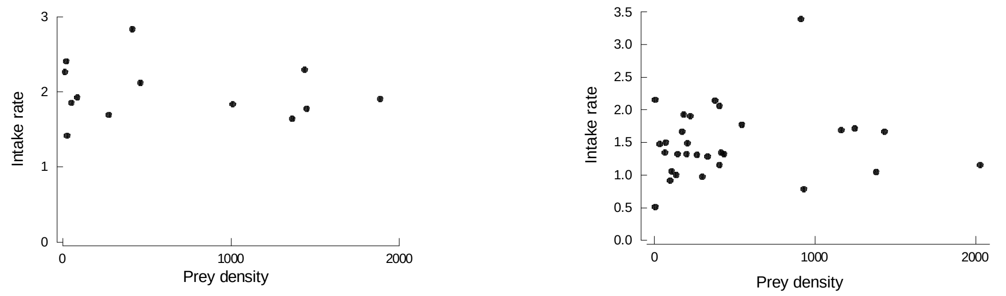
(p) Oystercatcher (Stabbers)
– *Cerastoderma* (Traeth Melynogg)



(q) Oystercatcher (Stabbers)
– *Mytilus* (Exe estuary)

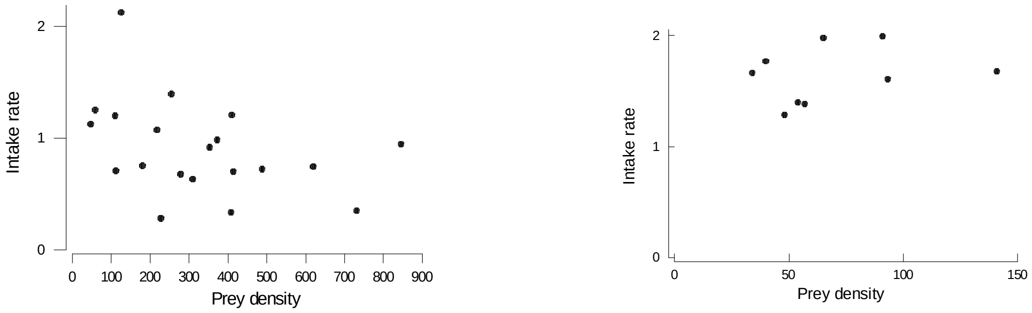
(r) Oystercatcher (Stabbers)
–*Mytilus* (Exe estuary)

Figure 3.1 (continued) Functional responses of waders eating macro-invertebrates: intake rate (mg AFDM s^{-1}) against numerical density of the prey (number m^2). In oystercatchers eating mussels or cockles, the method of feeding is given; *stabbing* between the shell valves or *hammering* into shells on the *dorsal* or *ventral* sides. Species are shown in ascending order of body size.



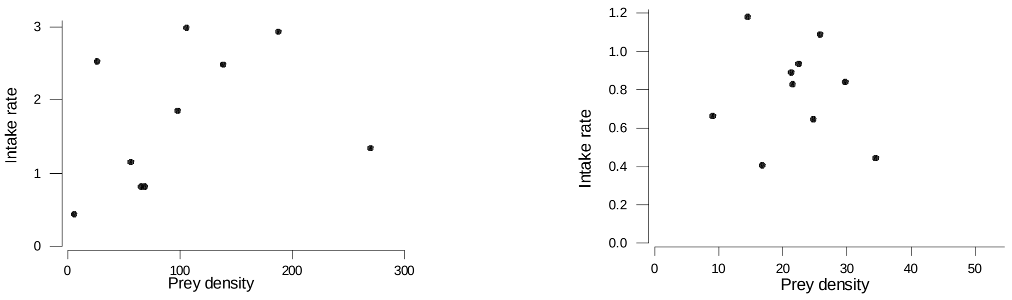
(s) Oystercatcher (Dorsal hammerers)
– *Mytilus* (Exe estuary)

(t) Oystercatcher (Ventral hammerers)
– *Mytilus* (Ythan estuary)



(u) Curlew
– *Nereis* (Exe estuary)

(w) Curlew
– *Nereis* (Wadden Sea)



(x) Curlew
– *Scrobicularia* (Exe estuary)

(y) Eastern curlew
- *Trypaea* (Australia)

3.4.3 INTAKE RATES

3.4.3.1 Main data set

Although the sample included 26 species of 11 genera, oystercatchers eating non-armoured prey (*i.e.* not cockles or mussels) dominated so the analysis was first conducted with oystercatchers excluded. Ten variables had a significant effect on intake rate. In addition to bird mass and prey mass (but not their interaction), variables representing prey taxon and other prey characteristics were selected: intake rates were lower when the prey could retreat down burrows, were molluscs or crustaceans. Taking all other significant variables into account, breeding birds had higher intake rates whereas birds using the plover foraging strategy had lower intake rates and birds fed more slowly as their distance from the equator increased.

The analysis on just oystercatchers eating non-armoured prey selected five variables of which two were again prey mass and whether the birds were breeding. With the data for oystercatchers combined with those from all the other species, nine variables were selected. Apart from bird mass and prey mass, and their interaction, a number of prey and bird characteristics were again selected, including whether the birds were breeding and were oystercatchers. Essentially the same variables were selected when oystercatchers eating cockles and mussels were also included in the analysis. Breeding birds again fed faster than non-breeders while oystercatchers eating mussels had a lower intake rate.

In all analyses, R^2 values (adjusted) were surprisingly high, varying between 68.0 and 81%. But despite their high levels of statistical significance, many variables had only a small absolute effect on intake rate and made little contribution to the amount of variance explained. Accordingly, R^2 was still 77.3% with only four of the most consistently selected variables included: bird mass, prey mass (but not their interaction) and whether the bird was an oystercatcher eating mussels or breeding (Table 3.1). Indeed, $\log_e$ bird and prey masses alone accounted for only 2% less of the variation in $\log_e$ intake rate (Table 3.1). Despite the very wide variety of prey species, habitats, study methods and research workers involved, a surprisingly high proportion of the variance in wader intake rate could be accounted by very few variables.

Adding the dummy variable expressing the bird's age in the much smaller data sets where bird age was known did not add significantly to any of the equations, although in all cases, the sign of the coefficient implied that any effect would have been for adults to feed faster than young, as previously shown by Hockey, Turpie & Velasquez (1998).

3.4.3.2 European oystercatchers eating cockles and mussels

Of the 152 spot estimates of intake rate available, 46 were birds eating cockles and 106 eating mussels. Feeding method, sensory modality and handling time did not have a significant effect on $\log_e$ intake rate and were rejected in that order in a step-down regression analysis with P values of 0.43, 0.19 and 0.11 respectively. The following had highly significant effects (adj. R^2=61.8%, $P<0.001$), the values in brackets showing the coefficient, its S.E. and P-value: $\log_e$ prey mass (+0.474, 0.032, <0.001), whether the prey was a mussel (-0.346, 0.085, <0.001), whether the bird was breeding (+0.525, 0.146, <0.001) and being held in captivity (-0.366, 0.153, 0.018): the constant was –1.801 (S.E.=0.157, <0.001). Intake rate increased with prey mass and was higher in breeding birds but lower in mussel-eaters and in captive oystercatchers.

Table 3.1 Multiple regression analysis of the correlates of $\log_e$ intake rates in waders. P-value is the significance of the coefficient from zero. – means the variable was not selected. * means that the variable was not included in the analysis. EMS is the Error Mean square, sometimes known as Residual Mean Square.

	Four variable model			Two variable model		
Variable	Coef.	SE	P	Coef.	SE	P
Constant	-2.802	0.192	0.000	-2.977	0.197	0.000
$\log_{10}$ Body Mass (g)	0.245	0.043	0.000	0.303	0.043	0.000
$\log_{10}$ Prey Mass (mg AFDM)	0.365	0.020	0.000	0.323	0.019	0.000
Oystercatcher eating mussels = 1	-0.227	0.070	0.001			
Breeding = 1	0.379	0.077	0.000			
N	468			468		
Adjusted R^2 (%)	77.3			75.5		
P	0.000			0.000		
EMS	0.270			0.290		

3.4.4 PHYLOGENETIC ANALYSES

There has been considerable debate in the literature concerning the circumstances under which it is valid to use raw species-specific data in comparative analyses, versus the circumstances in which it is prudent to take phylogenetic relationships into account (Harvey & Pagel 1991; Price 1997; Harvey & Rambaut 2000; Bennett & Owens 2002; Freckleton *et al.* 2002). In this work package, where associations between traits are tested across relatively distantly-related species that are not members of a single adaptive radiation, the potential danger of using raw species-specific data is that any associations may be due to common ancestry rather than convergent evolution (Bennett & Owens 2002). If this were the case, such phylogenetic non-independence could invalidate any implied causal basis to the identified relationships.

In order to test whether the results could be an artefact of phylogenetic relationships, the analyses were repeated using the independent contrasts method to control for the confounding effects of common ancestry (Felsenstein 1985; Harvey & Pagel 1991; Pagel 1992), with contrasts being calculated using the CAIC program (Purvis & Rambaut 1995). The molecular phylogenies of Paton *et al.* (2003) and Thomas *et al.* (2004) were used to construct a composite bifurcating phylogeny of the species in the analyses, with all branch lengths set to the same length. Linear least-squares regression models were then used to test for associations between contrasts in intake rate and contrasts in both body size and prey size. All regression models were forced through the origin (Pagel 1992).

These analyses based on phylogenetically independent contrasts largely supported the other analyses based on species-specific values. Both univariate and multivariate models confirmed that there were significant positive associations between intake rate and both body size and prey size. Also, the multivariate models based on phylogenetic contrasts were qualitatively the same as those based on using each population as an independent data point. These findings confirm that the key relationships described here are not due to the phylogenetic pattern of relationships among the species concerned.

3.4.5 PREDICTING THE PARAMETERS OF THE FUNCTIONAL RESPONSE

3.4.5.1 Asymptote

The equations Table 3.1 were used to predict the asymptotes of the functional responses shown Figure 3.1. Because of the effect that taking logarithms can have on sample variance, the following Error Mean Square back-transformation correction was applied to the predictions (Newman 1993). The uncorrected predicted $\log_e$ intake rate, Z, was calculated from the equations, and converted to the corrected intake rate, I, as follows:

$$I = e^{\left(Z + \frac{S^2}{2}\right)} \qquad (3.2)$$

where S^2 = Error Mean Square (or Residual Mean Square) of the regression (in bottom row of Table 3.1).

The correlation between observed and predicted asymptotes from the four-variable model was quite close (Figure 3.2, closed circles). The intercept, i, of the observed-predicted regression (not shown in Figure 3.2) was not significantly different from 0 (i=0.083, S.E.=0.116; P=.474) and the slope, s, was not significantly different from 1 (s=0.985, S.E.=0.075;

P=0.735). On average, the four-variable equation under-predicted observed asymptotes by 11.6% (range -204.0% to +53.1%; N = 30) but, as its S.E. was 9.5%, the mean discrepancy was not significantly different from zero. Much of this discrepancy arose from two very high values obtained in an early study of redshank *Tringa totanus* eating *Corophium volutator* on the Ythan estuary by JDG-C when the methodology for measuring intake rates in waders was poorly developed; for instance, feeding rate was over-estimated because it was measured from inter-catch intervals (Goss-Custard *et al.* 2002). With these two points excluded, the observed asymptotes were on average only 0.2% (S.E.=5.05; range –59.0% to +53.1%; N=28) higher than the predicted.

The correlation between observed and predicted asymptotes from the two-variable (body mass and prey mass) model (open circles in Figure 3.2) was also close. On average, it under-predicted observed asymptotes by 6.6% (range –166.6% to +57.5%; N=30) but, as the S.E. was 8.7%, the mean discrepancy was again not significantly different from zero. With the two Ythan redshank points excluded, the observed asymptotes were on average only 3.0% (S.E.=5.8; range –86.2% to +57.5%; N=28) higher predicted.

The slightly poorer performance of this two-variable model was due to five values (double circles in Figure 3.2) from the one study of breeding birds (oystercatchers eating *Macoma* in the Wadden Sea) and the four of oystercatchers eating mussels. Without these five points, the observed-predicted regression line had an intercept of –0.027 (S.E =0.104) and a slope of 1.057 (S.E.=0.078), not significantly different from zero or unity, respectively. The average deviation of the observed asymptotes from the predicted was –9.1% (S.E.=9.5%; range –166.6% to +57.5%; N=25) including the Ythan redshank and 2.3% (S.E. 5.4%; range –40.0% to +57.5%; N=23) excluding them. Thus, on average, it made little difference to the comparison between observed and predicted asymptotes whether the five data points on breeding birds and oystercatchers eating mussels were included. But it made a large difference to the precision of the predictions for birds in these two categories (Figure 3.2). The two-variable model could lead to large under-predictions of the asymptote in breeding waders (here -86%) or to large over-predictions in oystercatchers eating mussels (+19.1% to +43.1% here). For such birds, the four-variable model would give better predictions.

3.4.5.2 Gradient

A step-down multiple regression of the gradients of the functional responses in Figure 3.1 used a limited number of independent variables because of the small sample size (N = 23); bird and prey masses, prey taxon and whether the bird was an oystercatcher or breeding. As the two values from black-tailed godwits in east England were so exceptionally high, they were represented by a dummy 0/1 variable, in case they had undue influence.

In fact, the only overall significant variable selected with untransformed data was this dummy variable (adjusted R^2=63.1%, P<0.001). With these two data omitted, the only overall significant regression (adjusted R^2=23.3%, P=0.036) was obtained with prey mass (coefficient =0.087, S.E.=0.031, P=0.012), and the dummy variable representing oystercatchers as 1 (coefficient=24.25, S.E.= 11.86, P=0.056). With gradient, body mass and prey mass transformed to logarithms, the only overall significant regression (adjusted R^2=27.5%, P=0.028) for $\log_e$ gradient was with $\log_e$ body mass (coefficient=6.307, S.E.=3.224, P=0.065), $\log_e$ prey mass (coefficient=5.030, S.E.=1.495, P=0.003), and the dummy variable representing oystercatchers as 1 (coefficient=10.594, S.E.=4.699, P=0.036). The intercept was –24.77 (S.E.=15.84, P=0.134) and the error mean square was 52.47.

Although sample size was small, the results suggest that half the asymptotic intake rate was reached at higher prey densities when both the prey and birds were large, and especially if they were oystercatchers. That is, the gradient was more steep when the prey were small and less steep in large birds, especially oystercatchers. The predictive ability of the equation cannot be tested until the parameters from more functional responses become available.

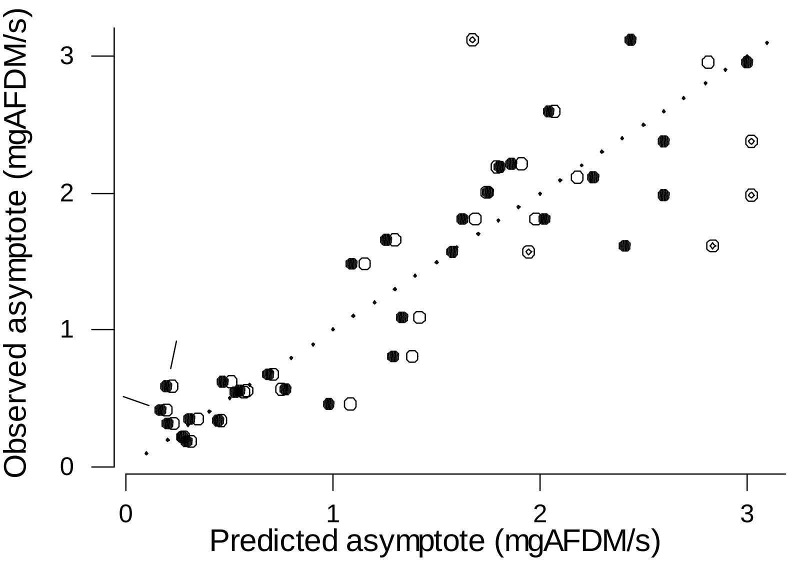


Figure 3.2 The observed asymptotes of the functional responses shown in Figure 3.1 in relation to the predicted asymptotes from the four-variable and two-variable equations shown in Table 3.1. Closed circles: equation including body mass, prey mass and whether the bird was an oystercatcher eating mussels or breeding. Open circles: equation only includes body mass and prey mass; the double circles show breeding birds or oystercatchers eating mussels. The two short lines indicate the two studies on redshank eating *Corophium volutator* on the Ythan estuary. Dotted line shows Y = X.

3.5 Discussion

3.5.1 CAUSAL BASIS OF THE CORRELATES OF INTAKE RATE

That large birds eating large prey generally had the highest intake rates was expected because of the well-established allometric relationship between intake rate and body mass in birds (Bryant & Westerterp 1980; Zwarts, Blomert & Hupkes 1990) and the generally greater profitability of large prey items and the ability of large birds to consume them (Zwarts & Blomert 1992). The causal basis of the associations between intake rate and some other statistically significant predictor variables is more uncertain, however. It is unclear why, taking bird and prey sizes into account, intake rates were consistently lower in birds eating molluscs, crustaceans and earthworms and higher in birds eating *Artemia*. Differences between prey taxa in availability to waders or in their anti-predator defence mechanisms might be responsible; for example, *Artemia* shows no obvious anti-predator responses and is highly visible as it swarms in the water. It is unclear why intake rates were sometimes lower in birds using a plover searching method, or in birds feeding further from the equator or in oystercatchers detecting prey visually. Of course, some associations may have no causal basis, as might be implied by the selection of 'Surface-living prey = 1' where the sign differed between oystercatchers and other waders.

The causal basis of the remaining associations may be more clear. Breeding birds consistently had higher intake rates than non-breeders. Prey availability may be higher in the breeding season if prey are more active in the warmer sediments or take greater risks when foraging to prepare for reproduction (Ens, Klaassen & Zwarts 1993). Alternatively, the priorities of birds themselves may change from reducing their risk of being attacked by predators while foraging (Cresswell 1994), or of damaging their bill (Swennen, Leopold & de Bruijn 1989) or consuming parasites (Norris 1999) to meeting the increased energy demands due to breeding. Oystercatchers generally had lower intake rates than other waders, taking prey and bird size into account, perhaps because many of their prey are heavily-armoured (Zwarts *et al.* 1996). Oystercatchers in captivity fed even more slowly, perhaps because of reduced food demand or because captivity affected their foraging behaviour or they were given prey to which they were not specialised.

The reduced intake rate in waders eating prey that could retreat into a burrow may imply that this anti-predator behaviour is effective in reducing intake rate in waders, and also introduces the possibility that interference through prey depression may have occurred in our sample (Yates, Stillman & Goss-Custard 2000). Interference from intra-specific and inter-specific kleptoparasitism may also have occurred. Excluding oystercatchers eating mussels or cockles in which interference through intra-specific kleptoparasitism does occur (Stillman, Goss-Custard & Caldow 1997; Triplet, Stillman & Goss-Custard 1999; but see Norris & Johnstone 1998), intraspecific and/or interspecifc interactions were noted in one third of the studies of intake rates across 18 species. As some authors did not record whether such interactions occurred, this is likely to be a minimum estimate. However, the magnitude of any interference effect cannot be determined without very careful study (Goss-Custard *et al.* 2003), especially as recent studies suggest that sometimes waders are able to minimise its effect (van Gils & Piersma 2004).

3.5.2 PREDICTING THE COEFFICIENTS OF THE FUNCTIONAL RESPONSE

As the asymptote was not set by handling time, as the parameters required to predict the maximum intake rate from a bird's satiation level are unknown, and as the possible role of perceptual time constraints on intake rate remains speculative, wader asymptote cannot yet be predicted from current process models of the functional response. However, the review of wader functional responses revealed that intake rate varied independently of the numerical density of the prey over a wide range and that the asymptote was usually reached at very low prey densities (<150/m2) compared with the densities of prey that typically occur; the only exceptions came from one study of black-tailed godwits eating small bivalve molluscs in east England (Gill *et al.* 2001). Therefore most of the spot estimates of intake rate were probably obtained at or near to the asymptote of the functional response, raising the possibility that correlates of these spot estimates could predict the asymptote.

The multivariate analysis of the 468 spot estimates of intake rates from 26 species of 11 genera identified ten variables representing natural history features of the prey and wader that accounted for 81% of the variance in logarithm-transformed intake rates. However, just four variables accounted for almost as much (77.3%), the variables being bird size (body mass), prey size (mean mass of the prey consumed), whether the bird was an oystercatcher eating mussels and whether it was breeding.

This four variable model under-predicted the observed asymptote across all 30 estimates by an average of 11.6% but the discrepancy was only 0.2% when two suspect estimates were removed. This model therefore predicted the observed asymptote successfully in 93% of cases. A two-variable model that included only bird mass and prey mass predicted the asymptotes with almost equal precision, suggesting that often one only need to know these two very-easily acquired parameters. (Interestingly, it also accurately predicted the asymptote of the functional response of rooks *Corvus frugilegus* eating pieces of tinned meat scattered at random on grass, suggesting that the model could have an even wider application (R A Stillman, unpublished information)). However, this model gave poor predictions for breeding waders and for oystercatchers eating mussels, and the four-variable model should be used here.

A multivariate analysis of the 23 estimates of the gradient suggested that half the asymptotic intake rate was reached at lower prey densities when the prey were small but, taking prey size into account, this occurred at higher prey densities when the birds were large, especially if they were oystercatchers. The resulting equation could be used to predict the gradient of the functional response, but its predictive power has yet to be tested. It is concluded that the asymptote of the functional response in waders can be reliably predicted from just four easily-measured variables, and that future work may confirm that the gradients may also be predicted this way.

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4 UNDERLYING BIOLOGY: WADER DECISION RULES

Liz Mattison & Ken Norris

4.1 Summary

This chapter describes the work conducted under work package 7 of the project. The aim of this work package was to compare the prey-selection decision rules used by oystercatchers feeding on cockles on two contrasting sites, the Burry Inlet and the Dee estuary, UK. The Dee estuary is considered a less favourable site because oystercatchers generally have lower prey intake rates than those on the Burry Inlet. Oystercatchers consume all cockle size classes on the Dee estuary, but ignore the largest size classes on the Burry inlet. As a result oystercatchers maximise their prey intake rate on the Dee estuary (intake rate maximising decision rules), but not on the Burry Inlet (risk avoidance decision rules). The difference between foraging strategies at each site show the flexibility of foraging shorebirds according to the conditions encountered and point to a cost that is incurred when foraging at the maximal energy intake rate, at least on the Burry Inlet. The work package tested the hypothesis that the different prey selection strategies at the two sites was generated by a trade-off between maximising energy consumption while minimising parasite consumption. Oystercatchers on the Burry Inlet are shown to maintain a lower ingestion rate of parasite transmission stages by selecting smaller cockle size classes. As discussed in previous work this would seem to indicate a trade-off between energy intake rate and the rate at which birds become infected with parasites, but is parasite infection really the cost that birds at the Burry Inlet are attempting to avoid? Further analysis reveals that although selective foraging can reduce the rate at which parasite transmission stages are ingested, this reduction is not sufficient to counteract the need to ingest a greater number of food items in order to obtain the amount of energy required to survive. In other words, the smaller the cockles selected, the greater the number of cockles eaten. This in turn results in a greater number of ingested parasites. Therefore, there is no evidence that the size selection strategies of oystercatchers on the Dee estuary and Burry Inlet is driven by a trade-off between energy and parasite consumption. Another, as yet unknown cost appears to be driving the foraging behaviour of the oystercatchers at the Burry Inlet. However, the work conducted in this work package still shows that wading birds can use either rate-maximising or risk avoiding decision rules.

4.2 Study Sites

4.2.1 THE DEE ESTUARY

The Dee Estuary drains into Liverpool bay. It contains 7 Sites of Special Scientific Interest (SSSIs) covering an area of 13,759ha and has been designated a wetland of international importance for wintering waders and wildfowl under the RAMSAR convention (Frazier 1999). It provides over-winter feeding grounds for internationally important numbers of 9 wader species including the oystercatcher (Mitchell, Moser & Kirby 1988). Approximately 80% of the estuary area is intertidal, consisting of mudflats such as those found at Hoylake (53-25°N, 3-10°W) and *Spartina* dominated saltmarshes (Buxton, Gillham & Green 1977). The intertidal area contains sometimes dense but extremely variable cockle (*Cerastoderma edule*) populations that have been the subject of intensive cockle fishing methods in the past. Oystercatchers forage on a range of prey in the area but at Hoylake they predominantly feed on cockles (Johnstone & Norris unpublished data). More detailed description of the area can be found in Jemmett (1996).

4.2.2 THE BURRY INLET

The Burry Inlet in South Wales (51-39°N, 4-10°W) has an intertidal area of approximately 6500ha, consisting of intertidal sandflats and saltmarsh. The invertebrate fauna of the sandflats is dominated by cockles *Cerastoderma edule* (Norris & Johnstone 1998*a*). The cockle population in the Llandrhidian Sands area of the estuary supports several thousand oystercatchers during the winter (Horwood & Goss-Custard 1977) and a commercial cockle fishery throughout the year (Franklin 1976; Norris, Bannister & Walker 1998). A more detailed description of the estuary can be found in Nelson-Smith & Bridges (1976).

4.3 Oystercatcher prey selection: methods

4.3.1 COCKLE AND PREY REMAINS COLLECTIONS

Sampling took place at Hoylake and the Burry Inlet during the winter, on a monthly basis. In the first season sampling took place from December 2001 until March 2002. During the second season sampling took place from September 2002 until February 2003. On each sampling date, areas were chosen on the basis that oystercatchers (*Haematopus ostralegus*) had been feeding on cockles (*Cerastoderma edule*) that day using a hammering technique (Drinnan, 1957; Swennen *et al* 1983; Norris & Johnstone 1998*a*). Such areas are relatively easy to identify because the birds leave opened shells on the substrate surface, either scattered around or in feeding piles at sites where the birds prefer to open cockles (see Johnstone & Norris 2000 and references therein). Freshly opened cockles are distinguishable by the presence of scraps of flesh in the region where the adductor muscles attach to the valves (Norris & Johnstone 1998*a*). During the first season six sample areas were identified at Hoylake (except during the November sampling occasion when bad weather limited fieldwork to 3 sampling areas). At the Burry Inlet, either 4 or 5 sites were sampled each month. During the second season, six or seven sites were sampled each month at Hoylake and five sites were sampled each month at the Burry Inlet.

At each sample site a 20m x 20m square of sand was examined for shells that had been hammered open during feeding. These were collected and used to estimate the prey size selection of oystercatchers. At the Burry Inlet three 0.1m^2 quadrat samples were dug out of the substrate to a depth of 5cm and the contents sieved through a 0.5mm mesh. The process was the same at Hoylake but four quadrat samples were taken in areas where cockle numbers were particularly low. This was necessary in order to gather as many individuals as possible for examination. All the cockles from each quadrat were separately bagged and retained. These were used to obtain biomass density estimates and to screen for parasite intermediate stages. Finally, the location of each sample area was recorded using a GPS receiver (Garmin eMapTM).

4.3.2 ESTIMATION OF COCKLE DENSITIES AND PREY SELECTION

After each sampling occasion, as soon as the cockles arrived at the laboratory, they were divided into five separate size-classes: 0-7mm, 7-15mm, 15-22mm, 22-29mm and 29+mm. The density of each cockle size class (m^{-2}) at each sample site was estimated using the mean number of cockles collected from the quadrat samples taken at each site. Prey remains were also divided into the same size-classes and counted. This allowed the comparison of cockles available in the substrate with those eaten by oystercatchers.

Energy content of cockles on each sampling occasion was estimated using the equation described in Johnstone & Norris (2000), which takes into account winter reduction of cockle flesh:

$$\ln y = -6.201 + 3.731 \ln x_1 - 0.0064 x_2 + 1.35 \times 10^{-5} x_3 \tag{4.1}$$

where y = grams of ash free dry mass (g AFDM), x_1 = cockle size class (integer values from 1 to 5), x_2 = September day (1st September = September day 1), x_3 = September day squared. The same equation was used to estimate energy content of cockles at both the Burry Inlet and Hoylake, as the flesh content of cockles does not differ significantly between these two sites (Johnstone unpublished data). The biomass density of cockles (g AFDM m^{-2}) at sites where oystercatchers foraged were estimated using the following equation:

$$b = \sum_{i=1}^{5} e_i d_i \tag{4.2}$$

where b = g AFDM m^{-2}; e_i = predicted energy content (g AFDM) of a cockle of size class i, and d_i = density (per m^{-2}) of cockles of size class i (Johnstone & Norris 2000).

4.3.3 TIME SPENT FEEDING

In order to establish the pattern of feeding at each study site, previously collected data was used. Firstly, the length of time birds spent feeding was calculated from 20 bird counts made during the ebbing tide and 20 bird counts during the flooding tide at the Burry Inlet during winter 1995-96. Secondly, the length of time spent feeding at Hoylake was calculated using seven bird counts during the ebbing tide and four bird counts during the flooding tide over the winter in 1998.

4.3.4 PARASITE SCREENING

A sub-sample of cockles to be examined for parasite infection was taken using the following method: from each of the quadrat samples 10 individuals of each size-class were randomly selected. If there were 10 or fewer individuals, all cockles of that size-class were examined. The selected cockles were rinsed in artificial seawater to remove any mud or sand and placed in separate labelled containers. These containers were submerged in tanks of well-aerated artificial seawater and kept at 11°C in a temperature-controlled room. The room was equipped with artificial lighting, timed to provide diurnal conditions with corresponding periods of twilight. Placing cockles in seawater tanks without substrate had the effect of cleaning out much of the mud and sand that can collect inside the shell valves and facilitated the examination process. A few individuals died during the period but were examined. All cockles were examined within 8 days of collection.

Cockles were removed from tanks prior to examination. Shell length was measured to the nearest 0.1mm; each individual was aged using growth rings on the valves and opened by severing the adductor muscles with a scalpel. The flesh was removed and placed in a petri dish. Larger cockles were divided into the following sections for examination under a binocular dissection microscope: siphons and mantle, foot, tissue found below the umbo, digestive gland and remaining tissue. Smaller cockles could be examined whole. The regions described correspond to different microhabitats preferred by parasite species that utilise cockles as an intermediate host (Lauckner 1983). A microscope slide was placed over the area to be examined. Downward pressure on the slide made the tissue thin, translucent and easy to examine under x30 magnification. Once parasites had been located, they were identified and counted. Particularly heavy infestations were even visible with the naked eye. This method allowed a record of exactly what parasite species were present in each individual and how many were present, along with information on where the individual was from, when it was collected, it's age, size and therefore flesh content.

A total of 3927 cockles from the Burry Inlet were examined over the two seasons and 1430 cockles from Hoylake. The discrepancy in sample sizes was due to the difference in cockle densities between sites. Those transmission stages deemed likely to infect foraging oystercatchers were identified and the results from both years were combined in order to maximise sample sizes and to account for between year variation in parasite numbers.

4.3.5 DEFINITIONS

From here on, the following definitions are used. Abundance – mean number of parasites per host taking into account both infected and uninfected individuals. Intensity – mean number of parasites per infected host (Margolis et al 1982). Prevalence – percentage of hosts that are infected. Range – minimum and maximum number of parasites encountered. Infrapopulation – number of a particular species found in one definitive (final) host. Dispersion of parasites within cockle samples was described using the variance to mean ratio (variance/mean). If the estimated value is significantly greater than unity, the distribution of parasites is aggregated, not a random (Poisson) distribution (Shaw & Dobson 1995).

4.4 Oystercatcher prey selection: results

4.4.1 COCKLE BIOMASS AND PREY SELECTION

When comparing the data collected from the Burry Inlet and Hoylake, differences in prey densities between the two areas and between the prey selection of the two oystercatcher populations became apparent.

Over both winter seasons, all cockle biomass densities recorded at the Burry Inlet were higher than those recorded at Hoylake. There was some evidence that cockle numbers at Hoylake decreased over the course of the winter. However, as samples were only taken in areas where birds were feeding, they may not have been representative of the area as a whole. At the Burry Inlet, a wide variety of biomass densities were recorded, but there was no indication of a general decline in cockle numbers (Figure 4.1).

The distribution of cockle size classes at both sites varied between years, probably because of variation in the levels of spat settlement over time. For example, at Hoylake during the first winter, the majority of cockles found were 7-15mm in length whereas during the second winter cockles 15-22mm in length were most common. However oystercatchers at the Burry Inlet consistently selected cockles from the intermediate size classes, whereas birds at Hoylake appeared to select cockles in direct proportion to their availability in the sand (Figure 4.2).

4.4.2 TIME SPENT FEEDING

At the Burry Inlet, the oystercatchers began feeding as soon as the cockle beds were exposed, but feeding birds were present for an average of 71 minutes. They then returned to feed during the flood tide, feeding birds being present for an average of 47 minutes. The average tidal cycle is 12 hours 50 minutes and for 7 hours 19 minutes, the cockle beds preferred by oystercatchers are exposed. The birds are therefore not feeding for large amounts of available time.

At Hoylake, the average tidal cycle is 12 hours 5 minutes and the average time birds were observed feeding was 8 hours per tidal cycle. The rest of the time, the feeding area was covered during the high water period. This indicates a marked difference in feeding behaviour between the study sites, with birds using all the available time to feed at Hoylake but only feeding at the beginning and the end of the available time at the Burry Inlet.

4.4.3 PARASITES FOUND IN COCKLES

Details of the parasites encountered during the current study are summarised in Tables 4.1 and 4.2. During both winters, at both sites, a total of 8 trematode parasites were observed in dissected cockles and one turbellarian. No cestode species were found and only one unidentifiable nematode. The nematode was not associated with host tissue so it is possible that the individuals noted were free-living and had been inhaled accidentally while cockles filtered seawater.

It was slightly surprising that no cestode larval stages were observed. Goater (1989) reported several species in cockles from the Exe Estuary and James, Sannia & Bowers (1977) reported cysticercoid larvae of the cestode *Hymenolepis brachycephala* in cockles from the Burry Inlet. However, owing to the size of such larvae and the number of hosts examined it is unlikely they were overlooked during this study.

The turbellarian observed in cockles from both the Burry Inlet and the Dee estuary was *Paravortex cardii*. This species lives in the digestive gland of cockles (Lauckner 1983). *P. Cardii* was less abundant at Hoylake than at the Burry Inlet. Only one individual was found at Hoylake in 2001-02 but in 2002-03 an abundance of 0.4 was recorded across all cockles, with a prevalence of infection of 17.5%. At the Burry Inlet, an abundance of 2.8 was recorded in 2001-02, with a prevalence of 74.2%; during 2002-03 abundance was 1.8 and prevalence 67.5%. *P. cardii* was not considered further as it does not infect any other hosts.

Two types of trematode sporocyst were found. *Gymnophallus choledochus* was present at very low incidences. Both the sporocyst stage containing cercariae and sporocysts containing mature metacercariae were observed. At the Burry Inlet during winter 2001-2002 one cockle was found to contain 145 sporocysts, a prevalence of 0.062%. During winter 2002-03 none were found. At Hoylake, during winter 2001-02 *G. choledochus* was not found but during winter 2002-03 10 cockles were infected, a prevalence of 1.08%. The species utilises cockles as both the first and second intermediate host. In addition, some sporocysts produce cercariae that migrate out of the cockle and penetrate polychaete worms (*Nereis diversicolor/Nephtys hombergi / Arenicola marina*). The final hosts of *G. choledochus* are Larus spp, *Tadorna tadorna*, Anatidae and Limicolidae (see Lauckner 1983 and references therein). As there is no record of *Haematopus ostralegus* being infected with *G. choledochus* this species was not considered further.

The sporocysts of the bucephalid trematode *Labratrema minimus* were found in cockles from both study sites. This species has previously been reported from cockles at the Burry Inlet under the synonym *Bucephalus haimeanus* (Hancock & Urquart 1965; Bowers 1969). During the winter 2001-02 presence of this sporocyst was noted but prevalence was not recorded. During winter 2002-03 at the Burry Inlet a prevalence of 3.71% was recorded. At Hoylake *L.*

minimus prevalence during winter 2002-03 was 0.43%. Sporocysts of *L. minimus* grow around the gonads of cockles, castrating any that become infected (Lauckner 1983). Eventually the branching sporocyst tissue virtually fills the body cavity of the host, it is surprising these cockles are found alive. Although the castrating effect of this parasite may have an interesting effect on the population dynamics of cockles in the area, the definitive host for this species is the sea bass *Dicentrarchus labrax* so no further analysis was carried out.

Five types of metacercariae were encountered, four of which probably infect oystercatchers. The total number of these metacercariae increased with cockle size and cockles were more heavily infected at Hoylake (Figure 4.3). Many metacercariae were found surrounded by host tissue in the area of the cockle positioned directly beneath the umbo. The majority of these were *Meiogymnophallus minutus*, probably the best-known trematode parasite of cockles and oystercatchers (e.g. Bowers & James 1967; James, Sannia & Bowers 1977; Lauckner 1983; Russell-Pinto 1990; Goater 1993). Prevalence of infection was high at both sites. Comparison of data collected during this study and data collected by James, Sannia & Bowers (1974) indicates that abundance of *M. minutus* in cockles from the Llandrhidian Sands area of the Burry Inlet is comparable between years. Because this species was the most common and the most numerous parasite found at both study sites and it is a well documented parasite of oystercatchers, we included it in our analysis and used it as the basis for a simple population model of parasites in oystercatchers. For details of infection patterns in cockles during this study see Tables 4.1 and 4.2 and Figures 4.3 and 4.4.

Occasionally similar metacercariae were found, within the same microhabitat but slightly smaller in size and brownish in colour. These were designated "*Gymnophallus* sp.". There are several unknown trematodes of this genus in the literature, recorded from both intermediate hosts and oystercatchers (e.g. Goater 1989; Lauckner 1983). Unfortunately, without further information on size, appearance, micro-habitat and life-cycle there is no way of linking *Gymnophallus* spp. found in cockles with *Gymnophallus* spp. found in oystercatchers (Goater 1989) so the example observed during this study was excluded from our analysis.

Encysted metacercariae were commonly observed in the mantle, digestive gland and the foot of cockles from both study sites. During the first year of parasite screening, formal identification was not possible and the number of cysts found in all microhabitats was pooled. During the second season, the cysts were identified as three separate species on the basis of microhabitat preference, appearance and size. *Himasthla continua* metacercariae were mostly found in the foot of cockles and were identified by size, having a diameter of 189 - 200µm (Lauckner 1983; Jensen, Castro & Bachelet 1999). *Himasthla interrupta* metacercariae occurred mainly in the mantle margins and are smaller in size (157 – 171µm in diameter - Lauckner 1983; Jensen, Castro & Bachelet 1999). Trematodes of the genus *Himasthla* are known to infect waders, gulls, herons and geese (Fried 2001; Ellis & Williams 1973) and three species have been recorded from the intestine of oystercatchers: *Echinostomum secundum* = *Himasthla elongata* (Nicoll 1906), *Himasthla leptosoma* (Threlfall 1963) and *Himasthla* sp (Goater 1989). *H. interrupta* and *H. continua* are considered to be likely parasites of the oystercatcher (Wegeberg, de Montaudouin & Jensen 1999) Because of this, numbers of both species were included in our analysis. Summary of the infection characteristics of these species during winter 2002-03 can be found in Tables 4.1 and 4.2 and Figure 4.5.

The third encysted metacercaria, found in the digestive gland of cockles, was identified as *Psilostomum brevicolle* on the basis of size, microhabitat and appearance – the diffuse granular excretory system is characteristic and cyst diameter is 200-230μm (Lauckner 1983). Oystercatchers are well-documented definitive hosts (Loos-Frank 1968; Goater, Goss-Custard & Kennedy 1995; Van Oers, Heg & Quenechdu 2002) so this species was also included in our analysis. For details of infection patterns in cockles from both study areas during winter 2002-03 see Tables 4.1 and 4.2 and Figure 4.6.

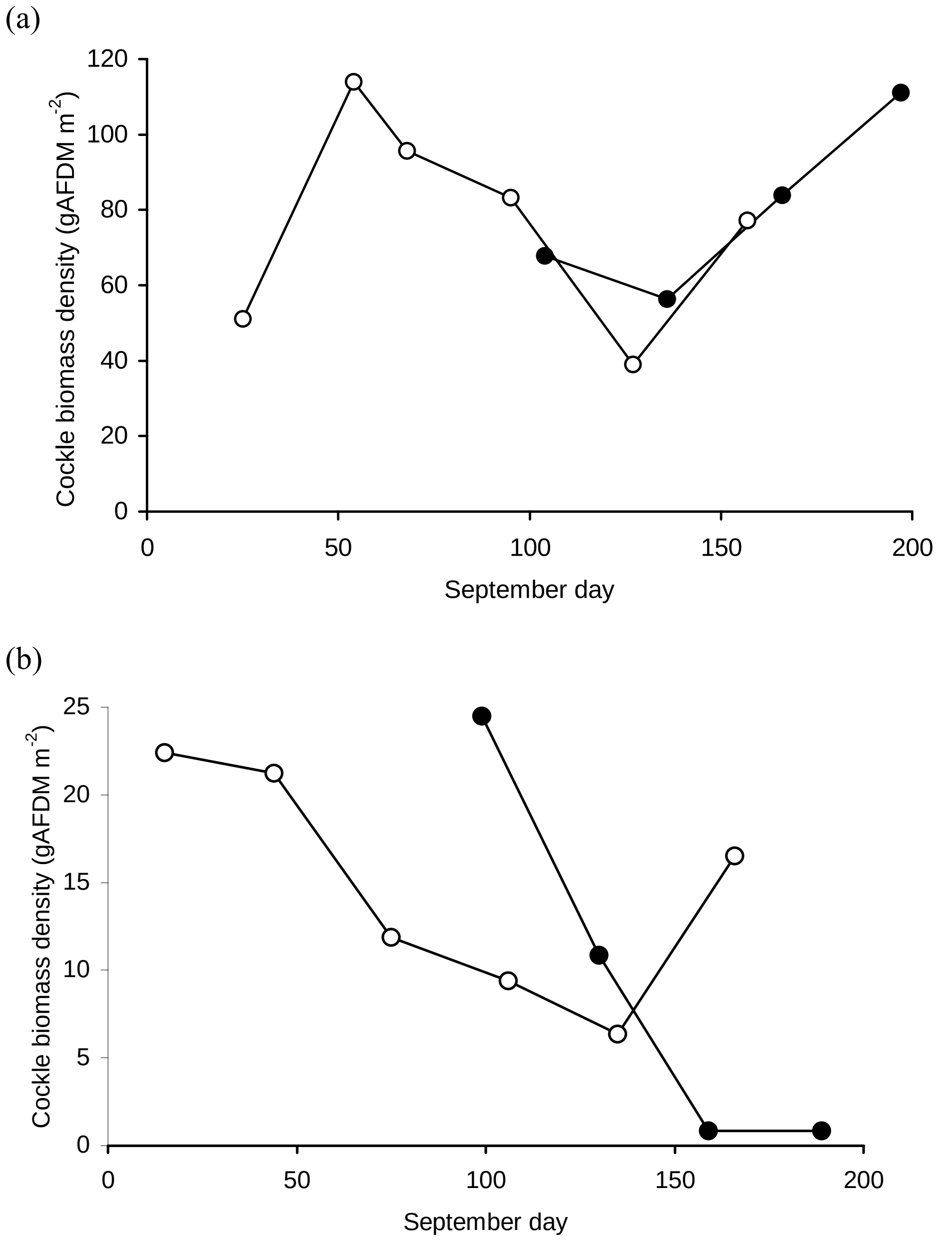


Figure 4.1 Cockle biomass densities at a. the Burry Inlet and b. Hoylake. Closed circles indicate data collected during winter 2001-02, open circles indicate data collected during winter 2002-03.

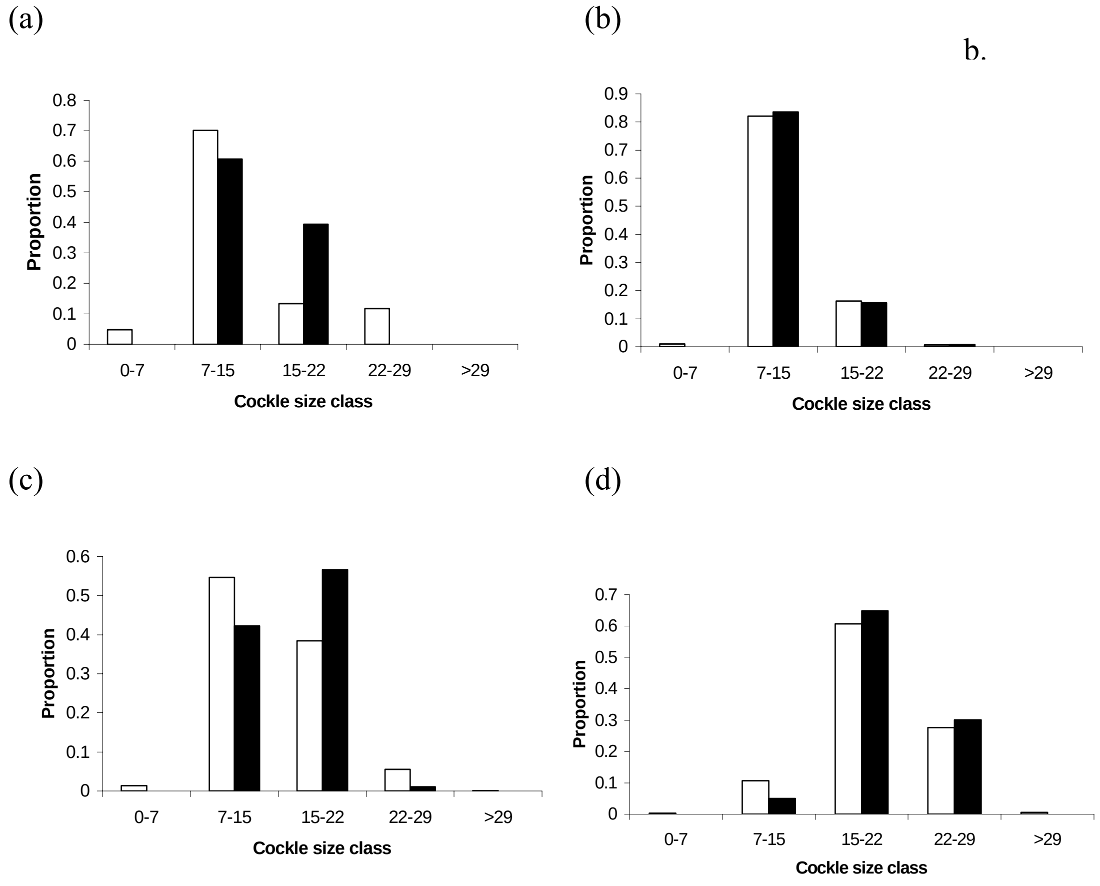


Figure 4.2. Comparison of the availability of each cockle size class (white bars) and the prey size selection of oystercatchers (black bars) at both study sites. Values shown are proportions based the mean numbers of each cockle size class collected and the mean number of prey remains collected during each winter at a. Burry Inlet 2001–2002; b. Hoylake 2001–2002; c. Burry Inlet 2002–2003; d. Hoylake 2002–2003.

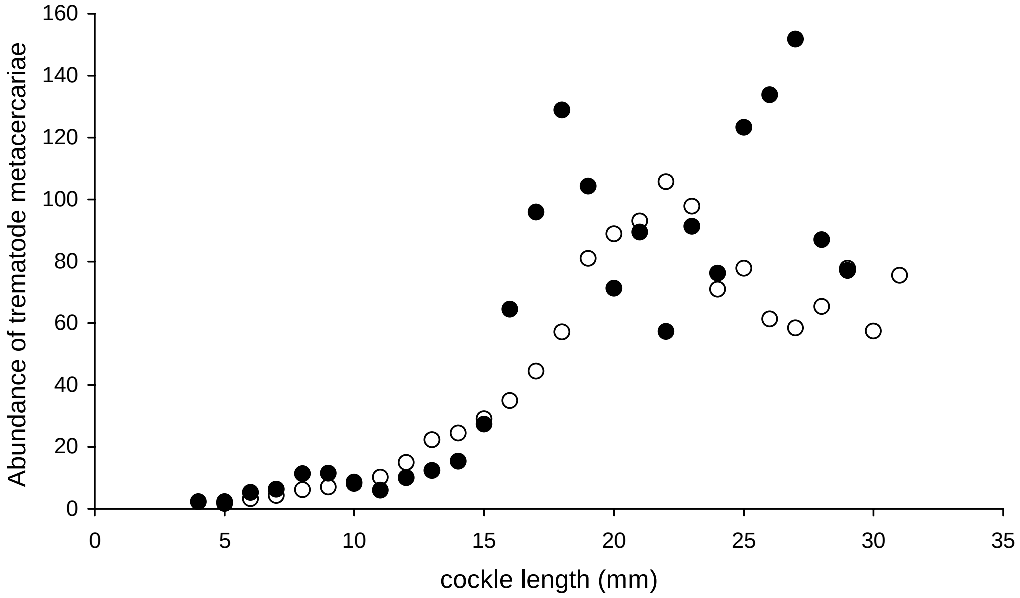
Table 4.1 Infection characteristics of the four trematode species present in cockles and liable to infect oystercatchers at the Burry Inlet (*n* = number of cockles in sample). *M. minutus* results were obtained by pooling both seasons data, results displayed for the other 3 species were from winter 2002-03 only (when each species was identified and recorded separately).

Species	Result	Cockle size class				
		0-7mm	7-15mm	15-22mm	22-29mm	>29mm
Meiogymnophallus minutus	*n*	379	1422	1294	815	17
	Abundance	0.4	5	46	67	64
	Prevalence	19	69.2	95.7	96.8	100
	Range	0-10	0-160	0-1039	0-682	5-200
	Variance/mean	3.2	16.8	100.9	78.7	31.4
Himasthla continua	*n*	147	871	827	453	16
	Abundance	0.4	0.5	0.9	1.1	0.5
	Prevalence	22.4	31.6	46.7	47.7	31.3
	Range	0-6	0-7	0-13	0-12	0-3
	Variance/mean	2.6	1.8	2.4	2.9	1.6
Himasthla interrupta	*n*	147	871	827	453	16
	Abundance	2	5	17	25	8
	Prevalence	79	87.4	97.3	97.8	100
	Range	0-16	0-41	0-96	0-137	1-34
	Variance/mean	2.2	5.3	13.6	20.4	10.9
Psilostomum brevicolle	*n*	147	871	827	453	16
	Abundance	0.1	0.2	0.5	0.6	0.5
	Prevalence	6.8	18.7	29.9	27.8	37.5
	Range	0-2	0-3	0-10	0-10	0-2
	Variance/mean	1.1	1.2	2.1	2.7	1.1

Table 4.2 Infection characteristics of the four trematode species present in cockles and liable to infect oystercatchers at Hoylake (*n* = number of cockles in sample).

Species	Result	Cockle size class				
		0-7mm	7-15mm	15-22mm	22-29mm	>29mm
Meiogymnophallus minutus	*n*	30	516	557	323	4
	Abundance	1	37	265	490	1575
	Prevalence	30	86.6	99.9	99.7	100
	Range	0-7	0-673	0-1335	0-3931	400-3080
	Variance/mean	4.1	67.1	104.6	373.5	856.3
Himasthla continua	*n*	3	142	465	314	3
	Abundance	21	21	9	8	9
	Prevalence	100	92.9	94.8	96.8	100
	Range	6-32	0-137	0-100	0-47	1-15
	Variance/mean	8.7	20.6	14.6	6.9	5.8
Himasthla interrupta	*n*	3	142	465	314	3
	Abundance	2	15	38	61	148
	Prevalence	66.7	93	99.6	100	100
	Range	0-4	0-70	0-171	10-235	90-259
	Variance/mean	2	10.2	16.4	24.1	62
Psilostomum brevicolle	*n*	3	142	465	314	3
	Abundance	0	0.1	0.1	0.2	0
	Prevalence	0	8.5	12	17.2	0
	Range	0	0-2	0-3	0-3	0
	Variance/mean	0	1.1	1.2	1.2	0

(a)



(b)

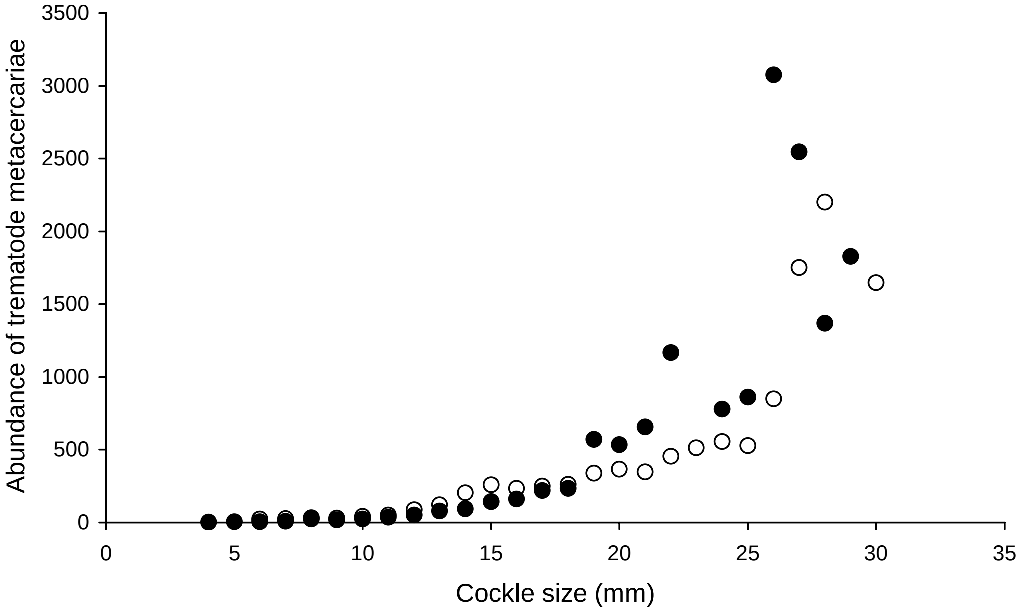


Figure 4.3 Abundance of trematode metacercariae that are likely to infect oystercatchers according to cockle shell length at a. the Burry Inlet and b. Hoylake. Closed circles indicate data collected during winter 2001-02; open circles indicate data collected during winter 2002-03

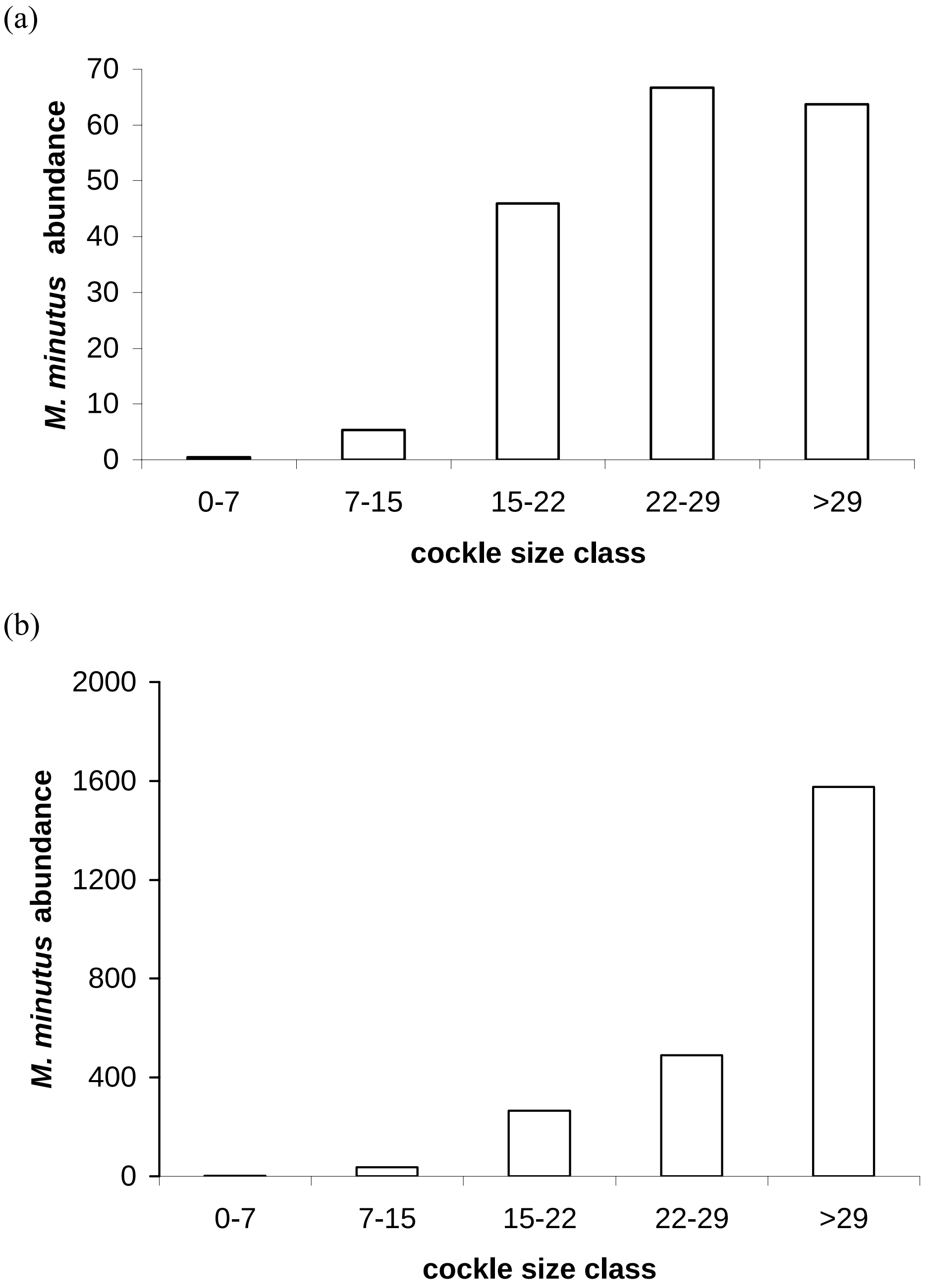


Figure 4.4 Abundance of *Meiogymnophallus minutus* metacercariae according to cockle size class (data pooled from both winter seasons) at a. the Burry Inlet and b. Hoylake.

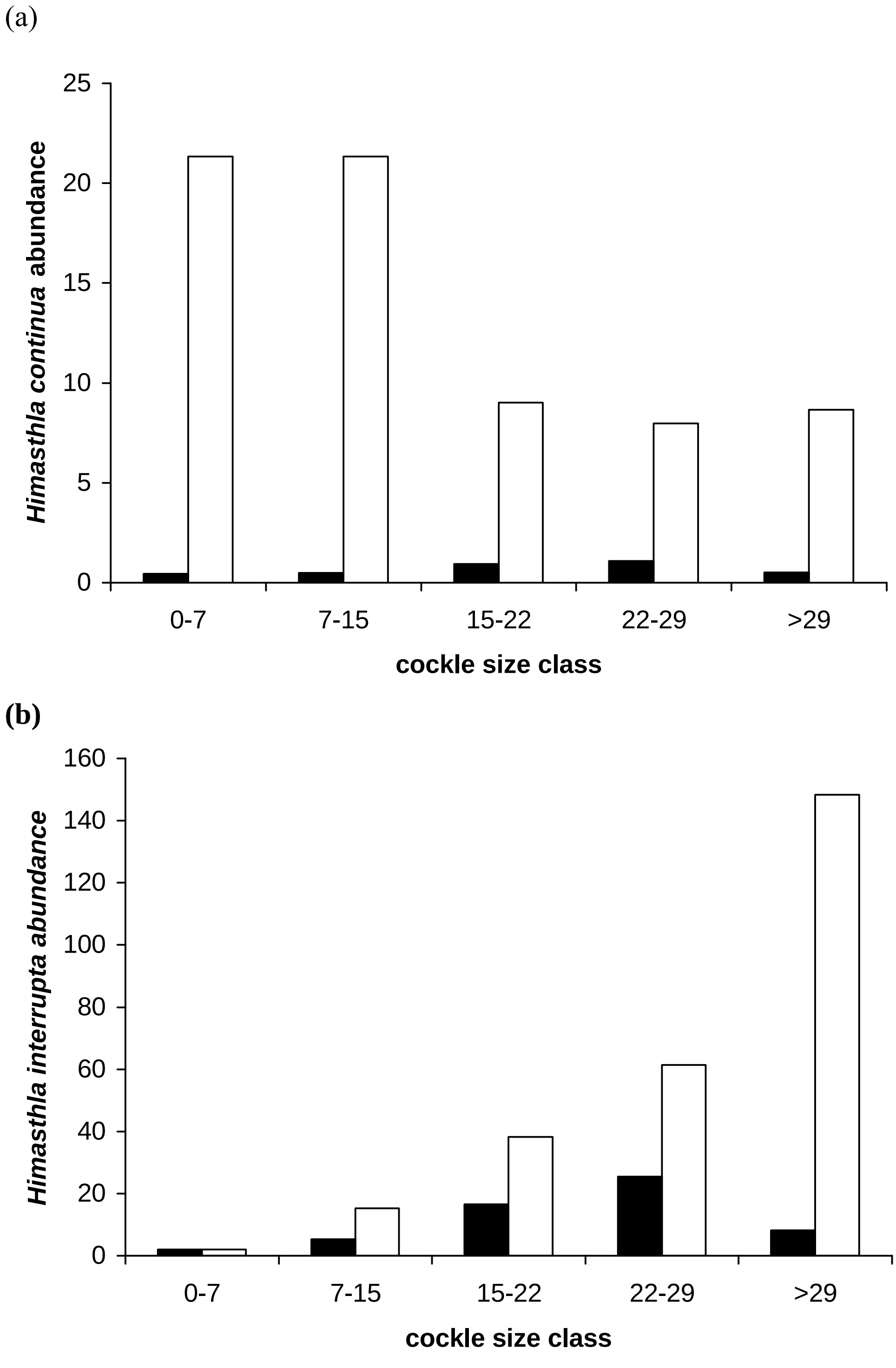


Figure 4.5 Abundance of a. *Himasthla continua* metacercariae and b. *Himasthla interrupta* metacercariae in cockles during winter 2002-03. Filled bars indicate abundances at the Burry Inlet; open bars indicate abundances at Hoylake.

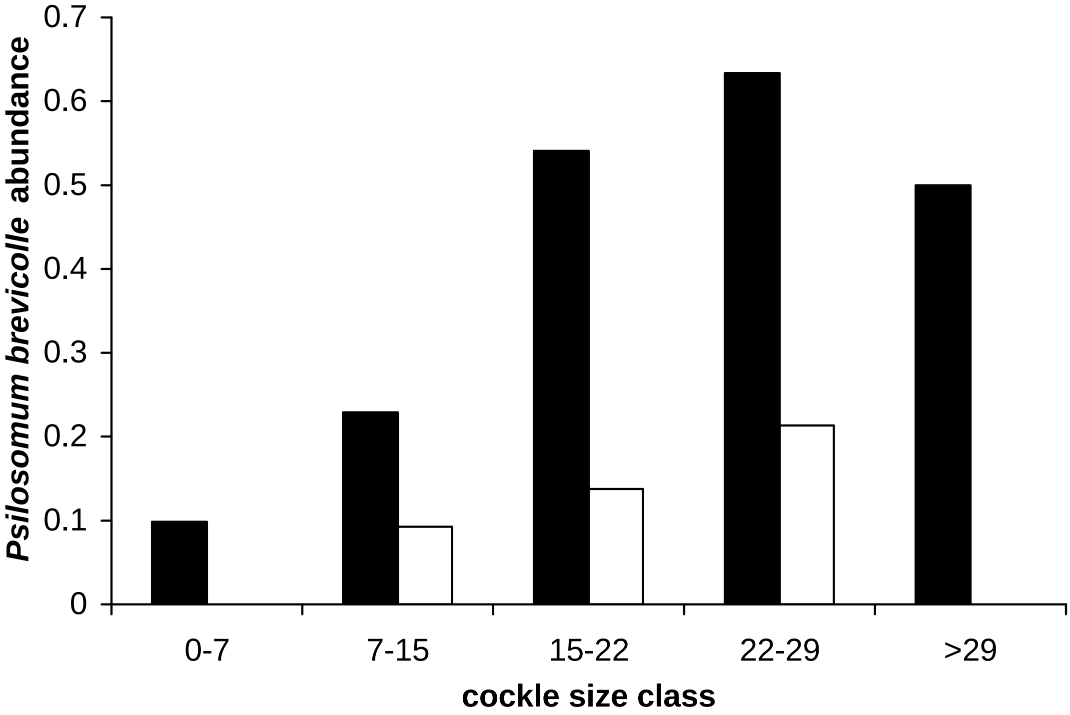


Figure 4.6 Abundance of *Psilostomum brevicolle* metacercariae in cockles during winter 2002-03. Filled bars indicate cockles from the Burry Inlet; open bars indicate cockles from Hoylake.

4.5 Energy and parasite intake rate: methods

4.5.1 OBSERVED ENERGY AND PARASITE INTAKE RATES ON THE BURRY INLET

In order to compare predicted energy intake rates and parasite ingestion rates with observed data, the observed energy intake rate each month and observed parasite ingestion rate each month at the Bury Inlet were calculated using foraging data from a previous study combined with the parasite data collected during this study. Energy intake rates from each cockle size class (g AFDM min^{-1}) were recorded during November 1994 to February 1995 on the Burry Inlet (estimated from observation of 144 birds taking 586 cockles – Norris & Johnstone 1998a). The sum of the energy intakes across all size classes provided observed total energy intake rates (g AFDM min^{-1}) from which observed mean intake rates per month were calculated. Because the energy content of each cockle size class was known and intake rates from each cockle size class were calculated separately (Norris & Johnstone 1998a), it was possible to calculate the number of cockles of each size class consumed per minute in order to obtain the observed intake rates. The abundance of trematode metacercariae likely to infect oystercatchers and the abundance of *Meiogymnophallus minutus* metacercariae recorded in each cockle size class during both winters of this study was multiplied by the number of cockles in the corresponding size class consumed per minute and the results summed across all size classes. This gave an estimate of the observed parasite ingestion rate (parasites min^{-1}) each month.

4.5.2 PREDICTED ENERGY AND PARASITE INTAKE RATES

To explore the possibility of a trade-off between energy intake and exposure to parasites, a modified version of the functional response model developed by Norris & Johnstone (1998*a*) was used. The modification is described by Norris (1999) but a short explanation is given here. The model was developed to predict the energy intake rate of oystercatchers feeding by touch, depending on the density of prey available. Cockles vary in size and hence in energy content. If there are *i* size classes of cockle (in this case there are five size classes) then the energy intake rate *E/T* (g AFDM sec^{-1}) can be described as

$$\frac{E}{T} = \frac{\sum E_i \lambda_i P_i Q_i}{1 + \sum \lambda_i (h_i P_i + (1 - P_i) w_i) Q_i}, \tag{4.3}$$

where E_i is the energy content of prey type *i* (g AFDM), h_i is the handling time of prey type *i* (s), w_i is the waste handling time of prey type *i* (s), P_i is the probability that a cockle of size *i* attacked by a bird will be successfully opened, λ_i is the encounter rate with prey type *i* (s^{-1})and Q_i is the probability that a predator will take an individual of prey type *i* after it is encountered.

Equation 4.3 with the cockle densities recorded at the Burry Inlet during winter 1994-95 and during winter 2002-03 at Hoylake (mean number of cockles of each size class m^{-2} throughout each winter) was used to determine the predicted energy intake rate according to cockle size classes included in an oystercatcher's diet (the "size selection strategy"). By replacing E_i with L_i (the mean abundance of trematode metacercariae recorded in cockles of size class *i* from each study area throughout both winters) the model was used to calculate the predicted rate at which parasites were ingested (parasites sec^{-1}) depending on the cockle size classes included in a bird's diet. This analysis was repeated for both the 4 trematode species likely to infect oystercatchers (*Himasthla interrupta*, *Himasthla continua*, *Meiogymnophallus minutus* and *Psilostomum brevicolle*) and specifically for the most common species, *M. minutus*.

4.5.3 PARAMETERS REQUIRED FOR FUNCTIONAL RESPONSE MODEL

Energy content of cockles was estimated using equation 4.1. The energy intake rates displayed were calculated using the energy content of cockles on September 1st. Parameter values are listed in Table 4.3 and abundance of *M. minutus* metacercariae can be found in Tables 4.1 and 4.2. The encounter rate with size class *i* (s^{-1}) was estimated using a simple random search model proposed by Hulscher (1976, 1982). This was appropriate as oystercatchers hammering cockles at both Hoylake and the Burry Inlet search for them by touch (Norris & Johnstone 1998*a*; Johnstone unpublished data). Hulscher's model estimates the encounter rate with a cockle of size class *i* as

$$\lambda_i = \frac{D_i a_i}{t_i}, \qquad (4.4)$$

where λ_i is the encounter rate with a cockle size *i* (s^{-1}), D_i is the density of size class *i* in the sand (m^{-2}), a_i is the mean effective touch area of a cockle size *i* (m^{-2}) and t_i is the duration of a single probe including the interprobe interval (s). The parameter values for this equation were obtained from Norris & Johnstone (1998*a*,*b*) and Norris (1999).

Smaller cockles (<22mm) are sometimes opened without being lifted out of the substrate and carried. Cockles opened this way ("*in situ*") have different parameter values than those carried to a preferred area prior to opening. At the Burry Inlet it was estimated that 55.9% of cockles <22mm were opened *in situ* (the level observed during Norris & Johnstone's (1998*a*) study). h_i and w_i of cockles carried prior to opening at the Burry Inlet were estimated using the linear regression models published in Norris & Johnstone (1998*a*). h_i of cockles <22mm in length opened *in situ* was estimated to be 43.8% as long and w_i 26.6% as long as for cockles that were carried prior to opening (Norris & Johnstone 1998*a*). The probability of successfully opening a cockle of size class *i* (P_i) at the Burry Inlet was assumed to be 75% if a cockle was attacked and opened *in situ* (Norris & Johnstone 1998*a*). For carried cockles, P_i was estimated using the logistic regression model described in Norris & Johnstone (1998*a*).

At the Dee estuary parameter estimates for the functional response model were based on the observation of 400 cockles hammered opened by oystercatchers feeding at the Dee estuary (Johnstone unpublished data). It was estimated that 45.5% of cockles <22mm at Hoylake were opened *in situ*. Regression models describing h_i and w_i and a logistic regression model describing P_i for carried cockles were constructed (for details see Table 4.3 legend). h_i of cockles <22mm opened *in situ* was estimated to be 47.3% as long and w_i was estimated to be 14.4% as long as for cockles carried prior to opening. P_i at the Dee estuary was assumed to be 40.2% for cockles attacked *in situ*.

Table 4.3 Parameter values for each study site, used in the functional response model (equations 3 and 4). Handling times at Hoylake were determined using a linear regression model in the form $y = 7.21+16.8x$ a significant fit with observed handling times at the Dee ($P = < 0.001$). Waste handling times were determined using a linear regression model in the form $y = 12.4+2.57x$ ($P > 0.05$) where y = handling time (s) and x = cockle size class (integer value 1-5). Probability that a cockle of size i would be successfully opened was determined using a logistic regression model in the form $y = 1/(1+e^{-(2.11-0.5927x)})$ where y = probability of success, x = cockle size class and e is the natural logarithm base. This model provided a significant fit with observed data ($P = <0.001$) (Johnstone unpublished data).

Study Site	Parameter	Unit	Cockle size class (mm)				
			0-7	7-15	15-22	22-29	>29
Burry Inlet	h_i	s	11.954	20.569	29.184	37.799	46.414
	w_i	s	19.365	16.35	13.335	10.32	7.305
	P_i		0.899	0.858	0.805	0.738	0.657
	D_i 1994-95	m^{-2}	2.35	121.508	96.073	124.158	33.288
	D_i 2001-02	m^{-2}	94.074	1384.259	262.407	231.667	0.185
	D_i 2002-03	m^{-2}	19.111	784.444	551.667	79.222	1.778
	a_i	m^2	0.000061	0.000188	0.000370	0.00059	0.000878
	t_i	s	0.1	0.12	0.15	0.15	0.15
	L_i (all trematodes) 2002-03		3.162	12.125	53.387	87.698	72.438
Hoylake	h_i	s	24.01	40.81	57.61	74.41	91.21
	w_i	s	14.97	17.54	20.11	22.68	25.25
	P_i		0.820	0.716	0.582	0.435	0.299
	D_i 2001-02	m^{-2}	4.167	345.833	68.333	2.667	0.167
	D_i 2002-03	m^{-2}	0.354	12.743	71.681	33.982	0.619
	a_i	m^2	0.000061	0.000188	0.000370	0.00059	0.000878
	t_i	s	0.1	0.12	0.15	0.15	0.15
	L_i (all trematodes) 2002-03		25.667	74.127	327.850	529.662	1648.333

4.6 Energy and parasite intake rates: results

4.6.1 OBSERVED ENERGY AND PARASITE INTAKE RATES

Observed energy intake rates varied according to the month they were recorded. The highest was recorded during February 1995, when birds fed at an average of 0.19gAFDM min^{-1}. All observed energy intakes at the Burry Inlet were lower than those predicted when intake rate was maximised. The observed ingestion rates of trematode metacercariae at the Burry Inlet were lower than those predicted when maximising energy intake rates during November and January but higher than predicted during December and February. Observed ingestion rates of *Meiogymnophallus minutus* metacercariae at the Burry Inlet were lower than that predicted when maximising energy intake rates except during February (see Figures 4.7b and 4.10a). These results do not give a clear indication that the observed cockle size selection strategy of oystercatchers at the Burry Inlet minimised parasite ingestion rates.

4.6.2 PREDICTED ENERGY INTAKES ACCORDING TO SIZE SELECTION STRATEGY

Predicted energy intake rates at the Burry Inlet were much higher than at Hoylake, this was mostly attributable to the higher biomass density of cockles but partly because the functional response parameters (for example h_i and P_i) were more favourable at the Burry Inlet (Table 4.3). At the Burry inlet during winter 1994-95 predicted energy intake was maximised when cockles >22mm were included in the diet (Figure 4.8a). During winter 2002-03 at Hoylake, energy intake was maximal if cockles >15mm in length were selected (Figure 4.9a). At Hoylake, energy intakes if all cockles were consumed when encountered were very similar to those when selecting larger cockles (Figure 4.9a).

4.6.3 PREDICTED PARASITE INGESTION RATES ACCORDING TO SIZE SELECTION STRATEGY

At the Burry Inlet predicted parasite ingestion rate when taking into account all trematode metacercariae and specifically *Meiogymnophallus minutus* metacercariae was maximal when cockles >15mm were consumed (Figure 4.10a). At Hoylake predicted parasite ingestion rate was also maximised if cockles >15mm were consumed, this applying to all trematode metacercariae and *Meiogymnophallus minutus* metacercariae only (Figure 4.11a). At both sites, the consequence of selecting all cockles encountered or smaller size classes only was both a lower parasite ingestion rate and a lower energy intake rate (Figures 4.8b, 4.9b, 4.10b & 4.11b). These results indicate a possible trade-off between energy intake and consumption of parasite transmission stages, the results presented here being comparable with those published by Norris (1999).

Figures 4.7, 4.10 and 4.11 show that the relationship between cockle size selection strategy and ingestion rate of *Meiogymnophallus minutus* metacercariae closely follows that shown when taking into account all trematode metacercariae at both study areas. This species was therefore chosen as the basis for an attempt to model the parasite infrapopulation likely to establish in the definitive host depending on the cockle sizes selected while feeding.

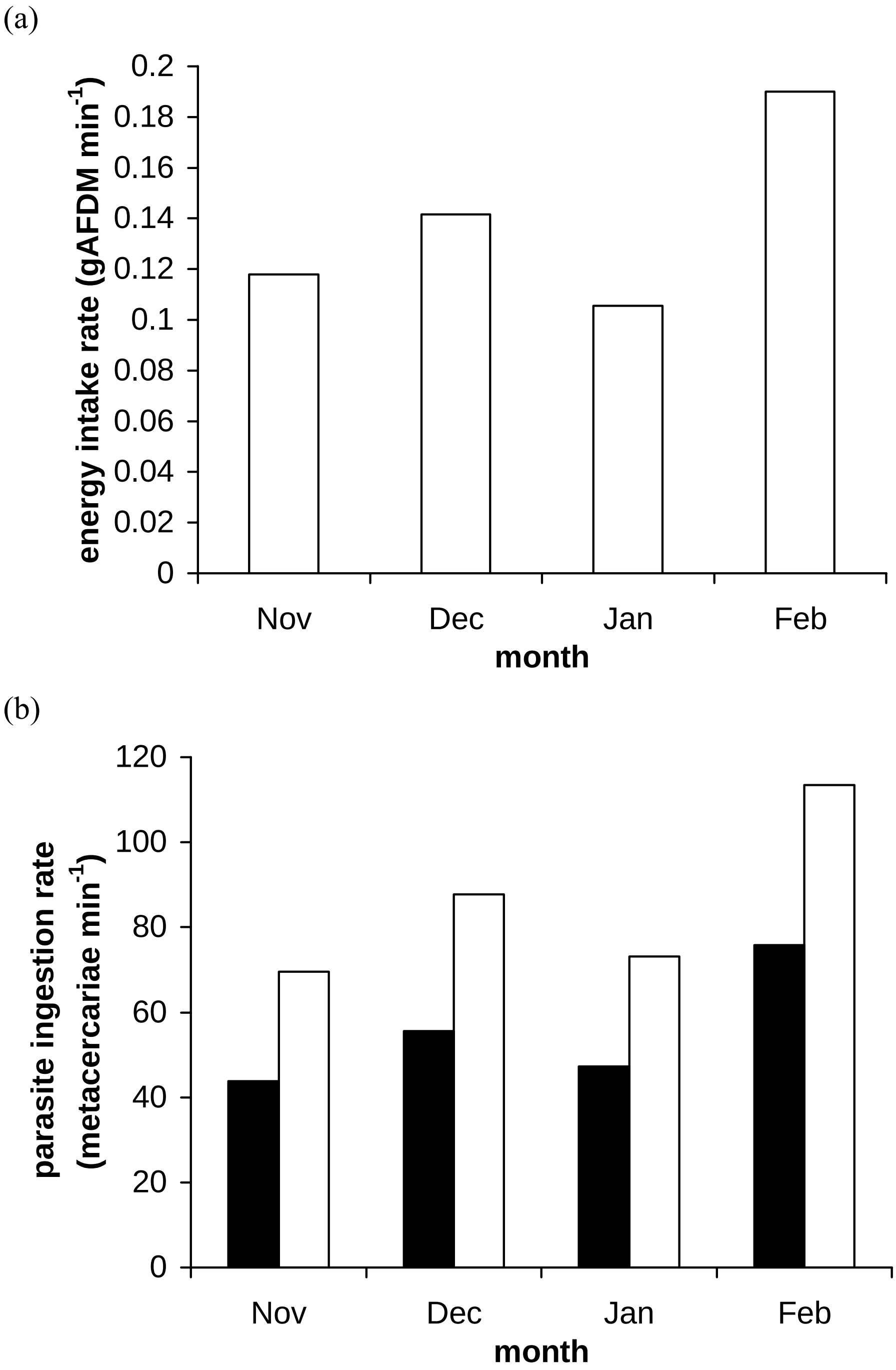


Figure 4.7 Graph a. Monthly average observed energy intake rates (g AFDM min^{-1}) and graph b. observed parasite ingestion rates at the Burry Inlet during winter 1994-95. Graph b. shows the ingestion rates of all trematode metacercariae (open bars) and the ingestion rates of *Meiogymnophallus minutus* metacercariae only (closed bars).

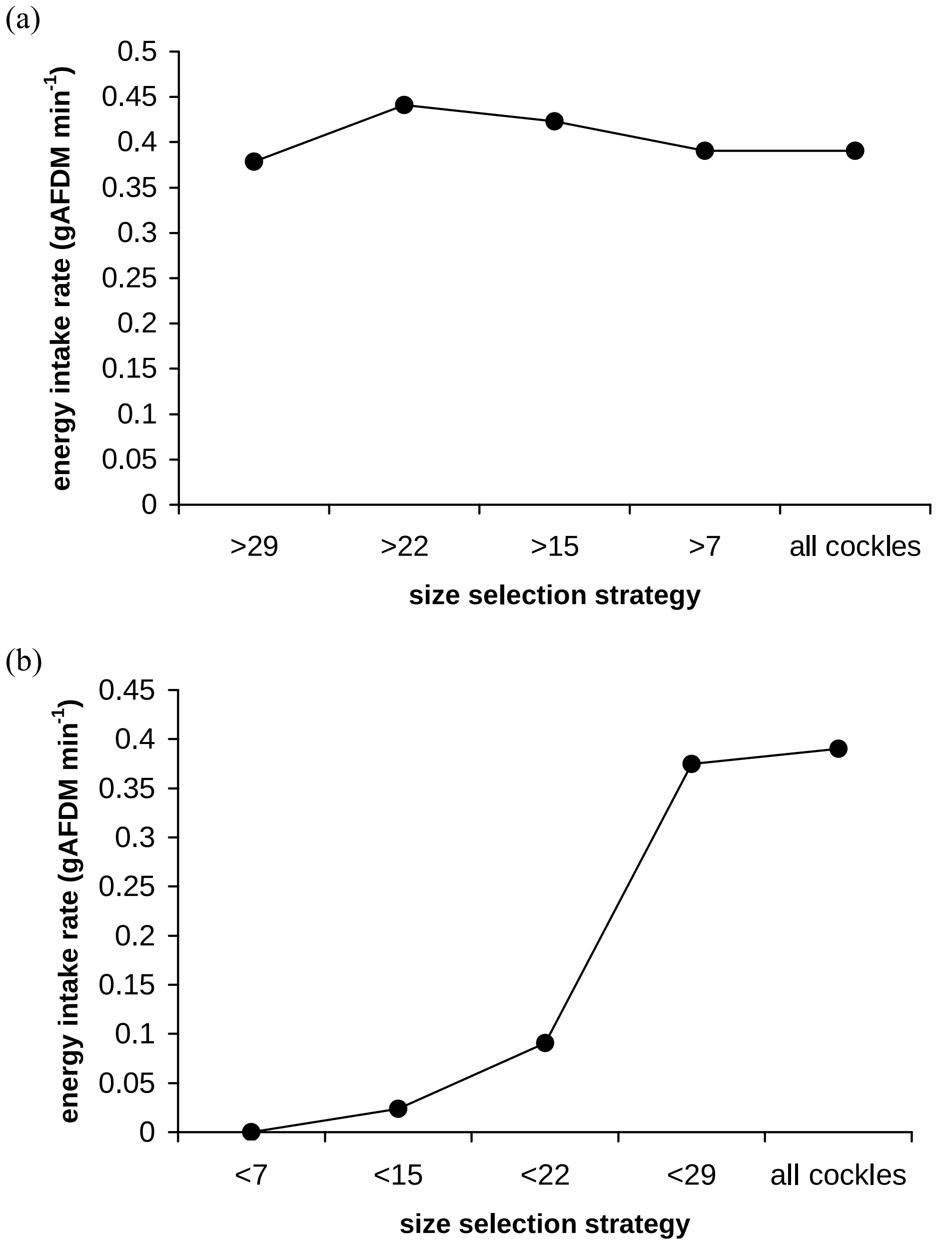
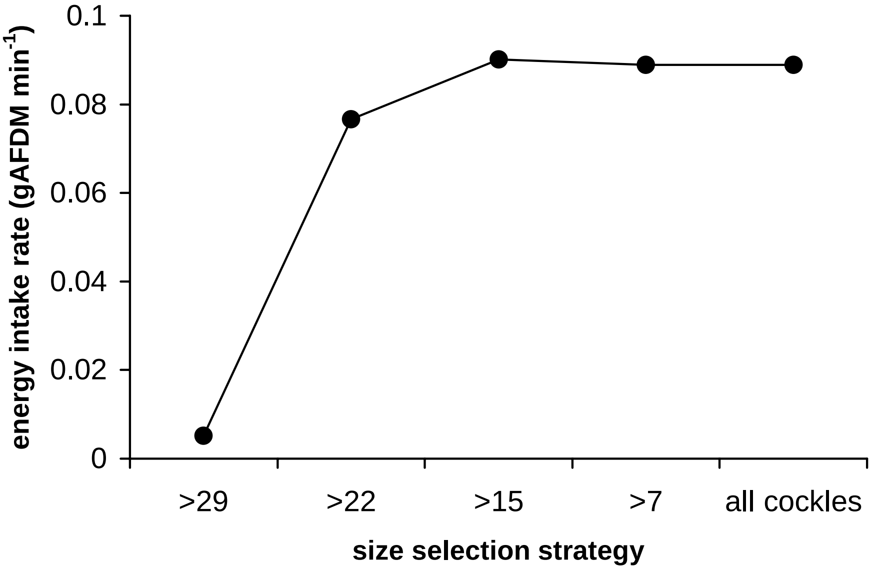


Figure 4.8 The effect of cockle size selection strategy on predicted energy intake rates at the Burry Inlet during winter 1994-95 (g AFDM min^{-1}): a. Finding the maximum possible energy intake rate, b. the effect of selecting smaller size classes on energy intake rate.

(a)



(b)

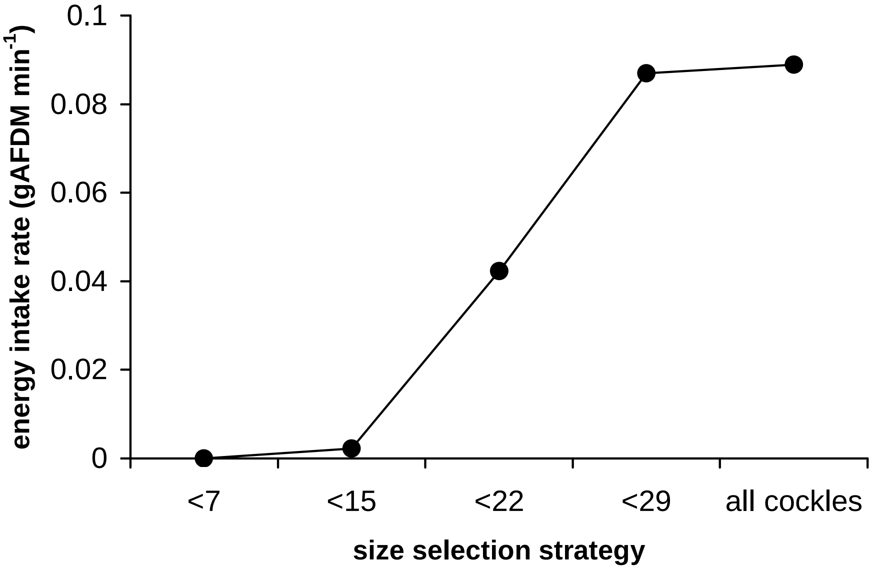
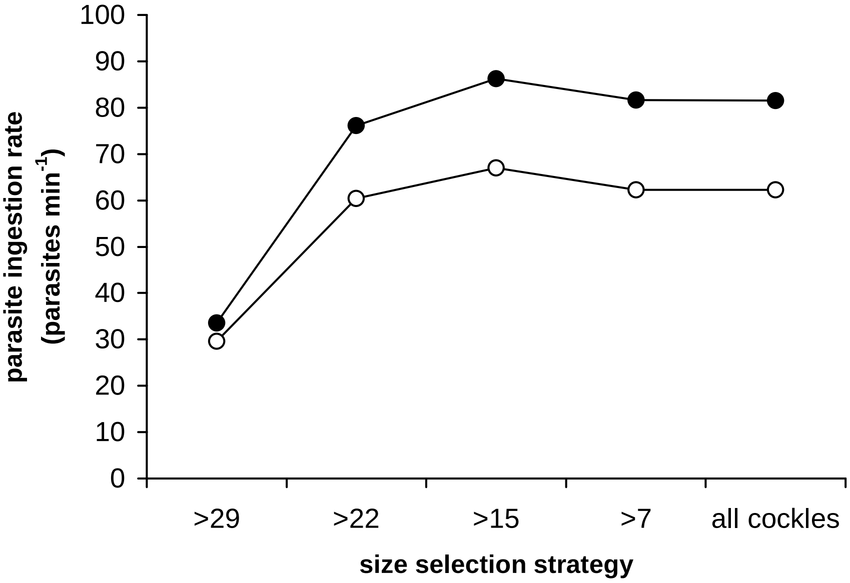


Figure 4.9 The effect of cockle size selection strategy on predicted energy intake rates at Hoylake during winter 2002-03 (g AFDM min^{-1}): a. finding the maximum possible energy intake rate, b. the effect of selecting smaller size classes on energy intake rate.

(a)



(b)

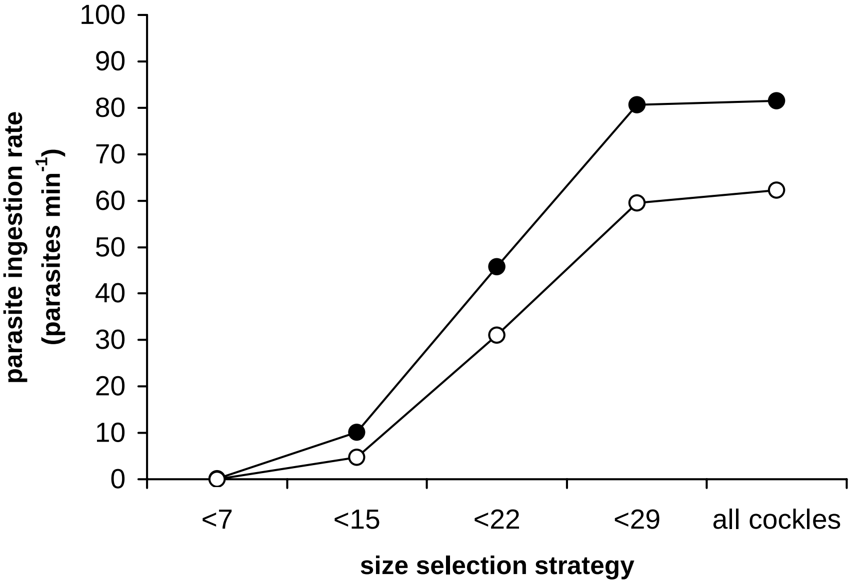


Figure 4.10 The effect of cockle size selection on predicted parasite ingestion rates at the Burry Inlet during winter 1994-95 (parasites min^{-1}). Closed circles indicate total trematode metacercariae; open circles indicate *M. minutus* only. Graph a. parasite ingestion rates when attempting to maximise energy intake rate; graph b. the effect of selecting smaller size classes on parasite ingestion rate.

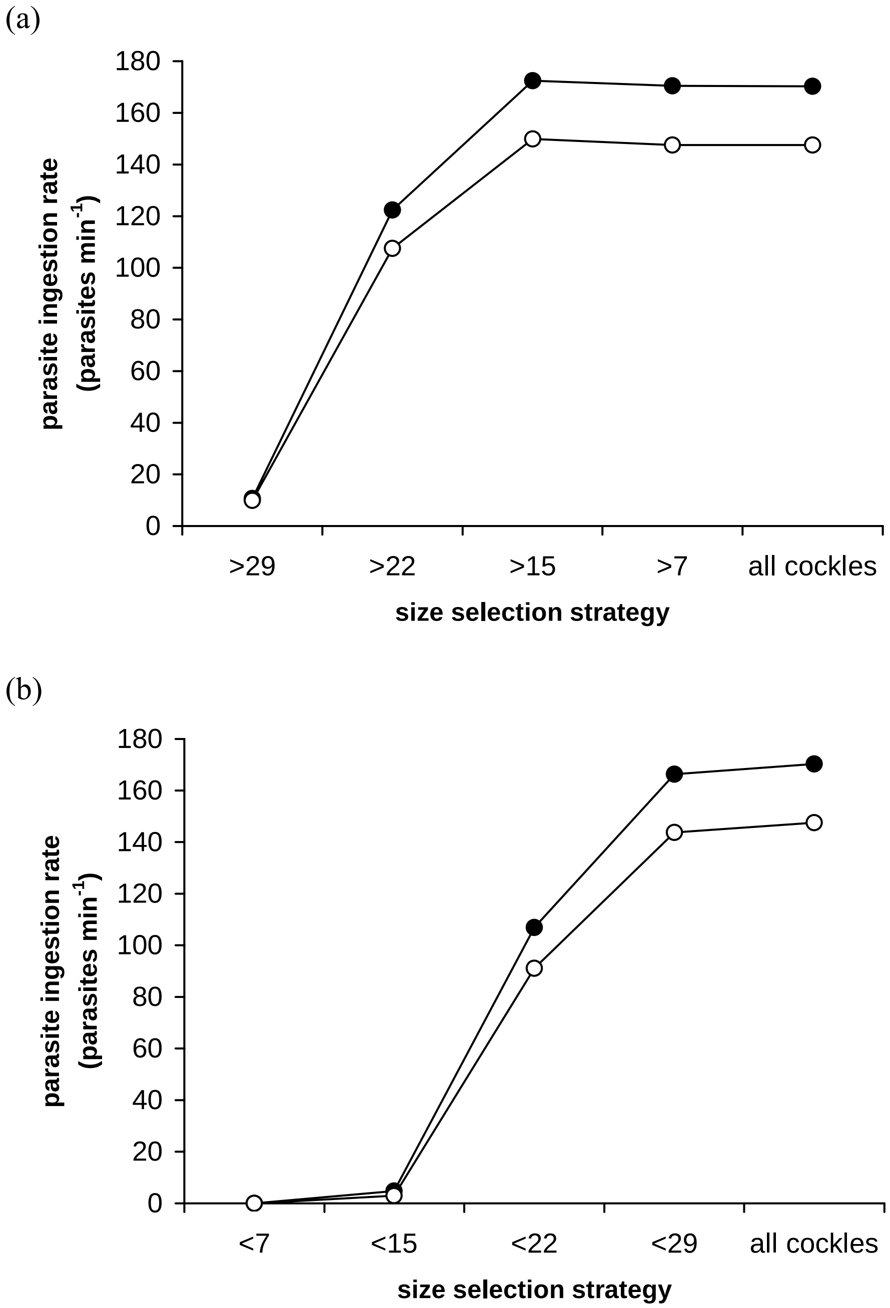


Figure 4.11 The effect of cockle size selection on predicted parasite ingestion rates at Hoylake during winter 2002-03 (parasites min^{-1}). Closed circles indicate total trematode metacercariae; open circles indicate *M. minutus* only. Graph a. parasite ingestion rates when attempting to maximise energy intake rate; graph b. the effect of selecting smaller size classes on parasite ingestion rate.

4.7 Daily energy and parasite intake: methods

4.7.1 FORAGING AND THE PRESENCE OF A DIGESTIVE BOTTLENECK

As described above, counts of feeding oystercatchers indicated a contrast in the time spent feeding at the Burry Inlet and at Hoylake. Previous studies have shown us that the rate at which food can be consumed by foraging oystercatchers is limited by the amount an individual's digestive tract can hold (11.92gAFDM) and the rate at which ingested food can be processed (0.03gAFDM min^{-1}) (Kersten & Visser 1996; Zwarts et al 1996). Because of this digestive bottleneck, oystercatchers have a choice of foraging strategy during the time their feeding sites are available. An individual may feed at the intake rate dictated by food availability and prey choice until full and then continue to feed at the rate dictated by the process of digestion for the rest of the available time (as observed at the Dee estuary). Alternatively, an individual may feed at the intake rate dictated by food availability and prey choice until full and then roost while digesting food before returning to the feeding area and re-filling its gut before the tide covers the area (as observed at the Burry Inlet).

4.7.2 ESTIMATION OF DAILY ENERGY INTAKES AT EACH STUDY SITE

Daily energy intakes were calculated using the observed monthly mean intake rates at the Burry Inlet and the intake rates predicted by the functional response model with the mean density of each cockle size class recorded throughout winter 1994-95 at the Burry Inlet and throughout winter 2002-03 at Hoylake. Predicted intake rates were recalculated every 10 days, from November 1st to February 28th, to take into account the decrease in intake rate through the winter due to the decrease in cockle flesh content. This time period was chosen to allow direct comparison with observed intake data from the Burry Inlet. Daily energy intake at the Burry Inlet was calculated assuming birds arrived at the feeding area with an empty gut, fed to capacity and then rested. The birds were then assumed to feed for a second period consuming the same amount that they had digested during the low water period. Finally the birds were assumed to leave the feeding grounds with a full gut and have sufficient time over the high water period to digest the entire gut contents. The relationship between the time spent roosting and the time spent feeding during the second period (z) was calculated thus:

$$z = \left(\frac{gr}{r} \right) \qquad (4.5)$$

where g is the gut processing rate and r is the initial intake rate. The amount of time spent roosting over low water was calculated by dividing the time available by z and the length of the second foraging interval assumed to be the time left before the feeding area was covered by the incoming tide (allowing sufficient time during high water to digest 11.92g AFDM). Daily energy intake at the Dee estuary was calculated assuming continuous foraging over the entire low water period. Birds arrived at the feeding area with room for 7.35g AFDM in their gut (the amount that could be digested during the time the feeding area was covered by water). They were assumed to feed to capacity and then continue to forage at the limited intake rate for the remaining time the area was exposed. For a comprehensive exploration of possibilities, the daily energy consumption at each study site was also calculated using the alternative strategy, so the possible energy consumption at the Burry Inlet assuming continuous foraging was estimated along with the possible consumption at Hoylake assuming a break for digestion.

4.7.3 ESTIMATING DAILY ENERGY REQUIREMENT AT EACH STUDY SITE

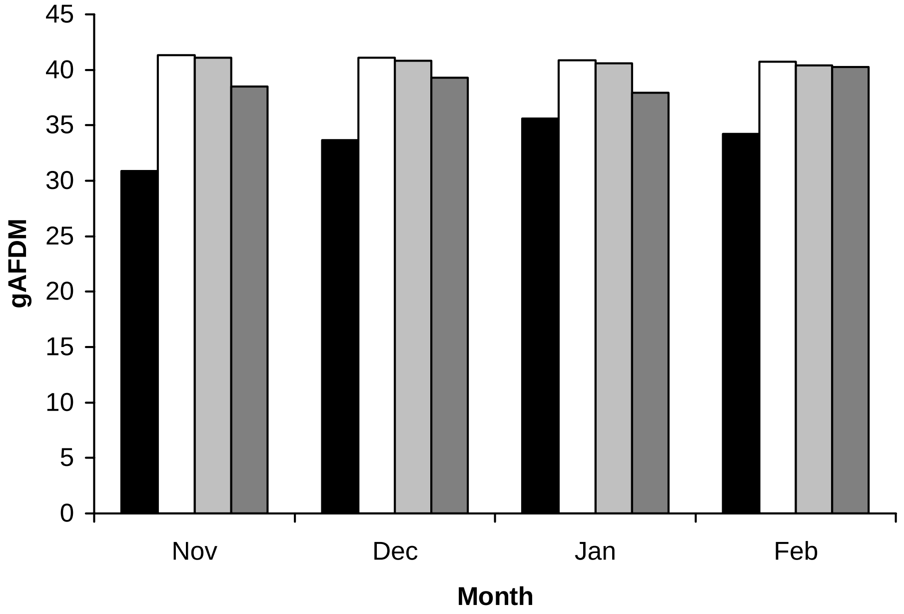
To check the feasibility of our models of daily energy consumption, daily energy expenditure was calculated using the method proposed by Stillman et al (2000). This is based on the results of experiments on oystercatchers kept in outdoor aviaries (Kersten & Piersma 1987) and an extrapolation to field conditions (Zwarts et al 1996). Daily energy expenditure was divided into general expenditure on activity, digestion etc. and thermoregulatory expenditure. General expenditure was assumed to be 673.2kJ per day (Zwarts et al 1996; Stillman et al 2000). Thermoregulatory expenditure was assumed to increase by a constant rate (31.8kJ $^{\circ}C^{-1}$) if the air temperature dropped below a critical temperature of 10ºC. If the temperature was above this level then it was assumed there were no thermoregulatory costs. The daily air temperature at the Burry Inlet during winter 1994-95 was extrapolated from synoptic weather measurements taken at Milford Haven. The daily air temperature at Hoylake was estimated by averaging synoptic weather measurements taken at Bidstone each day during winters 1997-2000 because data for winter 2002-03 is not yet available. All weather data was provided by the BADC meteorological data service. General expenditure was added to the thermoregulatory expenditure for each day to obtain the total daily energy expenditure. The mean value each month was then calculated.

4.8 Daily energy and parasite intake: results

At the Burry Inlet, if oystercatchers maximised their intake rates and fed continuously during the available time there was the potential to exceed their daily requirements by up to 34% each day. Even when observed energy intake rates were used, despite the evidence that these were lower than the maximum possible, daily requirements could be exceeded by up to 25% per day (Figure 4.12a.). In contrast, at Hoylake energy requirements were only exceeded during November, even if the birds attempted to maximise their energy intake and feed during all the available time (Figure 4.12b.). It appears that as far as food availability is concerned, oystercatchers overwintering at Hoylake may only be able to survive in the area during early winter while oystercatchers spending the winter at the Burry Inlet experience a plentiful food supply throughout their visit.

If oystercatchers at the Burry Inlet fed only at their initial intake rate and roosted while digesting over low water, they were still capable of exceeding their daily energy requirements over the coldest winter months when maximising energy intake rates (Figure 4.13a.). Modelling this strategy using observed intake rates provided a close fit with daily energy requirements over the corresponding time period, although a slight deficit in energy intake compared with energy requirement was detected during January. An increase in intake rates and therefore energy intake during February may be attributable to this deficit (Figures 4.7a and 4.13a). If oystercatchers at Hoylake employed the same strategy, it is clear that they would be unable to meet their energy requirements. Our model of this revealed a considerable deficit between energy intake and energy requirements from November to February (Figure 4.13b).

(a)



(b)

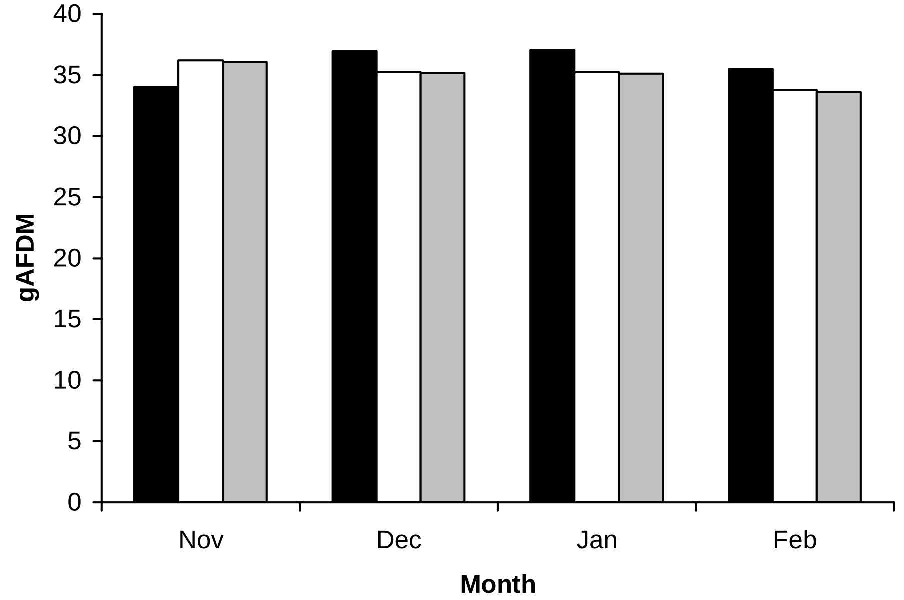
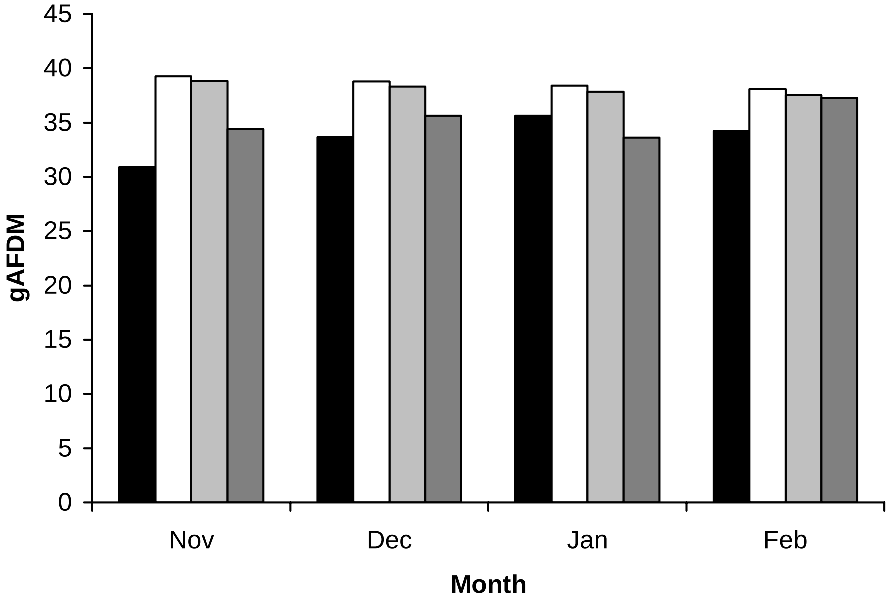


Figure 4.12 Daily energy requirement (black bars) in comparison with predicted daily energy intake when oystercatchers feed continuously during the time available at a. the Burry Inlet and b. Hoylake. White bars represent daily energy intake when intake rates are maximised, pale grey bars represent daily energy intake when all cockle size classes are included in the diet and dark grey bars represent daily energy intake using observed intake rates at the Burry Inlet.

(a)



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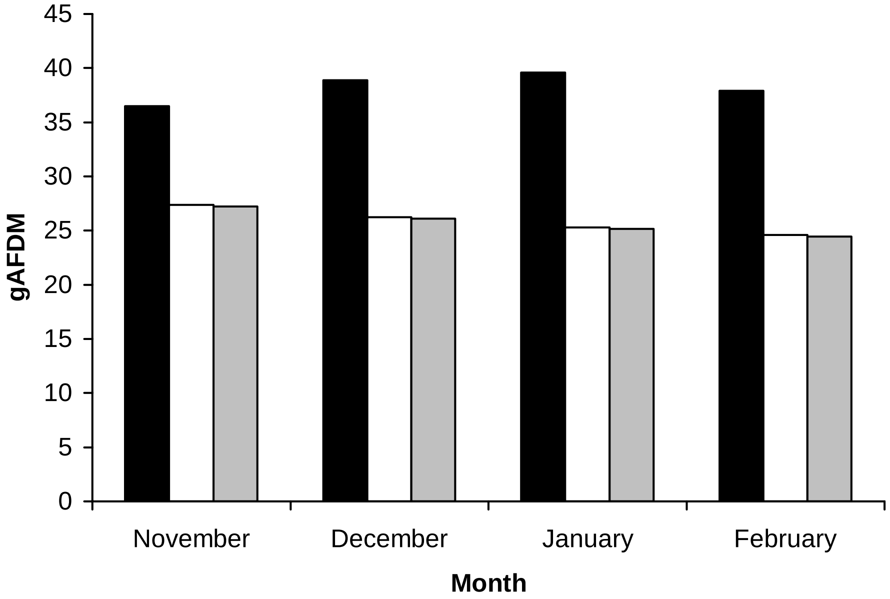


Figure 4.13 Daily energy requirement (black bars) in comparison with predicted daily energy intake when oystercatchers stop feeding after filling the gut to capacity and then refill their gut before the high water period at a. the Burry Inlet and b. Hoylake. White bars represent daily energy intake when intake rates are maximised, pale grey bars represent daily energy intake when all cockle size classes are included in the diet and dark grey bars represent daily energy intake using observed intake rates at the Burry Inlet.

4.9 Parasite infection: methods

An existing model that describes the change in infrapopulation over time in a definitive host, when there is one parasite transmission stage per infected prey item (Lafferty 1992) was adapted for our use. The modification simply replaced the proportion of infected prey items ingested with the number of parasite transmission stages ingested. The model was then used to describe the build up of a *Meiogymnophallus minutus* infrapopulation in an oystercatcher over time. The foraging strategies described in sections 4.7 and 4.8 were used. Observed parasite ingestion rates and predicted parasite ingestion rates (parasites min^{-1}) depending on the cockle size classes included in the diet were estimated as described in sections 4.5 and 4.6. The rate of change in the number of parasites that established in the host intestine – the change in parasite "infrapopulation" (Lafferty 1992) was calculated as

$$di / dt = pq - ui^{m} \tag{4.6}$$

where *i* is the existing parasite infrapopulation, *t* is time (day), *p* is the intake rate of parasites (parasites day^{-1}), *q* is the proportion of ingested parasites that establish within the host (0.2), *u* is the instantaneous per capita mortality rate of the parasite (0.1day^{-1}) (Smith 1994) and *m* is a coefficient of the intensity dependent increase in mortality rate (0.001).

To estimate *p* for a bird wintering at the Burry Inlet, the observed and the predicted parasite ingestion rate was simply multiplied by the time spent feeding each day (mins). Estimating *p* for a bird wintering at Hoylake was more complicated because the digestive bottleneck meant that energy intake rates changed during each feeding period. Parasite ingestion rates according to cockle size selection strategy when feeding at the initial energy intake rate were predicted using the functional response model. Parasite ingestion rates when feeding at the gut processing rate were estimated by proportionally reducing the densities of each cockle size class until the functional response model predicted energy intakes of 0.03gAFDM min^{-1} when the rate maximising strategy was used. The parasite ingestion rate was then recalculated using the corresponding proportional reduction in cockle density. For example, by assuming that densities of all cockle size classes were 19.8% of the observed densities, the energy intake rate at Hoylake during winter 2002-03 when feeding on cockles >15mm in length was 0.03gAFDM min^{-1}. The limited parasite ingestion rate was then estimated by assuming that cockle densities were 19.8% of the observed values. Daily parasite ingestion (*p*) was estimated as the time spent feeding at the initial intake rate per day multiplied by the initial parasite ingestion rate plus the time spent feeding at the gut processing rate multiplied by the limited parasite ingestion rate.

Parameter values for establishment and mortality rate were based on work by James, Sannia & Bowers (1977) who estimated the adult life span of *M. minutus* to be 10 days and thought that approximately 20% of parasites established in the intestine of the final host. The coefficient of the intensity dependent increase in mortality rate is deliberately low because adult *M. minutus* are small and oystercatchers are known to maintain very heavy infestations. Intensities of between 60,000 and 120,000 individuals have been recorded from oystercatchers at the Burry Inlet (Bowers & James 1967).

The parasite infrapopulation experienced over the winter assuming birds arrived at the feeding grounds free of infection was estimated using equation 6, the winter season starting on November 1st and continuing until February 28th. This allowed direct comparison of the expected parasite infrapopulations resulting from both observed and predicted energy intake rates.

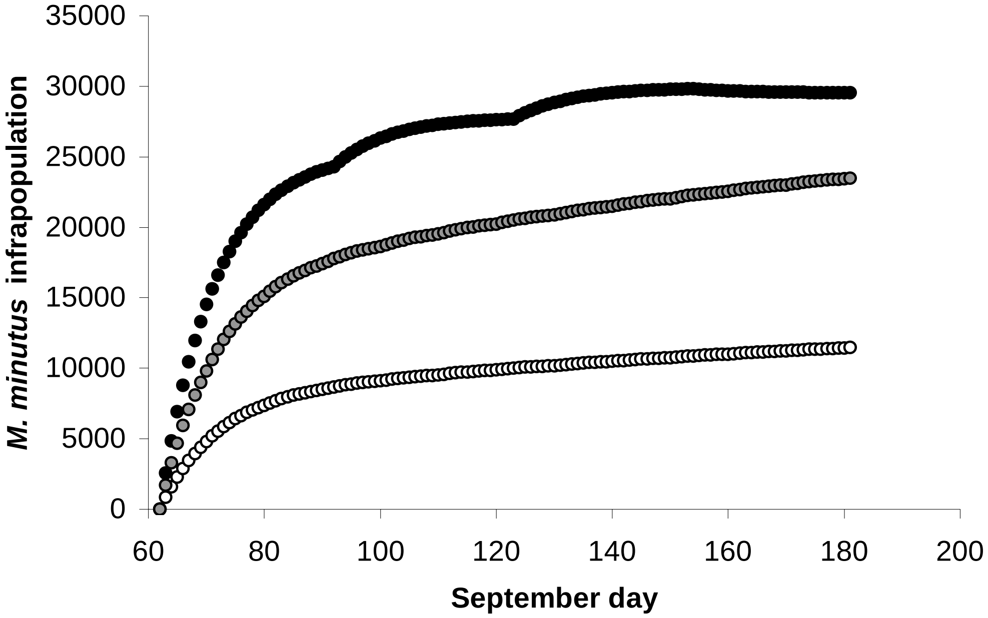
4.10 Parasite infection: results

The infrapopulations predicted at Hoylake were of a greater magnitude than those predicted at the Burry Inlet because of the greater abundance of metacercariae recorded from cockles at Hoylake and thus the higher predicted parasite ingestion rates (Figure 4.14).

At the Burry Inlet, the highest predicted parasite infrapopulation resulted from the observed cockle size selection strategy (Figure 4.14a). This directly contradicts the hypothesis that the observed size selection strategy of Burry Inlet oystercatchers is the result of an attempt to minimise exposure to parasites. The lowest predicted infrapopulation is the result of the cockle size selection strategy that would maximise energy intake (Figure 4.14a).

At Hoylake, the predicted parasite infrapopulations when maximising energy intake and if all cockle size classes are included in the diet are very similar, because both energy intake rates and parasite ingestion rates are so similar.

(a)



(b)

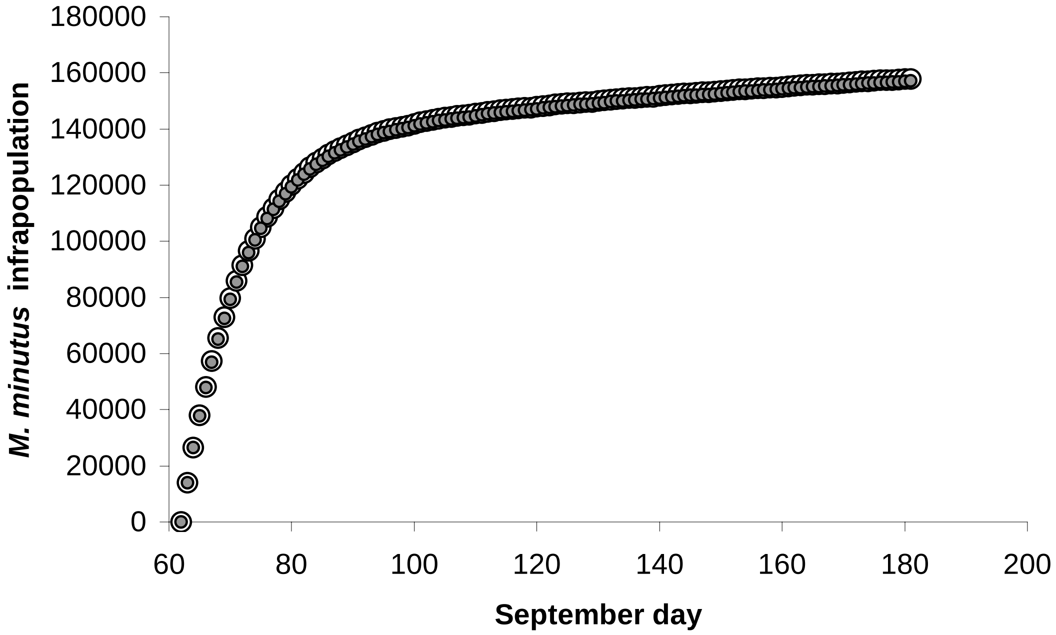


Figure 4.14. Estimated *Meiogymnophallus minutus* infrapopulation in an oystercatcher from a. The Burry Inlet during winter 1994-95 and b. Hoylake during winter 2002-03 according to cockle size selection strategy. White circles represent the energy intake maximising strategy; grey circles indicate the infrapopulation when all cockle size classes are included in the diet; black circles represent the expected parasite infrapopulation resulting from the observed size selection strategy at the Burry Inlet.

4.11 Conclusions

The results of this study again indicate that oystercatchers at the Burry Inlet forage selectively, in a way that keeps observed energy intake below the maximum achievable. However, oystercatchers at a less favourable site (Hoylake) do not seem to follow the same decision rules, probably because the maximum intake rate has to be maintained in order to survive. The difference between foraging strategies at each site show the flexibility of foraging shorebirds according to the conditions encountered and point to a cost that is incurred when foraging at the maximal energy intake rate. As the maximum intake rate at both study sites is that achieved when foraging on larger cockle size classes, it is logical to conclude that there is a significant risk encountered when feeding on large cockles.

Oystercatchers at the Burry Inlet are shown to maintain a lower ingestion rate of parasite transmission stages by selecting smaller cockle size classes. As discussed in previous work this would seem to indicate a trade-off between energy intake rate and the rate at which birds become infected with parasites, but is parasite infection really the cost that birds at the Burry Inlet are attempting to avoid? Further analysis reveals that although selective foraging can reduce the rate at which parasite transmission stages are ingested, this reduction is not sufficient to counteract the need to ingest a greater number of food items in order to obtain the amount of energy required to survive. In other words, the smaller the cockles selected, the greater the number of cockles eaten. This in turn results in a greater number of ingested parasites.

Exploring the population dynamics of the most common parasite of oystercatchers, although with a very simple modelling technique indicates that the birds wintering at the Burry Inlet are not reducing the number of parasites with which they become infected. Selection of smaller cockle size classes may actually be increasing the birds' exposure to infection. If this is the case, the costs of infection may not be of a sufficient magnitude to be worth avoiding. A greater, as yet unknown cost appears to be driving the foraging behaviour of the oystercatchers at the Burry Inlet.

4.12 References

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5 SINGLE-SITE MODELS: WADER DECISION RULES

Richard A. Stillman

5.1 Introduction

This chapter describes the work conducted in work package 7 of the project. The aim of this work package was to compare the prey-selection decision rules used by oystercatchers feeding on cockles on two contrasting sites, the Burry Inlet and the Dee estuary, UK. Chapter 4 presented the field data collected for this work package. The Dee estuary is considered a less favourable site because oystercatchers generally have lower prey intake rates than those on the Burry Inlet. Oystercatchers consume all cockle size classes on the Dee estuary, but ignore the largest size classes on the Burry inlet. As a result, oystercatchers maximise their prey intake rate on the Dee estuary (intake rate maximising decision rules), but not on the Burry Inlet (risk avoidance decision rules). The difference between foraging strategies at each site show the flexibility of foraging shorebirds according to the conditions encountered and point to a cost that is incurred when foraging at the maximal energy intake rate, at least on the Burry Inlet. This chapter develops a single-site model to determine how the population predictions of individual-based models (e.g. survival rate and body condition) depend on the decision rules birds use to determine their prey selection. Two versions of the model are developed differing in the decision rules used by birds. The *rate-maximising* model assumes that birds maximise their prey intake rate by consuming all prey size classes. This model mimics the behaviour of oystercatchers on the Dee estuary. The *risk-minimising* model assumes that, unless they are starving (i.e. losing mass), birds do not consume the largest prey size classes, which are assumed to have an associated cost. Starving birds are assumed to maximise their intake rate by consuming all prey size classes, as birds in the rate-maximising model. The risk-minimising model mimics the behaviour of oystercatchers on the Burry Inlet.

5.2 Model parameters

This section describes the parameter values and assumptions used for each of the five elements of the model.

5.2.1 GLOBAL

Global variables used in the model are shown in Table 5.1. The model started on 1 September, ran for 200 days and had a time step length of 1 hour.

5.2.2 PATCHES

The rate-maximising and risk-minimising models were not intended to represent any particular site(s) in great detail and so were kept as simple as possible. Therefore, each consisted of a single patch. Default patch variables used in the models are shown in Table 5.2.

5.2.3 RESOURCES AND COMPONENTS

Prey types and size classes used in the model, and their initial densities on each patch, are shown in Table 5.3. The model simply included two bivalve size classes. Small prey were assumed to be of less food value but safer to eat than large prey. The initial densities of bivalves were typical values recorded for cockles *Cerastoderma edule* in the Baie de Somme survey (Chapter 7). The initial ash-free dry mass content was that measured for cockles in the Baie de Somme (Chapter 7). The season change of ash-free dry mass during winter and the mortality rate due to factors other than oystercatchers were typical values for bivalves (Zwarts 1991).

5.2.4 FORAGERS

Forager numbers, diets, constants and variables are shown in Table 5.4. Individuals were assumed to arrive on 1 September and remain in the system for 200 days. Forager constants were foraging efficiency and dominance. Individuals were assumed to vary in their foraging efficiency, which influences intake rate in the absence of competitors, and dominance, which influences the effect of competitors on intake rate. The foraging efficiency of each individual within the population was drawn from a normal distribution, with a mean of one and a standard deviation of 0.125. The dominance score for each individual was drawn from a uniform distribution between 0 and 1. The forager variables used determined the strength of interference. The rate at which oystercatchers were able to feed depended on the abundance of food in a patch and the strength of interference from other competitors. The influence of the food supply on a bird's intake rate was calculated using a functional response (see Chapter 2). The energy assimilated from consumed food depended on the energy density of the food and the efficiency with which the energy from the food could be assimilated. Energy density was assumed to be 22 kJ g^{-1} for all prey species. Assimilation efficiency was assumed to be 0.85. Assimilated energy was converted into increased mass by assuming that 33 kJ of energy was stored in each g of storage tissues (Kersten & Piersma 1987). The thermoneutral energy requirements for each bird species were calculated from body mass using the "all species" equation of Nagy, Girard & Brown (1999). Bird body masses were based on data for the Wash, east England (Johnson 1985).

Table 5.1 Global variable values used in the rate-maximising and risk-minimising models.

Global variables	Value
Duration of time step	1 h
First day	1 September
Number of days	200

Table 5.2 Patch variable values used in the rate-maximising and risk-minimising models.

Patch variable	Value
Patch area	21.5 ha

Table 5.3 Resource and component parameter values used in the rate-maximising and risk-minimising models.

Resource		Component				
	Initial density (n m^{-2})	Winter mortality	Initial AFDM	Change	Energy density	Risk
Small bivalves	300	10%	0.04 g	-28%	22 KJg^{-1}	Low
Large bivalves	100	10%	0.08 g	-28%	22 KJg^{-1}	High

Table 5.4 Forager parameter values used in the rate-maximising and risk-minimising models.

Forager variables	
Initial numbers	1000
Arrival date	1 Sep
Diets eaten	1. Small bivalves 2. Small and large bivalves
Diet selection strategy:	
1. Rate-maximising model	Always consume diet 2
2. Risk-minimising model	Consume diet 1 if body mass > 90% of target Consume diet 2 if body mass < 90% of target
Range of foraging efficiencies (coefficient of variation)	0.125
Range of dominance values	0 - 1
Kleptoparasitism:	
Aggregation factor	10
Threshold density (n ha^{-1})	100
Coefficient for least dominant bird	-0.5
Coefficient for most dominant bird	0
Functional response:	
B_{50} (g AFDM m^{-2})	0.761
Forager coefficient	-1.141162
Prey coefficient	0.36542
Prey assimilation efficiency:	0.85
Energy density of fat reserves (kJ g^{-1})	33.4
Non-thermoregulatory energy requirements (kJ d^{-1})	724
Mean arrival mass (g)	500
Target mass(g)	500
Starvation mass (g)	350

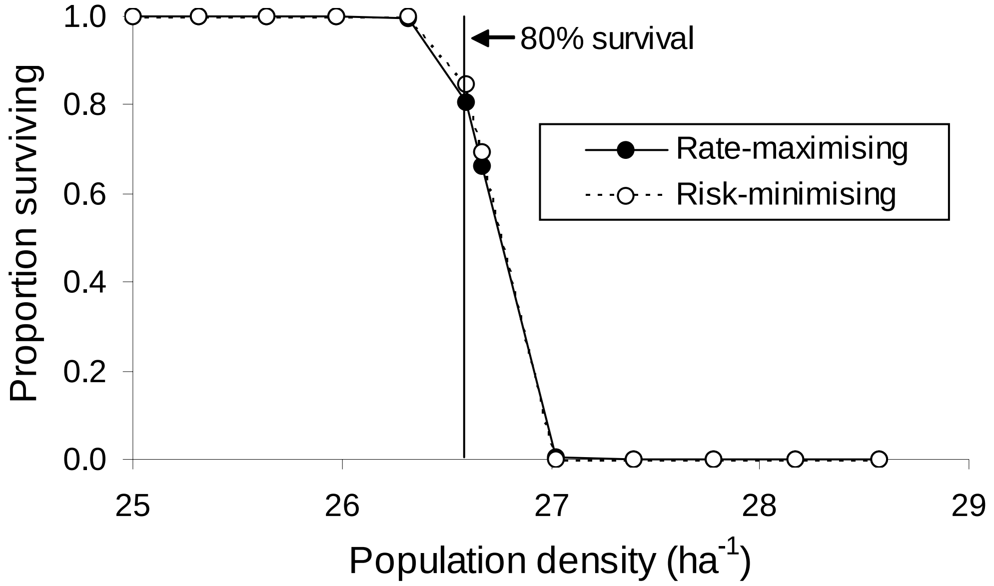
5.3 Results

This section compares the predictions of three alternative versions of the rate-maximising and risk-minimising models. The default models assume that prey quality (ash-free dry mass) remains constant throughout winter and that there are no additional sources of prey mortality other than predation by oystercatchers. Further models assume either that prey quality changes during the course of the season and / or that there are additional sources of prey mortality.

5.3.1 DEFAULT MODELS

Figure 5.1a shows the predicted effect of oystercatcher density on overwinter oystercatcher survival. In the absence of seasonal changes in prey quality and without additional prey mortality sources, both the rate-maximising and risk-minimising predict the same survival rates. Figure 5.1b shows the predicted diet selection, body mass and feeding effort at the oystercatcher density resulting in 80% oystercatcher survival. Both models predict the same survival and end-of-winter body mass. The risk-minimising model predicts that the risky diet is consumed by a smaller proportion of birds, and that birds have less spare time (i.e. they spend a higher proportion of the time feeding). Birds need to spend longer feeding in the risk-minimising model because the safe diet, consumed by most birds in this model, yields a lower intake rate and so birds need to spend longer feeding to meet their daily energy requirements. Figure 5.2 shows seasonal changes in the predictions of the rate-maximising and risk-minimising models. The rate-maximising model predicts that the risky diet (containing both risky and safe prey) is consumed throughout winter (Fig. 5.2a) and so the biomass densities of both risky and safe prey decline (due to oystercatcher predation) throughout winter (Fig. 5.2b). At the start of winter, the risk-minimising model predicts that just the safe diet (containing just safe prey) is consumed (Fig. 5.2a) and so only the density of safe prey declines during this period (Fig. 5.2b). As the density of safe prey approaches zero (Fig. 5.2b), the intake rate from the safe diet declines and so, to avoid starvation, birds are forced to switch to the risky diet (Fig. 5.2a). The two models predict different patterns in resource usage; safe prey are initially consumed at a higher rate in the risk-minimising model, and risky prey at a higher rate in the rate-maximising model. The survival predictions of the two models are the same because the total amount of resource that can be consumed during winter does not depend on the order in which resources are consumed. This happens because there are no seasonal changes in either prey quality and no additional sources of prey mortality.

(a) Density-dependence



(b) Predictions for 80% survival

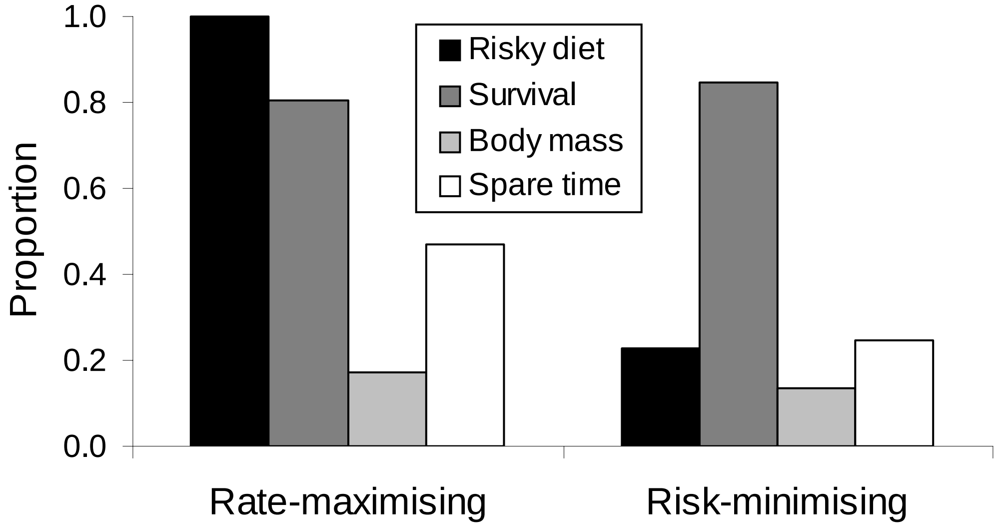
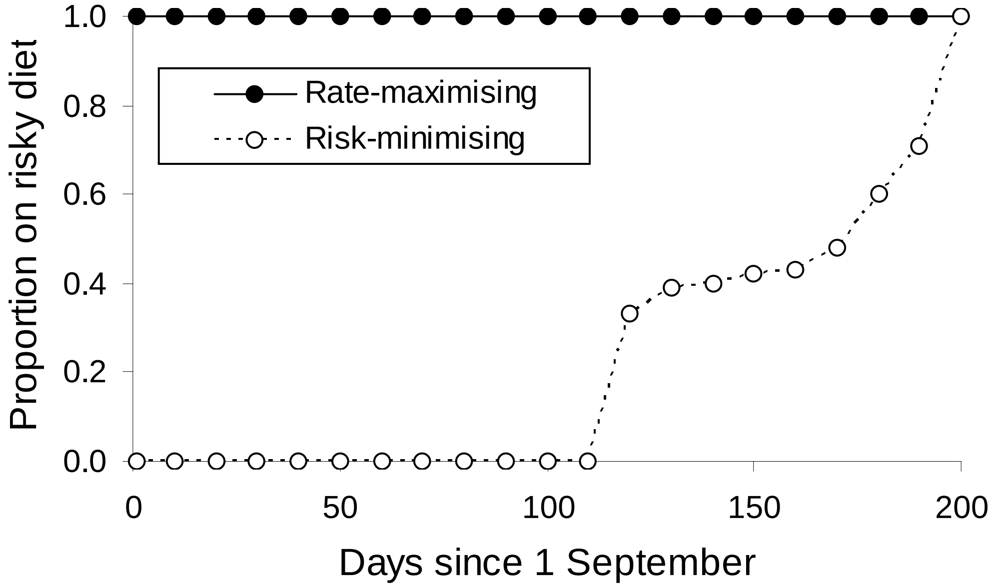


Figure 5.1 Comparison of rate-maximising and risk-minimising models. (a) The effect of oystercatcher population density on overwinter survival. (b) Overwinter average predictions when overwinter survival is 80%. Risky diet = average proportion of birds consuming the more risky diet including large bivalves. Body mass = body mass of surviving birds expressed as a proportion of the target mass. Survival = proportion of birds surviving to the end of winter. Spare time = average proportion of time spent not feeding. Prey quality was assumed to remain constant throughout winter and mortality due to factors other than oystercatchers was assumed to be zero.

(a) Diet selection



(b) Prey biomass density

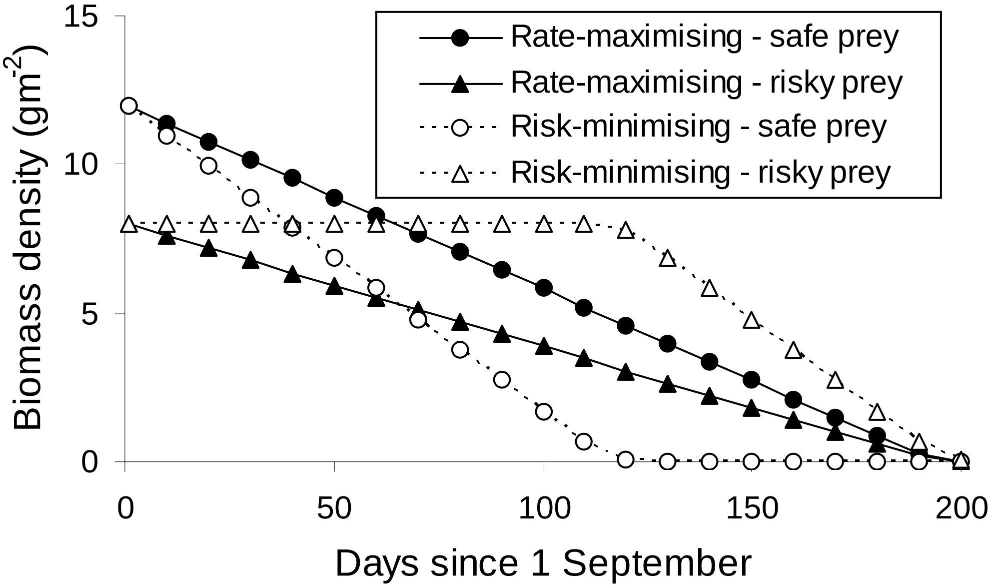


Figure 5.2 Comparison of rate-maximising and risk-minimising models at the oystercatcher density resulting in 80% oystercatcher survival. (a) Seasonal changes in the proportion of birds consuming the risky diet. (b) Seasonal changes in the biomass densities of risky and safe prey. Prey quality was assumed to remain constant throughout winter and mortality due to factors other than oystercatchers was assumed to be zero.

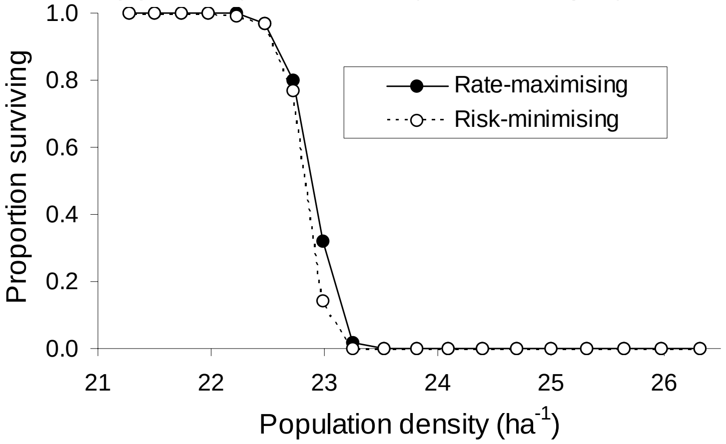
5.3.2 SEASONAL CHANGES IN PREY QUALITY

The default models were extended by incorporating seasonal declines in the quality of either risky and / or safe prey (Fig. 5.3). If both risky and safe prey were assumed to lose quality at the same rate, the two models produced very similar predictions (Fig. 5.3a), especially for survival rates above 80%, the usual range of shorebird survival rates. However, predictions differed if the changes in quality differed between the prey species. If just the risky prey quality declined, the rate-maximising model predicted higher survival (Fig. 5.3b). In contrast, if just the safe prey quality declined, the risk-minimising model predicted higher survival (Fig. 5.3c). These differences were caused by differences in the order in which the risky and safe prey were consumed. By predominantly consuming a particular type of prey early in winter, oystercatchers maximised the amount of this prey that was consumed before it was "lost" due to reduction in prey quality. Birds in the risk-minimising model consumed more safe prey early in winter and so were less affected by declines in this prey type than were birds in the rate-maximising model. Birds in the rate-maximising model consumed more risky prey and so were less affected by declines in this prey type than were birds in the risk-minimising model.

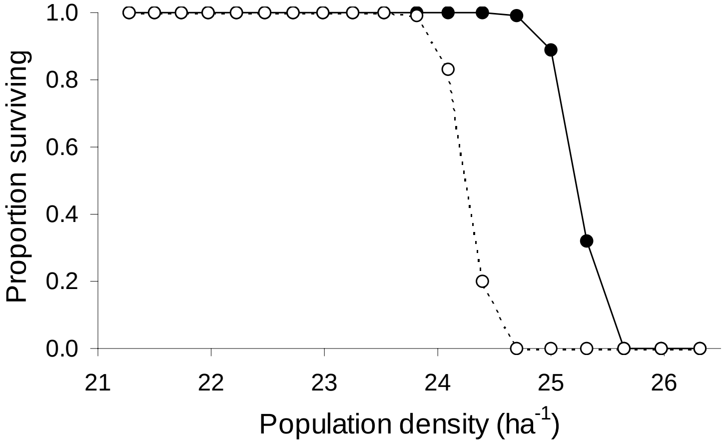
5.3.3 ADDITIONAL MORTALITY SOURCES

The previous models were extended by also incorporating sources of mortality other than predation by oystercatchers (Fig. 5.4). If both risky and safe prey were assumed to have additional mortality, the two models produced very similar predictions (Fig. 5.4a), especially for survival rates above 80%. However, predictions differed if the additional mortality sources differed between the prey types. If additional mortality was restricted to the risky prey, the rate-maximising model predicted higher survival (Fig. 5.4b). In contrast, if additional mortality was restricted to the safe prey, the risk-minimising model predicted higher survival (Fig. 5.4c). As above, these differences were caused by differences in the order in which the risky and safe prey were consumed. By predominantly consuming a particular type of prey early in winter, oystercatchers maximised the amount of this prey that was consumed before it was lost due to additional mortality sources. Birds in the risk-minimising model consumed more safe prey early in winter and so were less affected by additional mortality of this prey type than were birds in the rate-maximising model. Birds in the rate-maximising model consumed more risky prey and so were less affected by additional mortality of this prey type than were birds in the risk-minimising model.

(a) Quality loss of risky and safe prey



(b) Quality loss of risky prey only



(c) Quality loss of safe prey only

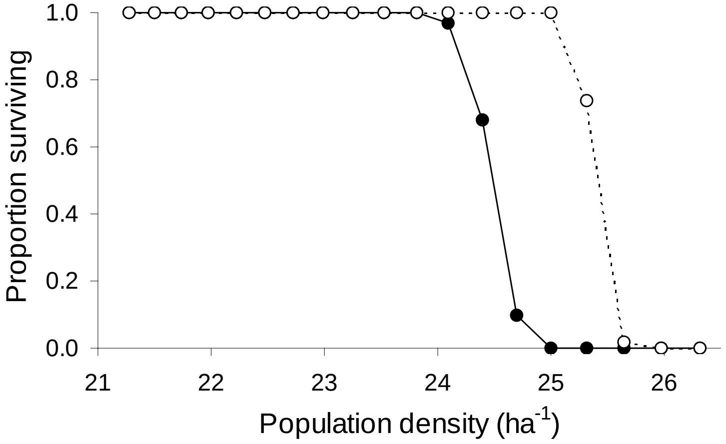
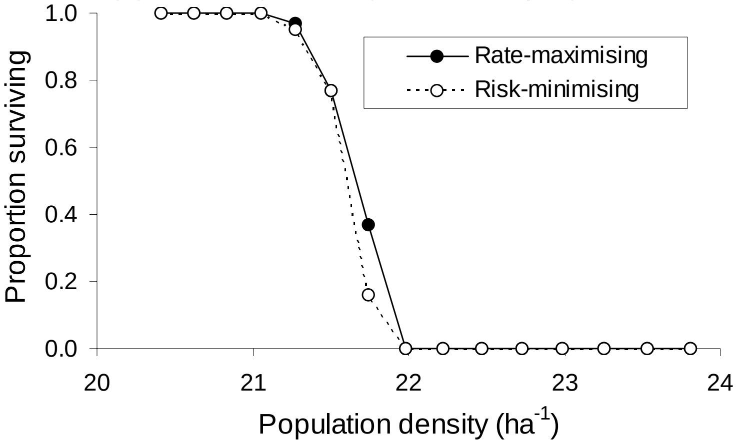
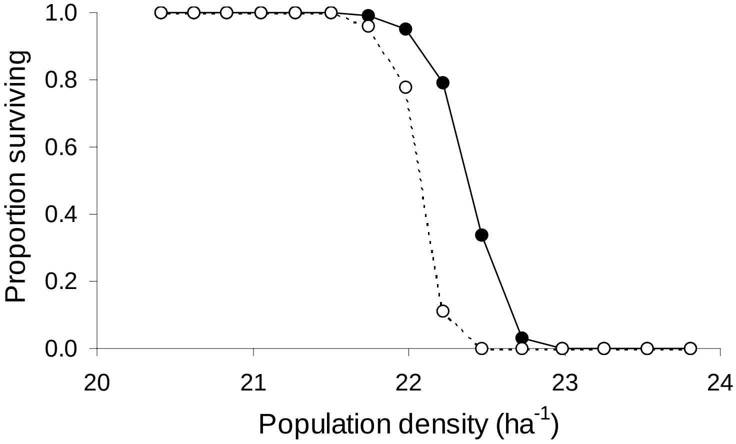


Figure 5.3 Comparison of rate-maximising and risk-minimising models. Effect of seasonal changes in prey quality (ash-free dry mass (AFDM)) on the predicted overwinter survival of oystercatchers. (a) AFDM of both risky and safe prey declines by 28% during winter. (b) AFDM of just risky prey declines by 28% during winter. (c) AFDM of just safe prey declines by 28% during winter. Mortality due to factors other than oystercatchers was assumed to be zero.

(a) Mortality of risky and safe prey



(b) Mortality of risky prey only



(c) Mortality of safe prey only

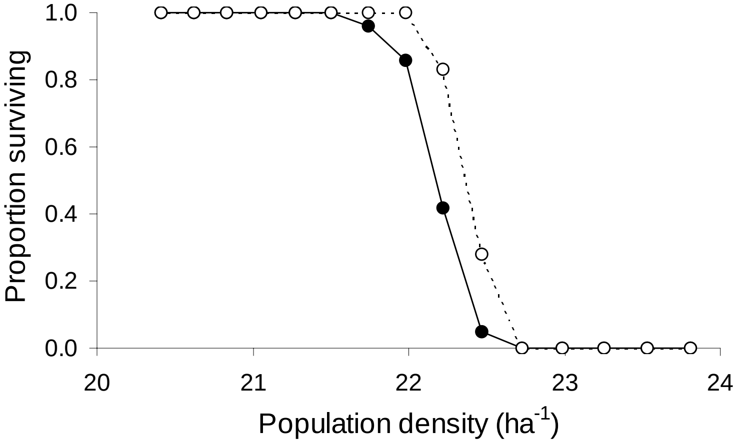


Figure 5.4 Comparison of rate-maximising and risk-minimising models. Effect of prey mortality due to factors other than oystercatchers on the predicted overwinter survival of oystercatchers. (a) 10% additional overwinter mortality of both risky and safe prey. (b) 10% additional overwinter mortality of risky prey only. (c) 10% additional overwinter mortality of safe prey only.

5.4 Summary

This chapter compared the predictions of models assuming that oystercatchers use either rate-maximising or risk-minimising decision rules to determine their prey selection. These models mimicked the observed behaviour of oystercatchers in the Burry Inlet (risk-minimising) and Dee estuary (rate-maximising) as described in Chapter 4. The risk-minimising model predicted that birds should select the safe diet when safe food is abundant, but switch to the risky diet when the density of safe food declines. This prediction is in accordance with the observation that oystercatchers avoid more risky prey on the Burry Inlet, where feeding conditions are better, but consume risky prey on the Dee estuary, where feeding conditions are poorer. The different decision rules changed the order in which the safe and risky diets were consumed. The two models produced different survival predictions if the prey differed in their seasonal changes in quality or their rates of loss to additional mortality sources. This means that it is important that individual-based models incorporate decision rules that mimic those used by birds in the real system, particularly if different prey types differ in their changes in quality or abundance. This strategy is used in the system-specific models developed in later chapters.

5.5 References

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6 SINGLE-SITE MODELS: BAHÍA DE CÁDIZ WADERS

6.1 Study site

The Bahía de Cádiz Natural Park, located in the southwest of the Iberian Peninsula, occupies an area of ten thousand hectares. The reserve is situated in the boroughs of Cádiz, El Puerto de Santa María, Puerto Real, San Fernando and Chiclana and was declared a national park in 1989. Its main component is the salt marshes, transformed into salt pans (salinas), of several rivers, including Guadalete, San Pedro and Arillo. Nowadays many of the salinas are abandoned or dedicated to intensive aquaculture, but there are still some small salinas in production in San Fernando, Chiclana, Puerto Real, and one large industrial salt producer in Puerto de Santa María.

Traditional salt production creates shallow pools rich in invertebrates that help to support the diversity of waders seen in the Park. There is a history of salt production in the area dating back to Roman times with activity reaching its height in the eighteenth and nineteenth centuries. During the twentieth century traditional salt production declined dramatically. When salinas are abandoned the sea penetrates the walls, leading to the gradual filling-in of the shallower zones and a change in the invertebrate community to one less attractive for waders

6.2 Issues

6.2.1 SALINA ABANDONMENT

Traditional salt production has declined rapidly and few active traditional salinas remain. Those that do remain are likely to be abandoned in the near future. Old abandoned salinas contain a very poor diversity of prey, largely *Hydrobia* and little else, and are much less attractive to birds than *Artemia*-rich active salinas. The model will be used to predict the effect on birds of the change prey abundance and diversity as currently active salinas are abandoned and their quality declines.

6.2.2 INTENSIVE AQUACULTURE

Aquaculture in the Bahía de Cádiz is changing from old extensive methods using open-air ponds to intensive methods based on indoor tanks. Open-air ponds were harvested by periodic draining, which provides a very rich, albeit short-lived, resource for waders in the period following drainage. Model simulations will predict what would happen to waders if the intensification of aquaculture continues and these drained fishponds are no longer available to them.

6.2.3 HABITAT CREATION

The potential problems of salina abandonment are well-known to the national park authorities and scientists in the Bahía de Cádiz and projects to mitigate the effects of this are in progress. Some areas of abandoned salina have already been bought for restoration and plans to buy more are ongoing at the time of writing. The aim of these projects is to manage the salinas in such a way as to provide maximum benefit to the birds. Using the model we can predict what area of managed salina is needed to support the current wader populations and what invertebrate species are most beneficial.

6.3 Data collection

6.3.1 PATCHES

Hundreds of invertebrate core samples were taken from 22 intertidal sampling sites and 16 supratidal sampling sites across the Bahía de Cádiz. Samples were taken to a depth of 30cm using a cylindrical corer with a diameter of 10cm. The bottom half of the core was broken up to look for large worms or bivalves. The top half was sieved through a 0.5mm mesh sieve and the invertebrates retained were preserved in formalin (4% formaldehyde) for later processing. As high densities of invertebrates can be present in the shallow water of supratidal habitats, the supratidal necton was sampled separately.

Exposures times were measured by observation of the times at which different patches exposed and covered on spring and neap tides in relation to the times of high and low tide. In a separate experiment on 23/7/04 the exposure status of intertidal patches was recorded every 30 minutes starting at high tide and continuing through low water to the start of the advancing tide.

6.3.2 RESOURCES

Once fixed by formalin, each sample was washed and preserved in industrial methylated spirits (IMS). All the invertebrates in each sample were counted and measured to the nearest millimetre, except when there were very high numbers of one species in a sample, in which case that species was sub-sampled.

6.3.3 COMPONENTS

Ash-free dry mass (AFDM)-length relationships in Cádiz were measured for a number of species. Individuals for AFDM were collected separately from the core samples and frozen before processing. The each individual animal was measured and placed into a crucible then dried at 90ºC to constant weight. After weighing each sample was ashed in a muffle furnace at 550ºC to constant weight and reweighed. The AFDM is the difference between the dry weight and the ash weight. Ash-free dry mass-length relationships were calculated by regressing $\log_e$ AFDM against $\log_e$ length. In the case of ragworms, the length of a worm is greater when frozen and thawed than when preserved, so the lengths used to calculate the relationship were adjusted to account for this.

6.3.4 FORAGERS

The numbers of each bird species used in the model were counted monthly at high and low tide.

6.4 Data analysis

6.4.1 PATCHES

Cluster and non-metric multidimensional scaling (MDS) techniques were used to determine patch types, based on a Bray-Curtis similarity matrix calculated from fourth root transformed invertebrate biomass density data (Clarke & Warwick, 1994).

Cluster analysis of the data identified six different patch types in terms of their invertebrate community, three intertidal and three supratidal. The three intertidal patch types were sand, intertidal mud and river channel mud. Sandy sites were characterised by the presence of bivalves and low abundance or absence of many polychaetes and other worms. River channel muds tended to contain high densities of *Scrobicularia plana* and *Cerastoderma edule* with few other bivalve species present. Intertidal muds had lower densities of *Scrobicularia,* a wider range of other bivalve species and higher densities of annelids than river channel muds.

Supratidal patch types were active or recently abandoned salinas, old abandoned salinas and extensive aquaculture. Active or recently abandoned salinas were distinguished from the other supratidal patch types by the presence of high densities of brine shrimps, *Artemia*, a species not found in older abandoned salinas or extensive fishponds. Older abandoned salinas contained high densities of *Hydrobia* species and sometimes low densities of small *Scrobicularia* or polychaete worms but nothing else. Samples from drained fishponds contained high densities of amphipods, chironomid midge larvae and *Hydrobia*.

6.4.2 RESOURCES

Resources used in the model were invertebrate prey size classes. Invertebrate data were combined for all sampling sites within each habitat patch and mean densities calculated for each prey size class. All worm species except ragworms, *Hediste diversicolor,* were combined and divided into five size-classes based on the preferred sizes of the wader species to be modelled. Ragworms were kept separate because the total biomass of *Hediste* was nearly double the biomass of all other worms combined.

Bivalves were divided into four size-classes, again based on the preferred sizes for different bird species. The two most abundant species, *Scrobicularia plana* and *Cerastoderma edule* (45% and 26% of bivalve biomass respectively), were modelled individually and all other bivalves species were combined.

Other resources in the model were *Artemia*, chironomid larvae, *Hydrobia* and amphipods. Each of these prey types had only one size-class as birds take all sizes over a particular minimum.

6.4.3 COMPONENTS

The only resource component included in this model was ash-free dry mass (AFDM), a measure of how much of the weight of a prey item is digestible. For most species, the AFDM for each prey size class was calculated using ($\log_e$) AFDM to ($\log_e$) body length relationships. In the case of *H. diversicolor*, the relationship was adjusted to account for the difference in length between fresh or frozen worms, which were used for AFDM, and preserved worms which were measured from the survey samples. For several small worm species, no size categories were used and biomass densities were based on the mean AFDM of a small worm.

Unlike more northerly sites, no overwinter decline in the AFDM of prey species was detected so AFDM in the model remained constant over the winter.

6.4.4 FORAGERS

Some species of bird showed large changes in numbers over the winter whilst the numbers of other species were relatively stable (Fig. 6.1). Where large changes occurred these were reflected in the model, but because all bird counts are subject to a degree of uncertainty small changes were averaged out.

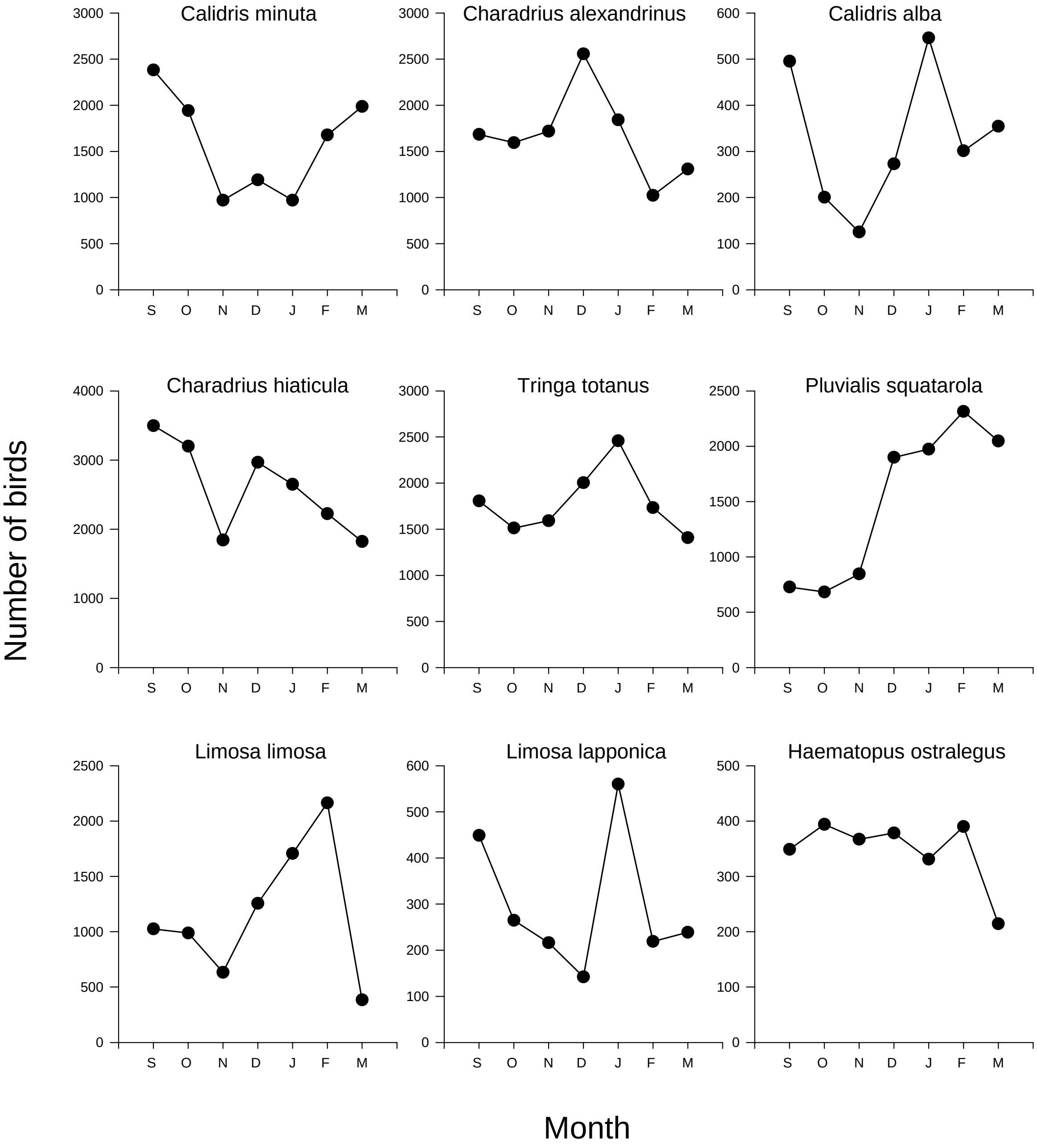


Figure 6.1 Observed bird numbers in the Bay of Cádiz

6.5 Model variables

6.5.1 GLOBAL

Global variables used in the model are shown in Table 6.1. The variable weekend was included so that certain variables, such as disturbance, could differ in intensity between weekdays and weekends. An equation predicting day length was included in order to calculate hours of daylight so that variables could differ between day and night-time. The area covered by the model was very large and tidal heights in the northern part of the area differed from those elsewhere. Hourly tidal heights at both Puerto de Santa María and La Carraca for 2003-04 were therefore included in the model. They were generated using 'TideWizard' software (Marine Computing International 2000-2002). Tidal stages calculated from this data were used in the model to control the exposure of some supratidal patches. It also meant that bird distribution data could be extracted for four different stages of the tide: low tide, high tide and receding tide and advancing tide. The spring-neap cycle variable, which varied from 0 (full neap) to 1 (full spring) allowed bird distribution to be related to this cycle.

Table 6.1 Global variables used in the Bahía de Cádiz model

Global variables	Value
Duration of time step	1 h
Day	Day 1 = 1 September
Weekend	0 = weekday, 1 = weekend
Time	Hour of the day. 0 to 23.
DayLength	21 June 14.67h, 21 December 9.65h
Daylight	0 = dark, 1 = daylight
TideHeightCarraca	Tide heights at La Carraca for 2004-05
TideHeightSMaria	Tide heights at Puerto de Santa Maria for 2004-05
TideStageCarraca	Tide stages at La Carraca (High, receding, low, advancing)
TideStageSMaria	Tide stages at Puerto de Santa Maria (Low tide, advancing, high, receding)
SNCycle	Stage of spring-neap cycle. From 0 (full neap) to 1 (full spring)

6.5.2 PATCHES

Cluster analysis of the invertebrate data identified six different patch types in terms of their invertebrate community, three intertidal and three supratidal. The three intertidal patch types were sand, intertidal mud and river channel mud. The supratidal patch types were active or recently abandoned salinas, old abandoned salinas and extensive aquaculture. This classification led to eighteen model patches, one for each patch type present in each functional unit (Fig. 6.2). Patch variables included in the model, and the baseline values used, are shown in Table 6.2. The area of each patch was calculated from GIS data. The tide height at which each intertidal patch was uncovered by the tide was derived by relating observations recorded on 23/07/2004 to the tidal curve for that day. The exposure of supratidal patches was derived from earlier observations.

Shellfishing takes place with varying intensity in every functional unit in the model. The numbers of shellfishers present on each patch varied randomly within the limits of the observed numbers of shellfishers in each patch. Shellfishing disturbed birds and could also affect the density of prey for some, principally the larger, bird species.

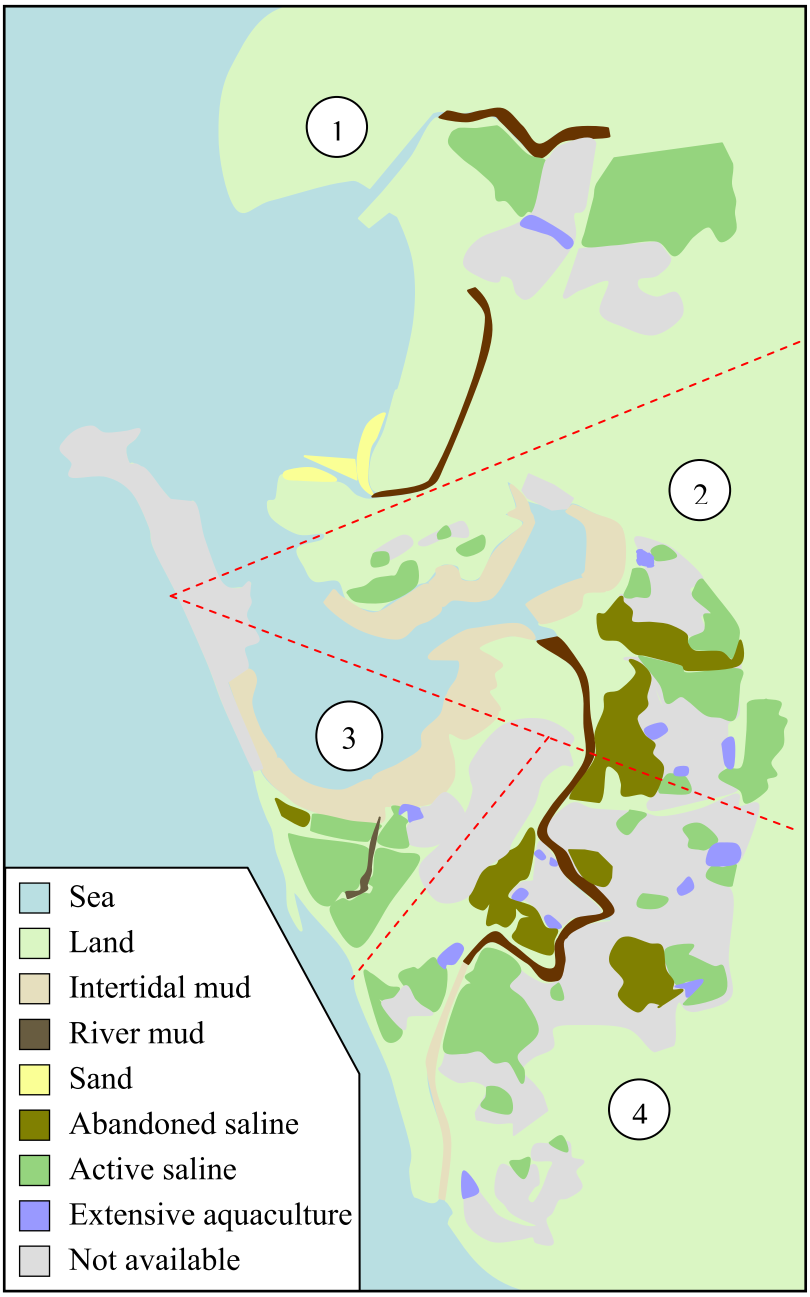


Figure 6.2 Feeding patches in the Bahía de Cádiz model. Numbers represent functional units – 1 Guadalete, 2 Trocadero, 3 Rio Arillo, 4 Sancti Petri

Table 6.2 Patch variables used in the Bahía de Cádiz model

Patch variables	**Patch**			
Patch variables	**Guadalete Channel Mud**	**Guadalete Sand**	**Guadalete Active Salina**	**Guadalete Aquaculture**
Patch area (m^2)	1138936	848426	9004600	288000
Tidal curve	La Carraca	La Carraca	La Carraca	La Carraca
Exposure tide ht (m) or tidal stages exposed	2.4	2.5	Always exposed	Always exposed
Area exposed on Full neap Full spring	 817116 1138936	 498316 848426	 9004600 9004600	 288000 288000
Functional unit	Guadalete	Guadalete	Guadalete	Guadalete
Disturbers (h^{-1})	1-7	2-20	0	0
Safety	0	1000	1000	1000

	Patch			
Patch variables	**Trocadero Intertidal Mud**	**Trocadero Active**	**Trocadero Abandoned Salinas**	**Trocadero Aquaculture**
Patch area (m^2)	6353649	5742620	4504600	210000
Tidal curve	P. de Santa Maria	P. de Santa Maria	P. de Santa Maria	P. de Santa Maria
Exposure tide ht (m) or tidal stages exposed	2.8	3.0	Receding, low	Always exposed
Area exposed on Full neap Full spring	 3799832 6353649	 5742620 5742620	 4504600 4504600	 210000 210000
Functional unit	Trocadero	Trocadero	Trocadero	Trocadero
Disturbers (h^{-1})	12-30	0	0	0
Safety	1000	1000	1000	1000

	Patch				
Patch variables	**Rio Arillo Channel Mud**	**Rio Arillo Intertidal**	**Rio Arillo Active Salinas**	**Rio Arillo Abandoned Salinas**	**Rio Arillo Aquaculture**
Patch area (m^2)	211499	4807407	5317700	400000	12000
Tidal curve	P. de Santa Maria	P. de Santa Maria	P. de Santa Maria	P. de Santa Maria	P. de Santa Maria
Exposure tide ht (m) or tidal stages exposed	2.7	2.7	Receding, low, advancing	Receding, low, advancing	Always exposed
Area exposed on Full neap Full spring	 148116 211499	 3369571 4807407	 5317700 5317700	 400000 400000	 12000 12000
Functional unit	Rio Arillo	Rio Arillo	Rio Arillo	Rio Arillo	Rio Arillo
Disturbers (h^{-1})	0	13-31	0	0	0
Safety	0	1000	1000	1000	1000

	Patch				
Patch variables	**Sancti Petri Channel Mud**	**Sancti Petri Intertidal Mud**	**Sancti Petri Active Salinas**	**Sancti Petri Abandoned Salinas**	**Sancti Petri Aquaculture**
Patch area (m^2)	1416905	669011	7109100	1880000	1330000
Tidal curve	P. de Santa Maria	P. de Santa Maria	P. de Santa Maria	P. de Santa Maria	P. de Santa Maria
Exposure tide ht (m) or tidal stages exposed	2.0	2.7	Receding, low, advancing	Receding, low, advancing	Always exposed
Area exposed on Full neap Full spring	 689129 1416905	 327947 669011	 7109100 7109100	 1880000 1880000	 1330000 1330000
Functional unit	Sancti Petri	Sancti Petri	Sancti Petri	Sancti Petri	Sancti Petri
Disturbers (h^{-1})	5-8	5-7	0	0	0
Safety	0	1000	1000	1000	1000

6.5.3 RESOURCES

Prey types and size classes used in the model, and their initial densities on each patch, are shown in Table 6.3. Although winter weather in Cádiz is warm enough to allow some growth and recruitment of invertebrates data to parameterise this were not available, so winter growth and recruitment were not included in the model.

Table 6.3 Resource variables used in the Bahía de Cádiz model

Resource		Initial density (m^{-2})							
Species	**Size class (mm)**	**Guadalete Channel Mud**	**Guadalete Sand**	**Guadalete Active Salina**	**Guadalete Aquaculture**	**Trocadero Intertidal Mud**	**Trocadero Active**	**Trocadero Abandoned Salinas**	**Trocadero Aquaculture**
Hediste diversicolor	5-9.9	0.0000	0.0000	0.0000	0.0000	8.6477	0.0000	0.0000	0.0000
Hediste diversicolor	10-19.9	7.1217	0.0000	0.0000	0.0000	3.6438	0.0000	0.0000	0.0000
Hediste diversicolor	20-49.9	60.5773	0.0000	0.0000	0.0000	6.2613	0.0000	0.0000	0.0000
Hediste diversicolor	50-79.9	13.2551	0.0000	0.0000	0.0000	7.4750	0.0000	0.0000	0.0000
Hediste diversicolor	80+	55.5928	0.0000	0.0000	0.0000	4.3764	0.0000	0.0000	0.0000
Other polychaetes	5-9.9	311.4362	39.0503	0.0000	0.0000	414.3321	0.0000	3.9980	0.0000
Other polychaetes	10-19.9	250.6290	39.2000	0.0000	0.0000	854.2687	0.0000	0.0000	0.0000
Other polychaetes	20-49.9	16.1449	9.8000	0.0000	0.0000	694.4951	0.0000	0.0000	0.0000
Other polychaetes	50-79.9	0.0000	0.0000	0.0000	0.0000	140.5331	0.0000	0.0000	0.0000
Other polychaetes	80+	0.0000	0.0000	0.0000	0.0000	38.6768	0.0000	0.0000	0.0000
Cerastoderma edule	5-9.9	42.7304	32.7665	0.0000	0.0000	5.8846	0.0000	0.0000	0.0000
Cerastoderma edule	10-14.9	31.4947	43.6886	0.0000	0.0000	14.8468	0.0000	0.0000	0.0000
Cerastoderma edule	15-19.9	117.5087	147.4492	0.0000	0.0000	29.7778	0.0000	0.0000	0.0000
Cerastoderma edule	20+	14.2435	49.1497	0.0000	0.0000	10.9314	0.0000	0.0000	0.0000
Scrobicularia plana	5-9.9	159.6860	0.0000	0.0000	0.0000	35.1156	0.0000	128.0338	0.0000
Scrobicularia plana	10-14.9	10.3531	0.0000	0.0000	0.0000	7.5592	0.0000	6.3871	0.0000
Scrobicularia plana	15-19.9	74.1498	5.4611	0.0000	0.0000	3.6438	0.0000	0.0000	0.0000
Scrobicularia plana	20+	648.0536	52.3665	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Other bivalves	5-9.9	3.5609	61.0443	0.0000	0.0000	59.9496	0.0000	0.0000	0.0000
Other bivalves	10-14.9	6.0155	145.0551	0.0000	0.0000	62.2727	0.0000	0.0000	0.0000
Other bivalves	15-19.9	0.0000	116.4778	0.0000	0.0000	32.8335	0.0000	0.0000	0.0000
Other bivalves	20+	42.7304	223.9784	0.0000	0.0000	28.2064	0.0000	0.0000	0.0000
Artemia	All	0.0000	0.0000	1614.8132	0.0000	0.0000	33610.7614	0.0000	0.0000
Amphipods	All	3.0077	256.5951	0.0000	2032.5200	306.5120	0.0000	0.0000	2032.5200
Larvae	All	21.8309	0.0000	851.7759	1470.0000	244.7381	866.6361	50.2189	1470.0000
Gastropods	All	1920.6787	5.4611	39.2000	1955.1000	171.8860	79.6575	4533.3532	1955.1000

Resource		**Initial density (m^{-2})**				
Species	**Size class (mm)**	**Rio Arillo Channel Mud**	**Rio Arillo Intertidal**	**Rio Arillo Active Salinas**	**Rio Arillo Abandoned Salinas**	**Rio Arillo Aquaculture**
Hediste diversicolor	5-9.9	0.0000	13.0324	0.0000	0.0000	0.0000
Hediste diversicolor	10-19.9	0.0000	30.8107	0.0000	0.0000	0.0000
Hediste diversicolor	20-49.9	9.8000	25.4482	0.0000	0.0000	0.0000
Hediste diversicolor	50-79.9	0.0000	29.8111	0.0000	0.0000	0.0000
Hediste diversicolor	80+	0.0000	30.6052	0.0000	0.0000	0.0000
Other polychaetes	5-9.9	29.4000	2733.4922	0.0000	0.0000	0.0000
Other polychaetes	10-19.9	519.4000	1803.4168	0.0000	0.0000	0.0000
Other polychaetes	20-49.9	9.8000	400.4969	0.0000	0.0000	0.0000
Other polychaetes	50-79.9	0.0000	131.7394	0.0000	0.0000	0.0000
Other polychaetes	80+	0.0000	19.9083	0.0000	0.0000	0.0000
Cerastoderma edule	5-9.9	0.0000	0.0000	0.0000	0.0000	0.0000
Cerastoderma edule	10-14.9	9.8000	0.0000	0.0000	0.0000	0.0000
Cerastoderma edule	15-19.9	29.4000	14.6206	0.0000	19.6000	0.0000
Cerastoderma edule	20+	9.8000	9.1320	0.0000	0.0000	0.0000
Scrobicularia plana	5-9.9	720.0000	116.7310	0.0000	0.0000	0.0000
Scrobicularia plana	10-14.9	10.0000	28.1948	0.0000	0.0000	0.0000
Scrobicularia plana	15-19.9	0.0000	0.0000	0.0000	0.0000	0.0000
Scrobicularia plana	20+	0.0000	0.0000	0.0000	0.0000	0.0000
Other bivalves	5-9.9	0.0000	126.1714	0.0000	0.0000	0.0000
Other bivalves	10-14.9	0.0000	114.0592	0.0000	0.0000	0.0000
Other bivalves	15-19.9	0.0000	35.5051	0.0000	0.0000	0.0000
Other bivalves	20+	0.0000	113.4472	0.0000	0.0000	0.0000
Artemia	All	0.0000	0.0000	33610.7614	0.0000	0.0000
Amphipods	All	0.0000	261.3164	0.0000	0.0000	2032.5200
Larvae	All	0.0000	203.6790	866.6361	19.6000	1470.0000
Gastropods	All	5272.4000	1403.9706	79.6575	3498.6000	1955.1000

Resource		Initial density (m^{-2})				
Species	**Size class (mm)**	**Sancti Petri Channel Mud**	**Sancti Petri Intertidal Mud**	**Sancti Petri Active Salinas**	**Sancti Petri Abandoned Salinas**	**Sancti Petri Aquaculture**
Hediste diversicolor	5-9.9	0.0000	0.0000	0.0000	0.0000	0.0000
Hediste diversicolor	10-19.9	1.8364	0.0000	0.0000	0.0000	0.0000
Hediste diversicolor	20-49.9	52.4052	0.0000	0.0000	0.0000	0.0000
Hediste diversicolor	50-79.9	105.5610	9.5483	0.0000	0.0000	0.0000
Hediste diversicolor	80+	98.2419	0.2517	0.0000	0.0000	0.0000
Other polychaetes	5-9.9	519.5402	337.9668	0.0000	0.0000	0.0000
Other polychaetes	10-19.9	536.3827	623.6767	0.0000	37.1752	0.0000
Other polychaetes	20-49.9	46.5901	776.4353	0.0000	4.1306	0.0000
Other polychaetes	50-79.9	20.9137	47.9934	0.0000	0.0000	0.0000
Other polychaetes	80+	8.3283	47.7417	0.0000	0.0000	0.0000
Cerastoderma edule	5-9.9	1.8608	0.0000	0.0000	0.0000	0.0000
Cerastoderma edule	10-14.9	5.5522	0.0000	0.0000	0.0000	0.0000
Cerastoderma edule	15-19.9	59.5207	0.0000	0.0000	0.0000	0.0000
Cerastoderma edule	20+	40.3428	9.5483	0.0000	0.0000	0.0000
Scrobicularia plana	5-9.9	1569.6787	47.9934	0.0000	90.8727	0.0000
Scrobicularia plana	10-14.9	3.6727	0.0000	0.0000	4.1306	0.0000
Scrobicularia plana	15-19.9	14.1822	0.0000	0.0000	0.0000	0.0000
Scrobicularia plana	20+	143.5486	0.0000	0.0000	4.1306	0.0000
Other bivalves	5-9.9	2.7761	0.5033	0.0000	0.0000	0.0000
Other bivalves	10-14.9	0.0000	9.5483	0.0000	0.0000	0.0000
Other bivalves	15-19.9	0.0000	0.0000	0.0000	0.0000	0.0000
Other bivalves	20+	4.0082	0.0000	0.0000	0.0000	0.0000
Artemia	All	0.0000	0.0000	33610.7614	0.0000	0.0000
Amphipods	All	0.9304	0.5033	0.0000	0.0000	2032.5200
Larvae	All	22.9520	19.6000	866.6361	365.0298	1470.0000
Gastropods	All	5361.2167	86.4384	79.6575	7490.4397	1955.1000

Resource		**Ash-free dry mass (g)**							
Species	**Size class (mm)**	**Guadalete Channel Mud**	**Guadalete Sand**	**Guadalete Active Salina**	**Guadalete Aquaculture**	**Trocadero Intertidal Mud**	**Trocadero Active**	**Trocadero Abandoned Salinas**	**Trocadero Aquaculture**
Hediste diversicolor	5-9.9	0.000000	0.000000	0.000000	0.000000	0.006681	0.000000	0.000000	0.000000
Hediste diversicolor	10-19.9	0.005001	0.000000	0.000000	0.000000	0.005001	0.000000	0.000000	0.000000
Hediste diversicolor	20-49.9	0.011008	0.000000	0.000000	0.000000	0.010714	0.000000	0.000000	0.000000
Hediste diversicolor	50-79.9	0.051448	0.000000	0.000000	0.000000	0.065688	0.000000	0.000000	0.000000
Hediste diversicolor	80+	0.271425	0.000000	0.000000	0.000000	0.143945	0.000000	0.000000	0.000000
Other polychaetes	5-9.9	0.000120	0.000129	0.000000	0.000000	0.000703	0.000000	0.000113	0.000000
Other polychaetes	10-19.9	0.000176	0.000411	0.000000	0.000000	0.000395	0.000000	0.000000	0.000000
Other polychaetes	20-49.9	0.000535	0.001337	0.000000	0.000000	0.002379	0.000000	0.000000	0.000000
Other polychaetes	50-79.9	0.000000	0.000000	0.000000	0.000000	0.004078	0.000000	0.000000	0.000000
Other polychaetes	80+	0.000000	0.000000	0.000000	0.000000	0.026599	0.000000	0.000000	0.000000
Cerastoderma edule	5-9.9	0.003996	0.005798	0.000000	0.000000	0.003638	0.000000	0.000000	0.000000
Cerastoderma edule	10-14.9	0.022575	0.023797	0.000000	0.000000	0.025096	0.000000	0.000000	0.000000
Cerastoderma edule	15-19.9	0.054460	0.059441	0.000000	0.000000	0.055426	0.000000	0.000000	0.000000
Cerastoderma edule	20+	0.093849	0.096862	0.000000	0.000000	0.147955	0.000000	0.000000	0.000000
Scrobicularia plana	5-9.9	0.002118	0.000000	0.000000	0.000000	0.002401	0.000000	0.001781	0.000000
Scrobicularia plana	10-14.9	0.010756	0.000000	0.000000	0.000000	0.006725	0.000000	0.010968	0.000000
Scrobicularia plana	15-19.9	0.031086	0.028046	0.000000	0.000000	0.023602	0.000000	0.000000	0.000000
Scrobicularia plana	20+	0.121207	0.164182	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
Other bivalves	5-9.9	0.001349	0.002365	0.000000	0.000000	0.002525	0.000000	0.000000	0.000000
Other bivalves	10-14.9	0.007952	0.005103	0.000000	0.000000	0.012211	0.000000	0.000000	0.000000
Other bivalves	15-19.9	0.000000	0.011229	0.000000	0.000000	0.014155	0.000000	0.000000	0.000000
Other bivalves	20+	0.032705	0.038017	0.000000	0.000000	0.070022	0.000000	0.000000	0.000000
Artemia	All	0.000000	0.000000	0.000396	0.000000	0.000000	0.000497	0.000000	0.000000
Amphipods	All	0.000145	0.000040	0.000000	0.000096	0.000060	0.000000	0.000000	0.000096
Larvae	All	1.789E-07	0.000000	0.001285	0.001400	0.000006	0.001766	0.000066	0.001400
Gastropods	All	0.000675	0.001634	0.001215	0.000649	0.000909	0.000512	0.000816	0.000649

Resource		**Ash-free dry mass (g)**				
Species	**Size class (mm)**	**Rio Arillo Channel Mud**	**Rio Arillo Intertidal**	**Rio Arillo Active Salinas**	**Rio Arillo Abandoned Salinas**	**Rio Arillo Aquaculture**
Hediste diversicolor	5-9.9	0.000000	0.006223	0.000000	0.000000	0.000000
Hediste diversicolor	10-19.9	0.000000	0.005319	0.000000	0.000000	0.000000
Hediste diversicolor	20-49.9	0.017475	0.014869	0.000000	0.000000	0.000000
Hediste diversicolor	50-79.9	0.000000	0.051040	0.000000	0.000000	0.000000
Hediste diversicolor	80+	0.000000	0.353466	0.000000	0.000000	0.000000
Other polychaetes	5-9.9	0.000059	0.000115	0.000000	0.000000	0.000000
Other polychaetes	10-19.9	0.000219	0.000338	0.000000	0.000000	0.000000
Other polychaetes	20-49.9	0.000455	0.001348	0.000000	0.000000	0.000000
Other polychaetes	50-79.9	0.000000	0.005524	0.000000	0.000000	0.000000
Other polychaetes	80+	0.000000	0.086232	0.000000	0.000000	0.000000
Cerastoderma edule	5-9.9	0.000000	0.000000	0.000000	0.000000	0.000000
Cerastoderma edule	10-14.9	0.016107	0.000000	0.000000	0.000000	0.000000
Cerastoderma edule	15-19.9	0.049505	0.067046	0.000000	0.055485	0.000000
Cerastoderma edule	20+	0.253129	0.095877	0.000000	0.000000	0.000000
Scrobicularia plana	5-9.9	0.001030	0.002388	0.000000	0.000000	0.000000
Scrobicularia plana	10-14.9	0.008287	0.009925	0.000000	0.000000	0.000000
Scrobicularia plana	15-19.9	0.000000	0.000000	0.000000	0.000000	0.000000
Scrobicularia plana	20+	0.000000	0.000000	0.000000	0.000000	0.000000
Other bivalves	5-9.9	0.000000	0.003922	0.000000	0.000000	0.000000
Other bivalves	10-14.9	0.000000	0.013467	0.000000	0.000000	0.000000
Other bivalves	15-19.9	0.000000	0.017357	0.000000	0.000000	0.000000
Other bivalves	20+	0.000000	0.085106	0.000000	0.000000	0.000000
Artemia	All	0.000000	0.000000	0.000497	0.000000	0.000000
Amphipods	All	0.000000	0.000110	0.000000	0.000000	0.000096
Larvae	All	0.000000	0.000254	0.001766	0.000000	0.001400
Gastropods	All	0.000862	0.001205	0.000512	0.000810	0.000649

Resource		Ash-free dry mass (g)				
Species	**Size class (mm)**	**Sancti Petri Channel Mud**	**Sancti Petri Intertidal Mud**	**Sancti Petri Active Salinas**	**Sancti Petri Abandoned Salinas**	**Sancti Petri Aquaculture**
Hediste diversicolor	5-9.9	0.000000	0.000000	0.000000	0.000000	0.000000
Hediste diversicolor	10-19.9	0.004920	0.000000	0.000000	0.000000	0.000000
Hediste diversicolor	20-49.9	0.016299	0.000000	0.000000	0.000000	0.000000
Hediste diversicolor	50-79.9	0.047802	0.048726	0.000000	0.000000	0.000000
Hediste diversicolor	80+	0.207395	0.446100	0.000000	0.000000	0.000000
Other polychaetes	5-9.9	0.000124	0.000102	0.000000	0.000000	0.000000
Other polychaetes	10-19.9	0.000211	0.000360	0.000000	0.000236	0.000000
Other polychaetes	20-49.9	0.001060	0.001110	0.000000	0.000328	0.000000
Other polychaetes	50-79.9	0.003153	0.002230	0.000000	0.000000	0.000000
Other polychaetes	80+	0.028513	0.005821	0.000000	0.000000	0.000000
Cerastoderma edule	5-9.9	0.003736	0.000000	0.000000	0.000000	0.000000
Cerastoderma edule	10-14.9	0.021607	0.000000	0.000000	0.000000	0.000000
Cerastoderma edule	15-19.9	0.053678	0.000000	0.000000	0.000000	0.000000
Cerastoderma edule	20+	0.109573	0.147061	0.000000	0.000000	0.000000
Scrobicularia plana	5-9.9	0.001355	0.000954	0.000000	0.001972	0.000000
Scrobicularia plana	10-14.9	0.008465	0.000000	0.000000	0.006274	0.000000
Scrobicularia plana	15-19.9	0.028479	0.000000	0.000000	0.000000	0.000000
Scrobicularia plana	20+	0.152475	0.000000	0.000000	0.084562	0.000000
Other bivalves	5-9.9	0.000886	0.002008	0.000000	0.000000	0.000000
Other bivalves	10-14.9	0.000000	0.003623	0.000000	0.000000	0.000000
Other bivalves	15-19.9	0.000000	0.000000	0.000000	0.000000	0.000000
Other bivalves	20+	0.232592	0.000000	0.000000	0.000000	0.000000
Artemia	All	0.000000	0.000000	0.000497	0.000000	0.000000
Amphipods	All	0.000183	0.000798	0.000000	0.000000	0.000096
Larvae	All	0.000000	0.000000	0.000944	0.000000	0.001400
Gastropods	All	0.001372	0.000555	0.001762	0.001223	0.000649

6.5.4 COMPONENTS

Values of AFDM for each resource are shown in Table 6.3. For each size class they are a weighted mean based on the densities of each individual 1mm size category within the larger size-class.

6.4.5 FORAGERS

Nine species of shorebirds were included in the model: Little Stint *Calidris minuta*, Kentish Plover *Charadrius alexandrinus*, Sanderling *Calidris alba*, Ringed Plover *Charadrius hiaticula*, Redshank *Tringa totanus*, Grey Plover *Pluvialis squatarola*, Black-tailed Godwit *Limosa limosa*, Bar-tailed Godwit *Limosa lapponica*, and Oystercatcher *Haematopus ostralegus*.

Forager numbers, diets, constants and variables are shown in Table 6.4.

Forager diets were determined from published information on the diets of waders in the bahía de Cádiz (Masero, 2003; Masero et al., 2000; Perez-Hurtado et al., 1997). Forager constants were feeding efficiency, dominance, initial functional unit, arrival date and departure date. It is thought that birds tend not to move between functional units in Cádiz (A. Perez-Hurtado pers. comm.) so the numbers in each functional unit were initialised by assigning each bird to a functional unit on arrival. The arrival and departure days of each bird species were set up to match the patterns of bird numbers observed through the winter (see Section 6.3.4). The foraging efficiency of each individual within the population was drawn from a normal distribution, with a mean of one and a standard deviation of 0.125. The dominance score for each individual was drawn from a uniform distribution between 0 and 1.

Forager variables used were the area available for feeding and three different types of interference: mobile-prey interference, weak kleptoparasitism and strong kleptoparasitism (see Chapter 2). The area available for feeding was the currently exposed patch area minus any area affected by shellfishers. This area was then used to calculate the degree of interference from conspecifics. Mobile prey interference affected the intake rates of birds feeding on worms and *Crustacea*, weak kleptoparasitism affected the intake rates of birds other than oystercatchers feeding on molluscs, whilst strong kleptoparasitism affected the intake rate of oystercatchers feeding on molluscs. The parameter values describing these three types of interference are shown in Table 6.4.

The rate at which shorebirds were able to feed depended on the abundance of food in a patch and the strength of interference from other competitors. The influence of the food supply on a bird's intake rate was calculated using a functional response (see Chapter 2) for annelids and molluscs. For other, supratidal, prey types intake rates measured in the bahía de Cádiz were used (Castro, 2001; Estrella, 2001; Masero, 1998, 2003; Masero & Perez-Hurtado, 2001). The parameter values describing the functional response for each shorebird species are shown in Table 6.4.

The energy assimilated from consumed food depended on the energy density of the food and the efficiency with which the energy from the food could be assimilated. Energy density was assumed to be 22kJg^{-1} for all prey species. Assimilation efficiencies were derived from (Masero, 2003) (Table 6.4).

Assimilated energy was converted into increased mass by assuming that 33KJ of energy was stored in each gram of storage tissues (Kersten & Piersma, 1987). The daily energy requirements for each bird species were calculated from the species' body mass using the 'all bird species' equation given by Nagy, Girard and Brown (1999). Body mass data for all species except oystercatchers were supplied by the authors. In general, species were 10-15% lighter in Cádiz than on the Wash, England, so the weight of oystercatchers in the model was based on the average measured on the Wash (Johnson, 1985) reduced by 10%.

Shellfishing disturbed part of a patch, making it unavailable for feeding. The area affected by disturbance was calculated from disturbance distances for some species obtained on the Bahía de Cádiz. Species for which disturbance distances were not measured were assigned the same disturbance distance as the nearest equivalent species for which a distance was available. The energy cost of disturbance was calculated using the following equation (Nudds & Bryant, 2000):

$$C = 61.718tM^{0.7902} \tag{6.1}$$

Where C = energetic cost in J, t = duration of flight and M = mean body mass in kg. The duration of flight following a disturbance was assumed to be two minutes.

The only source of forager mortality in the model was starvation. A forager died if it failed to maintain any fat reserves i.e. body mass $\leq$ starvation mass. The starvation mass of each species was measured from previous studies or predicted from the basal body mass for species with no direct measurement (Table 6.4).

Table 6.4 Forager variables used in the Bahía de Cádiz model

Forager variables	**Correlimos menudo**	**Chorlitejo patinegro**	**Correlimos tridáctilo**	**Chorlitejo grande**	**Archibebe común**	**Chorlito gris**	**Ajuga colinegra**	**Ajuga colipinta**	**Ostrero**
	Little Stint	**Kentish Plover**	**Sanderling**	**Ringed Plover**	**Redshank**	**Grey Plover**	**Black-tailed Godwit**	**Bar-tailed Godwit**	**Oystercatcher**
	Calidris minuta	**Charadrius alexandrinus**	**Calidris alba**	**Charadrius hiaticula**	**Tringa totanus**	**Pluvialis squatarola**	**Limosa limosa**	**Limosa lapponica**	**Haematopus ostralegus**
Initial numbers	2380	1670	496	3500	1640	750	880	449	368
Arrival dates	Sep-Nov	Sep	Sep	Sep	Sep	Sep	Sep	Sep	Sep
	Jan-Mar	Nov-Dec	Nov-Jan		Nov-Jan	Dec-Jan	Nov-Feb	Dec-Jan	
Diets eaten:									
Polychaetes 5-10mm	x		x						
Polychaetes10-50mm		x							
Polychaetes10-80mm					x				
Polychaetes 20mm+				x		x		x	
Polychaetes 50mm+									x
Bivalves 5-10mm			x		x				
Bivalves 10-20mm						x	x	x	
Bivalves 15mm+									x
Artemia	x		x						
Larvae	x	x		x	x		x		
Hydrobia			x	x	x		x		
Amphipods									
Range of foraging efficiencies (coef. of variation)	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125
Range of dominance values	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1
Mobile prey interference:									
Aggregation factor	10	10	10	10	10	10	10	10	10
Threshold density (n ha^{-1})	100	100	100	100	100	100	100	100	100
Coefficients	0.48,0,0	0.48,0,0	0.48,0,0	0.48,0,0	0.48,0,0	0.48,0,0	0.48,0,0	0.48,0,0	0.48,0,0

Forager variables	**Correlimos menudo**	**Chorlitejo patinegro**	**Correlimos tridáctilo**	**Chorlitejo grande**	**Archibebe común**	**Chorlito gris**	**Ajuga colinegra**	**Ajuga colipinta**	**Ostrero**
	Little Stint	**Kentish Plover**	**Sanderling**	**Ringed Plover**	**Redshank**	**Grey Plover**	**Black-tailed Godwit**	**Bar-tailed Godwit**	**Oystercatcher**
	Calidris minuta	**Charadrius alexandrinus**	**Calidris alba**	**Charadrius hiaticula**	**Tringa totanus**	**Pluvialis squatarola**	**Limosa limosa**	**Limosa lapponica**	**Haematopus ostralegus**
Weak kleptoparasitism:									
Aggregation factor	10	10	10	10	10	10	10	10	10
Threshold density (n ha^{-1})	100	100	100	100	100	100	100	100	100
Coefficients	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0
Strong kleptoparasitism:									
Aggregation factor									10
Threshold density (n ha^{-1})									100
Coefficients									0.50,-0.50,0
Functional response:									
B_{50} (g AFDM m^{-2})	0.761	0.761	0.761	0.761	0.761	0.761	0.761	0.761	0.761
Forager coefficient	-2.0005	-1.8785	-1.8373	-1.8201	-1.6194	-1.4962	-1.4105	-1.4354	-1.3020
Prey coefficient	0.36542	0.36542	0.36542	0.36542	0.36542	0.36542	0.36542	0.36542	0.36542
Prey assimilation efficiency:									
Worms	0.8	0.8	0.8	0.8	0.8	0.8		0.8	0.8
Bivalves			0.85		0.85	0.85	0.85	0.85	0.85
Artemia	0.7		0.7						
Larvae	0.7	0.7		0.7	0.7		0.7		
Hydrobia			0.76	0.76	0.76		0.76		
Amphipods									

Forager variables	**Correlimos menudo**	**Chorlitejo patinegro**	**Correlimos tridáctilo**	**Chorlitejo grande**	**Archibebe común**	**Chorlito gris**	**Ajuga colinegra**	**Ajuga colipinta**	**Ostrero**
	Little Stint	**Kentish Plover**	**Sanderling**	**Ringed Plover**	**Redshank**	**Grey Plover**	**Black-tailed Godwit**	**Bar-tailed Godwit**	**Oystercatcher**
	Calidris minuta	**Charadrius alexandrinus**	**Calidris alba**	**Charadrius hiaticula**	**Tringa totanus**	**Pluvialis squatarola**	**Limosa limosa**	**Limosa lapponica**	**Haematopus ostralegus**
Energy density of fat reserves (kJ g^{-1})	33.4	33.4	33.4	33.4	33.4	33.4	33.4	33.4	33.4
Non-thermoregulatory energy requirements (kJ d^{-1})	97	136	152	160	279	393	498	465	673
Area affected by disturbance (m^2)	4839.8	4839.8	14892.2	14892.2	17394.5	5771	10003.9	10003.9	2239.6
Energy cost of disturbance (kJ $disturbance^{-1}$)	0.75	0.88	0.95	0.98	1.53	2.17	2.85	2.63	4.14
Basal mass (g)	26.14	42.97	50.84	54.53	123.5	204	289.26	261.33	450
Mean arrival mass (g)	26.14	42.97	50.84	54.53	123.5	204	289.26	261.33	450
Target mass(g)	26.14	42.97	50.84	54.53	123.5	204	289.26	261.33	450
Starvation mass (g)	17	32	33	37	85	127	161	195	350

6.6 Simulations

The effects of salina abandonment were simulated by progressively decreasing the area of active and recently abandoned salinas in each functional unit and increasing the area of old abandoned salinas by a corresponding amount. The area of active salinas was reduced by 25%, 50%, 75% and 100%. The area lost to active salina in each case was converted into an equal area of old abandoned salina with the prey community and exposure regime appropriate to that type of habitat.

The intensification of aquaculture was simulated simply by reducing the area of drained extensive fishponds available to the birds by 25%, 50%, 75% and 100%. As the intensive aquaculture that replaces extensive fishponds provides no food sources for birds the lost habitat was not converted to another habitat type, but simply removed from the model.

To simulate the effects of habitat creation we started with a baseline worst-case scenario in which all active salina and extensive aquaculture had been removed. Areas which were currently old abandoned salinas were then gradually turned into active salinas. The area of habitat created in the simulations ranged from 300 to 1800ha in steps of 300ha. Habitat creation was spread equally across all four functional units rather than being confined to one or more.

As many of the species in the model feed mainly intertidally, salina abandonment and aquaculture intensification were also simulated with the density of intertidal prey reduced by half to see if the supratidal played a role in the survival of these species at low intertidal prey densities.

6.7 Results

6.7.1 MODEL CALIBRATION

Initial uncalibrated model runs showed high mortality rates in little stint, *Calidris minuta*, and kentish plover, *Charadrius alexandrinus*. On examination of the data, it was found that the ash-free dry mass of small polychaetes (excluding *Hediste*) was very low. The ‘polychaetes’ prey type covers a variety of different species from long threadlike worms to thicker more robust ones and the AFDM, and therefore the profitability, of these different types is likely to vary considerably. On the assumption that the birds would avoid small threadlike worms and concentrate on those with higher food value, the AFDM of small polychaetes (5-10mm and 10-15mm) was increased to a figure more in line with, although still lower than, that of *Hediste*. Mortality rates in little stint and kentish plover dropped to zero as a result of this increase.

6.7.2 MODEL VALIDATION

6.7.2.1 Distribution between functional units

Birds in the model were assigned to a functional unit on arrival, based on the observed distribution of birds between functional units. Thereafter, they remained in the same functional unit unless their energetic needs were not being met and their fat reserve dropped below 10% of their target. If this happened, the birds were free to move to any other functional unit that offered a better chance of survival. We compared the distribution of birds between functional units in December, after birds had had time to move functional units if necessary, but before numbers had begun dropping in spring with the observed distribution.

For most species the predicted distribution between functional units matched the observed well (Fig. 6.3). Exceptions to this were little stint (*Calidris minuta*) and sanderling (*Calidris alba)* of which higher numbers were present in the Trocadero functional unit in the model than were observed there in reality.

6.7.2.2 Habitat selection at low tide

Data on the proportion of birds of each species feeding intertidally and supratidally in the Guadalete functional unit was available from Masero *et al.* (2000). From the data therein we calculated the proportion of the population of each species seen feeding at low tide. We then derived from this our test statistic – the proportion of feeding birds using the intertidal areas as opposed to the supratidal at low tide. We compared predicted and observed values for the start, middle and end of the period modelled, i.e. September, December and March. Blacktailed godwit were excluded from the comparison because none were observed in Guadalete in the year of modelling.

For the majority of species the model predicted low-tide habitat use well (Fig. 6.4). Exceptions were sanderling, C*alidris alba*, and redshank, T*ringa totanus* which used the intertidal more in the model than was observed, particularly at the end of winter in March. According to Masero (2003) some species use the salinas more during their pre-migration fattening period in March. The model did not include pre-migratory weight gain as data on weight targets was not available, so this may in part explain the discrepancy between predicted and observed.

6.7.2.3 Time spent feeding

Masero (2003) measured the daily amount of time spent feeding by, amongst other species, little stint, *Calidris minuta*, and sanderling, *Calidris alba* in winter and in their pre-migration period in spring. The model predicted feeding time well in the spring but overpredicted sanderling feeding time in December (Fig. 6.5).

6.7.2.4 Diet selection

Birds in the model were given a choice of diets based on observations collected under this project and previously available data. They could only feed on prey included in their diet selection diets, but could choose to feed on a subset of the permitted diets. We compared the model's predicted diet selection with observed diet selection from Perez-Hurtado *et al.* (1997). Figure 6.6 below shows the proportion of each prey type in the diet of each bird species.

The diets of little stint, *Calidris. minuta*, and kentish plover, *Charadrius alexandrinus*, could not be observed directly in the wild but faecal analysis showed that they fed on a mixture of chironomid larvae and polychaetes. Model birds had the same diet, but the proportion of polychaetes in the diet was higher than was suggested by faecal analysis. Sanderling, *Calidris alba,* were observed to feed on a mixture of polychaetes, bivalves and *Hydrobia* and also chose to eat a mixture of these diets in the model. Ringed plover, *Charadrius hiaticula*, fed mainly on polychaetes in the model and were also observed to feed on them in the wild. They also ate *Hydrobia* in Perez-Hurtado *et al.*'s study, but the model birds were not permitted to eat *Hydrobia* as no functional response was available. The same was true for model redshank, T*ringa totanus*. Observations showed redshank feeding intertidally on *Hydrobia*, bivalves and polychaetes, whilst model redshank fed largely on Polychaetes with some bivalves included in the diet. Grey plover, *Pluvialis squatarola*, and bar-tailed godwit, *Limosa lapponica*, fed on a mixture of polychaetes and bivalves both in the model and in reality. Faecal analysis suggested that black-tailed godwits, *Limosa limosa*, ate chironomid larvae supratidally, as did model birds, but they did not feed intertidally at the study site. Oystercatchers were not included in Perez-Hurtado *et al.*'s study.

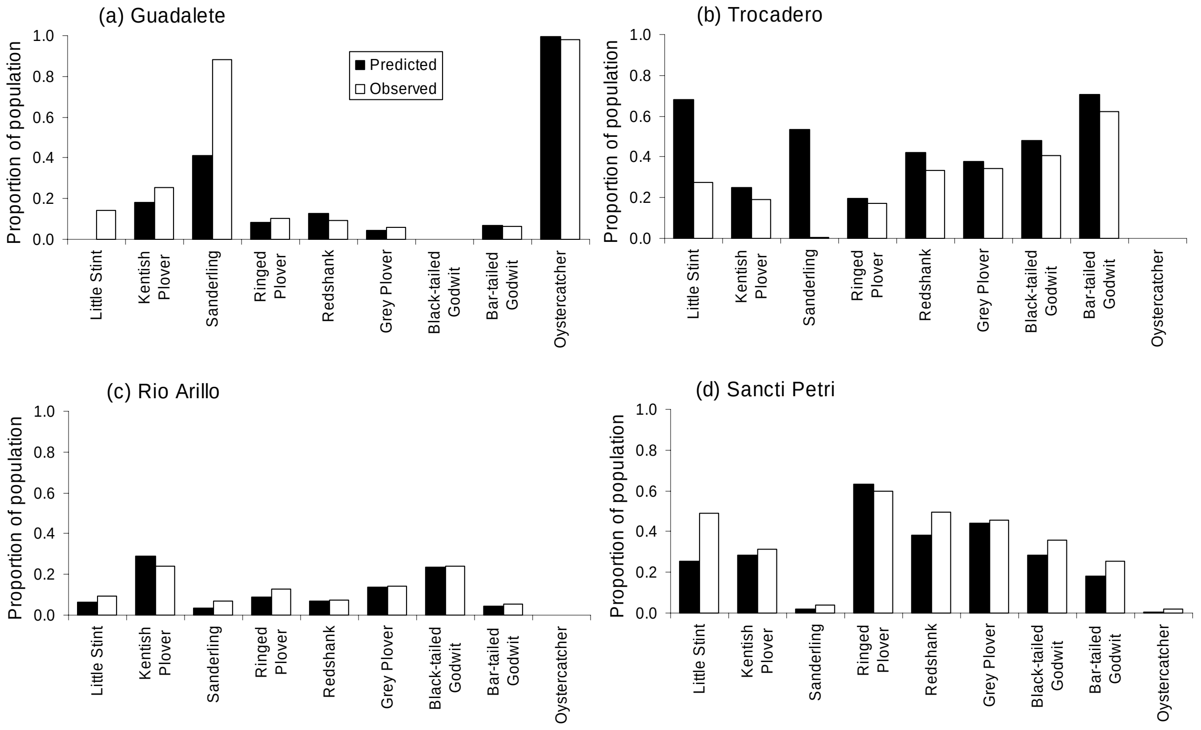
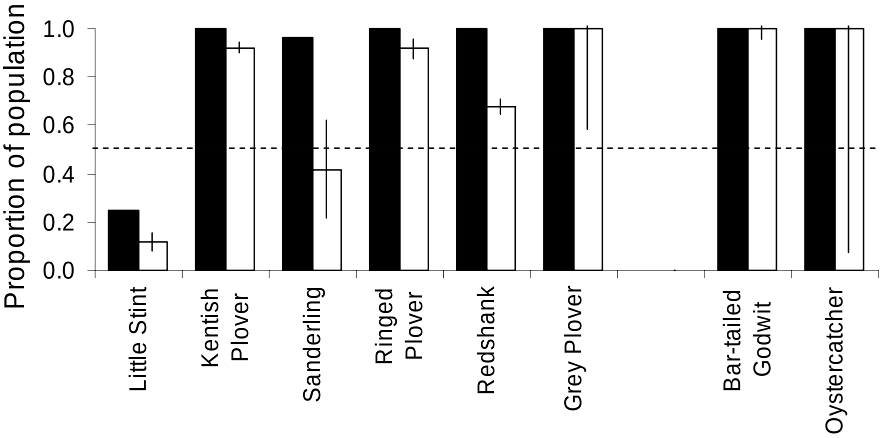
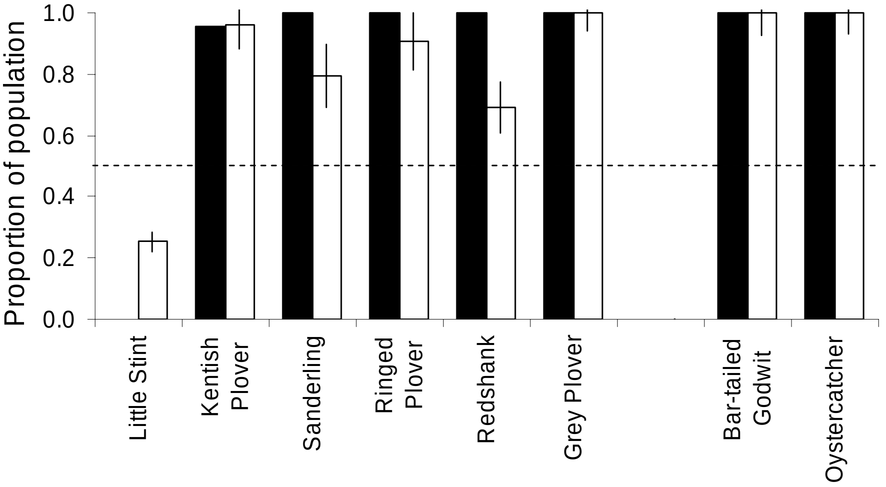


Figure 6.3 Predicted (black bars) and observed (white bars) numbers of birds in each functional unit.

(a) September



(b) December



(c) March

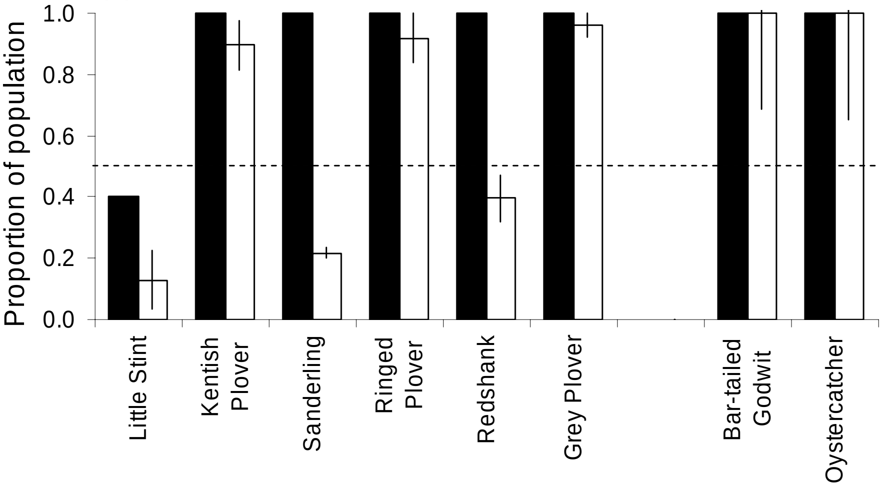
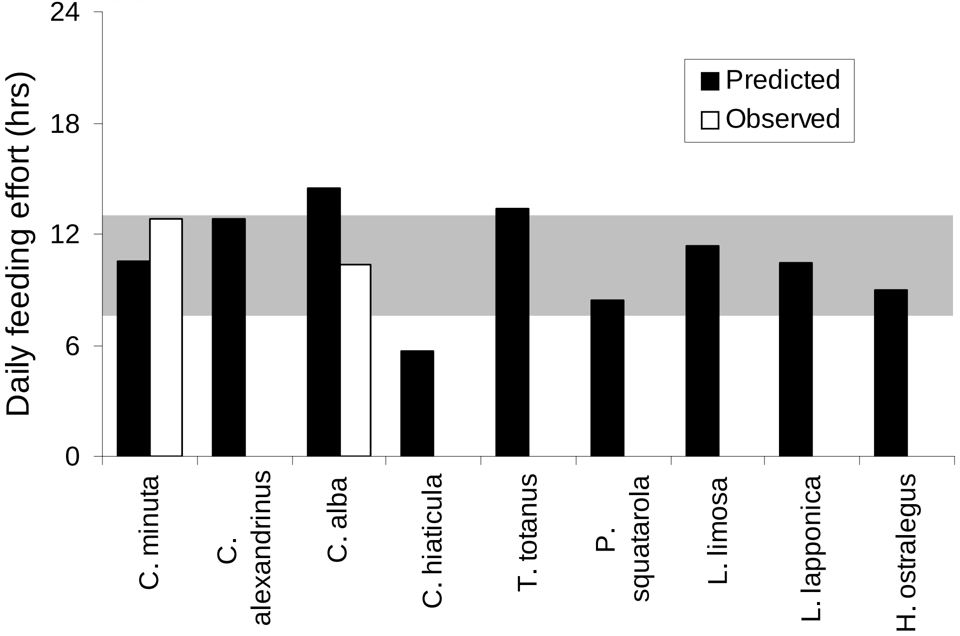


Figure 6.4 Predicted (black bars) and observed (white bars) proportion of feeding birds using intertidal habitat at low tide in a) September, b) December and c) March.

(a) December



(b) March

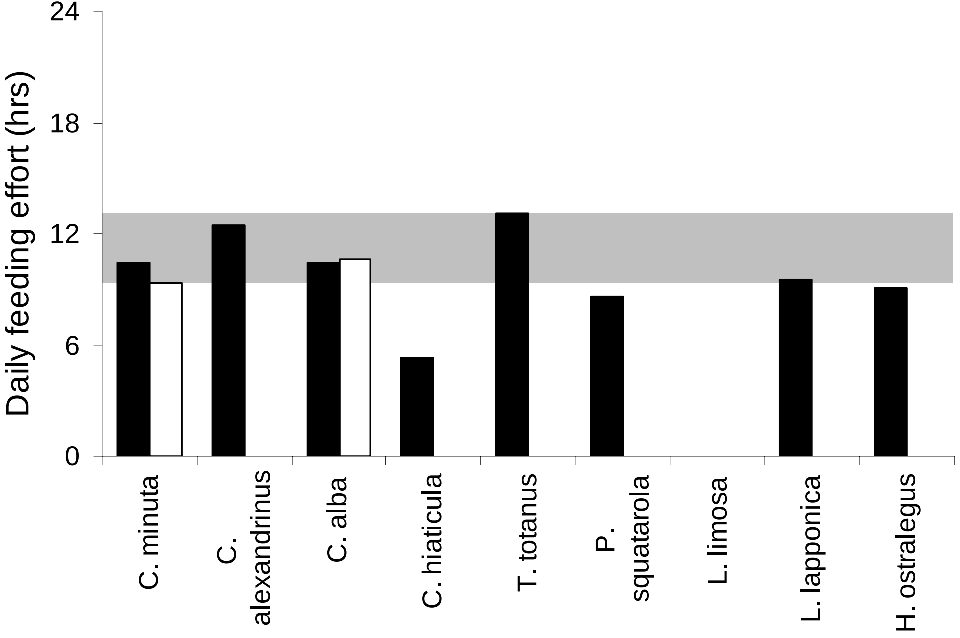


Figure 6.5 Predicted (black bars) and observed (white bars) amount of time spent feeding in a) December and b) March. The grey box shows the range of daily feeding times observed in Masero's study (Masero, 2003).

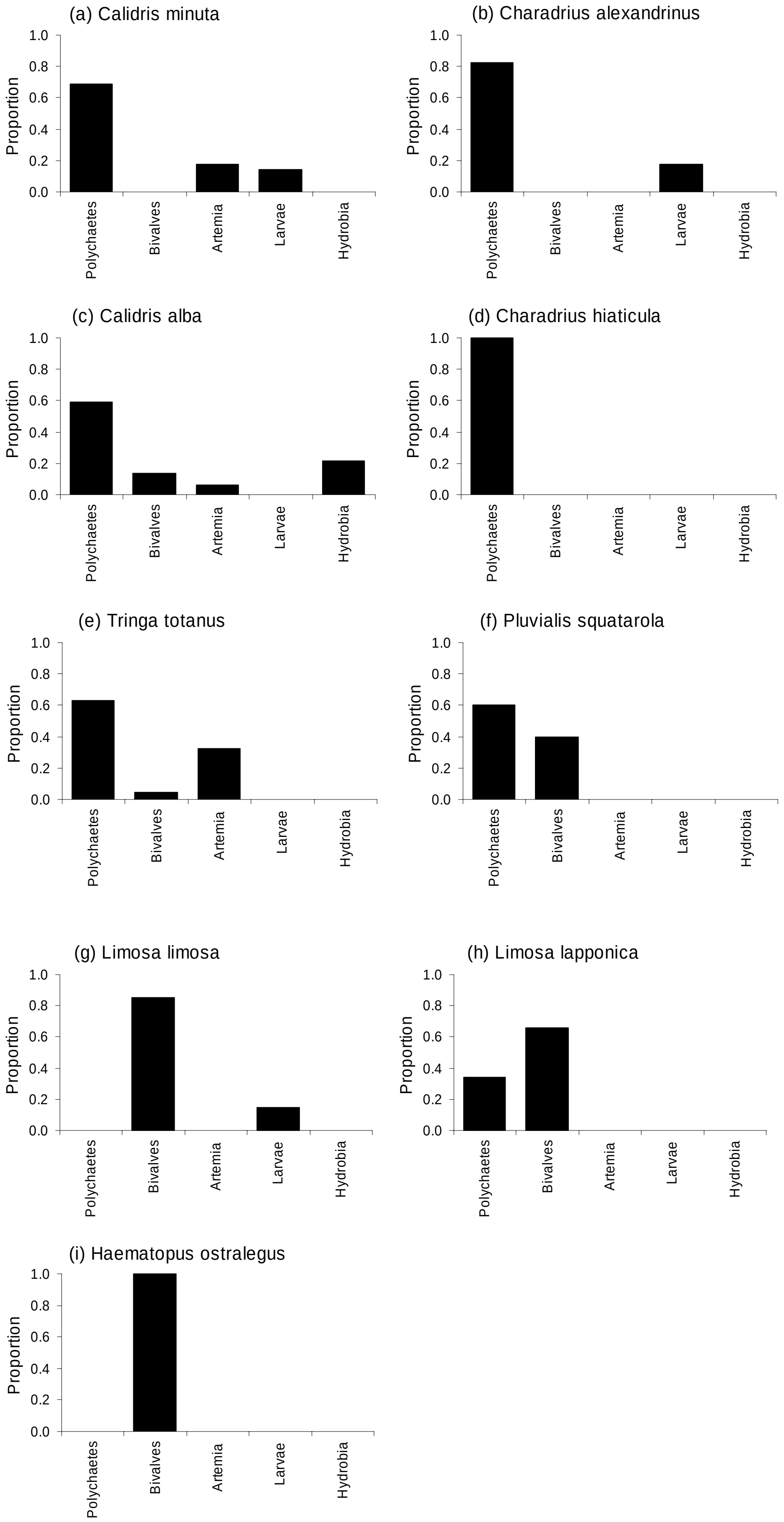


Figure 6.6 Diet selections of model birds.

6.7.3 ISSUES

6.7.3.1 Salina abandonment

We simulated the abandonment of between 25% and 100% of the current area of active salinas, with the exception of the industrial salina in Guadalete which is unlikely to be abandoned. The simulations showed no effect of salina abandonment on mortality rates at any level when prey density on the intertidal areas was at normal levels. When the simulations were re-run with intertidal prey densities halved there was a small effect of complete salina abandonment with redshank, *Tringa totanus*, mortality increasing by 2.4%.

6.7.3.2 Aquaculture intensification

We simulated the intensification of aquaculture by removing between 25% and 100% of the area of available fishponds. This too had no effect on mortality when intertidal prey densities were at normal levels. With intertidal prey densities halved, there was a low-level mortality of redshank in some simulations, around 0.8%, but this was not related to the amount of aquaculture removed.

6.7.3.4 Habitat creation

The baseline for habitat creation was a worst-case scenario in which all traditional salinas had been abandoned and no extensive aquaculture remained. In this case, there was 4.1% mortality of redshank when intertidal prey density was halved. This mortality was compensated for by the lowest level of habitat creation simulated – 300ha of active salina created in equal amounts in all four functional units.

6.8 Conclusions

Using data collected for this Report, we have developed an individuals-based model of nine shorebird species over wintering in the Bahía de Cádiz. As well as high number of bird species there were several different intertidal and supratidal habitat types in the model making it the most complex individuals-based shorebird model developed to date.

The model predicted reasonably well the distribution of birds around the bay, the proportion feeding on intertidal and supratidal habitats, their diet choices and the proportion of time that they spend feeding during the tidal cycle where available. However, some aspects of the system were not included in the model because of limited availability of data and these could affect the model's predictions considerably. For example, functional responses are difficult and time-consuming to collect, especially for birds eating very small prey, and some birds therefore had a limited range of diets in the model as a result of data not being available. In addition, it is known that some species change their feeding behaviour when gaining weight for their spring migration (Masero, 2003), but we could not include this in the model as pre-migration weight targets are currently not known.

Time constraints, and the length of time taken for each model run, meant that no repeat runs could be done for any of the simulations done for this Report. As a result, variation in stochastic elements of the model, such as feeding efficiency of individual birds, is reflected in the figures presented here. It also meant that no statistical analyses could be made of the results. Future work will involve repeat simulations and statistical analysis of our results.

In this Report, we used the model to address several issues related to the widespread changes in the supratidal habitat currently happening in Cádiz. Simulations suggested that the abandonment of traditional salinas and the intensification of aquaculture would have very little effect on the bird species included in the model, but it should not be concluded from this that the loss of salinas from the Bahía de Cádiz natural park would cause no harm. There are several reasons for this. First, the majority of the species included in the model feed predominantly on intertidal muds, so salina abandonment should not be an issue for these birds. Other species that were not included in the model, avocet, *Recurvirostra avosetta*, or spoonbill, *Platalea leucorodia*, for example, might be more dependent on the salinas. Second, we were not able to include pre-migration fattening in the model, although it could be added at a later date if the necessary information becomes available. There are indications that the salinas might play an important role in pre-migration fattening for some species, so their loss could cause some birds to fail on their spring migration, or indeed to be unable to migrate at all. Other aspects of the ecology of active salinas are also not yet well-understood. We do not yet know whether there is interference competition between birds feeding there, nor how large numbers of birds feeding in a salina might affect the population dynamics of the prey species living there. It is also possible that some species may prefer to feed in salinas regardless of energetic considerations, in the same way that redshank, *Tringa totanus*, prefer to feed on *Corophium* despite their low energy value (Goss-Custard, 1977). If this were the case, loss of active salinas might well cause some species that currently winter in the Bahía de Cádiz to winter elsewhere in the future. Finally, some of the richest areas in the Bahía de Cádiz are the river muds. Although these are very rich in invertebrates, they are also narrower than the intertidal mudflats and it is possible that many waders avoid feeding in these areas because of perceived predation risk. Many birds in the model did feed in these areas when supratidal prey were removed, but if real birds perceive them as too risky, the effect of supratidal habitat loss would be greater.

Overall, we succeeded in the aim of developing an individuals-based shorebird model for the large and complex Bahía de Cádiz area. Birds in the model generally feed in the correct habitats on the right sort of prey and where time spent feeding could be compared with the observed, the two corresponded quite well. As further research into the ecology of the salinas and their shorebird communities is conducted it can be incorporated into the model to refine the model's predictions and elucidate further the complex relationships between mudflats, salinas and shorebirds.

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7 SINGLE-SITE MODELS: BAIE DE SOMME WADERS

Sarah Durell, Patrick Triplet, Michel Desprez, Cédric Fagot, Nicolas Loquet, François Sueur and Richard Stillman

7.1 Study site

The Baie de Somme is the second largest estuary (70 km^2) on the French channel coast (Fig. 7.1). It is designated a Ramsar Waterfowl Habitat site, and an SPA European marine site under the EU Birds Directive. It is a major macrotidal estuary, with a mean tidal range of 8.98m. It is also a very exposed estuary, with a wide opening towards the prevailing westerly currents and south-westerly winds. As a result, the estuary is subject to substantial processes of deposition and erosion of sediment (McClusky *et al.*, 1994). Most freshwater enters the Baie de Somme from the Somme Canal in the south east, with smaller flows from canals at Le Crotoy and La Maye in the north. The intertidal flats in the Baie de Somme range from sandy muds to mobile sands and, in the lower reaches of the estuary, there are substantial cockle beds which are commercially fished (Desprez, 1995).

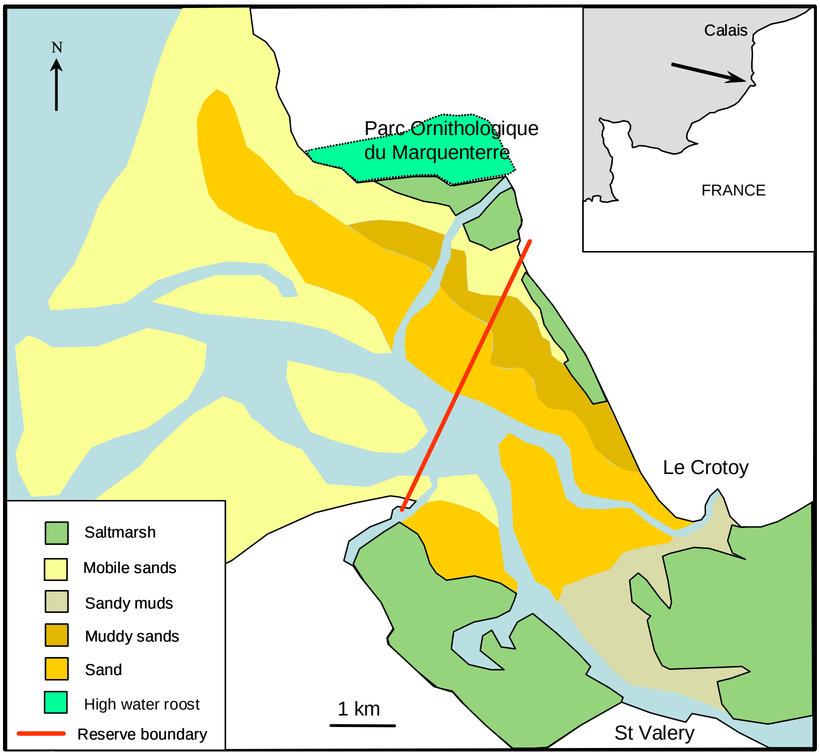


Figure 7.1 The Baie de Somme

7.2 Issues

7.2.1 HUNTING

Hunting is a major leisure activity on the Baie de Somme with over 3,000 licences being issued each season. The hunting season is from 1 September until 31 January and affects the whole of the estuary, apart from the Nature Reserve in the north-west (Fig. 7.1). Two of the three shorebird species included in this study, oystercatchers *Haematopus ostralegus* and curlew *Numenius arquata,* are shot, whilst the third, dunlin *Calidris alpina*, is a protected species. However, all three species are affected by disturbance by hunters. In our simulations we investigated the effect of reducing the hunted area and the length of the hunting season on shorebird survival.

7.2.2 SPARTINA ENCROACHMENT

In recent years, the area of cordgrass *Spartina spp.* in the Baie de Somme has been increasing. Research has shown that *Spartina* encroachment reduces the area for dunlin to feed (P. Triplet unpublished data). In our simulations we investigated how long it would take, if no measures are taken to prevent the present rate of increase in *Spartina*, before shorebird survival would be affected.

7.2.3 DISTURBANCE

The Nature Reserve in the Baie de Somme is the main place that shorebirds can feed during the winter without the risk of being shot. It is also subject to a great deal of disturbance, both from fishermen and from recreational visitors. It is important, therefore, for the Reserve management to know what level of disturbance can be allowed without affecting the survival of the birds that feed and roost there.

7.2.4 FISHING

Cockle fishing within the Nature Reserve disturbs the birds and depletes their food supply. Cockle fishing was included in the model and we investigated the effect of varying cockle stocks, and the amount of fishing that takes place.

7.2.5 ACCRETION

At the moment, sediments are accreting in the Baie de Somme, which means that the inter-tidal flats are becoming sandier and the shore-level is rising. In our simulations we tried to predict how this would affect the shorebird populations.

7.2.6 POPULATION CHANGE

The final issue we wanted to address in our simulations was population change. We investigated how many more shorebirds, under present conditions, could overwinter on the Baie de Somme without affecting their survival.

7.3 Data collection

7.3.1 PATCHES

Sediment characteristics were drawn from Nature Reserve monitoring data. Tide and topographic data for 1992 were taken from the Baie de Somme management project (Sogreah/EDF, 1995). These consisted of tidal curves, at different locations and for different tide levels (from the DDE/DSO Bureau d'Etudes Techniques Maritimes) and in a set of 3,600 height points covering the whole estuary (from aerial surveys by Topophot).

7.3.2 RESOURCES

Intertidal invertebrate communities in the Baie de Somme were sampled in the winter of 2001/2002 using a grid system of sampling (Fig. 7.2). Full surveys of benthic invertebrates were made each month from October 2001 until March 2002. At each sampling station two cores of 0.02 m^2 cross-sectional area and 30 cm depth were taken and the samples sieved in the field using a 1 mm mesh. Sieved material was fixed in a 4% formalin solution coloured by B phloxin.

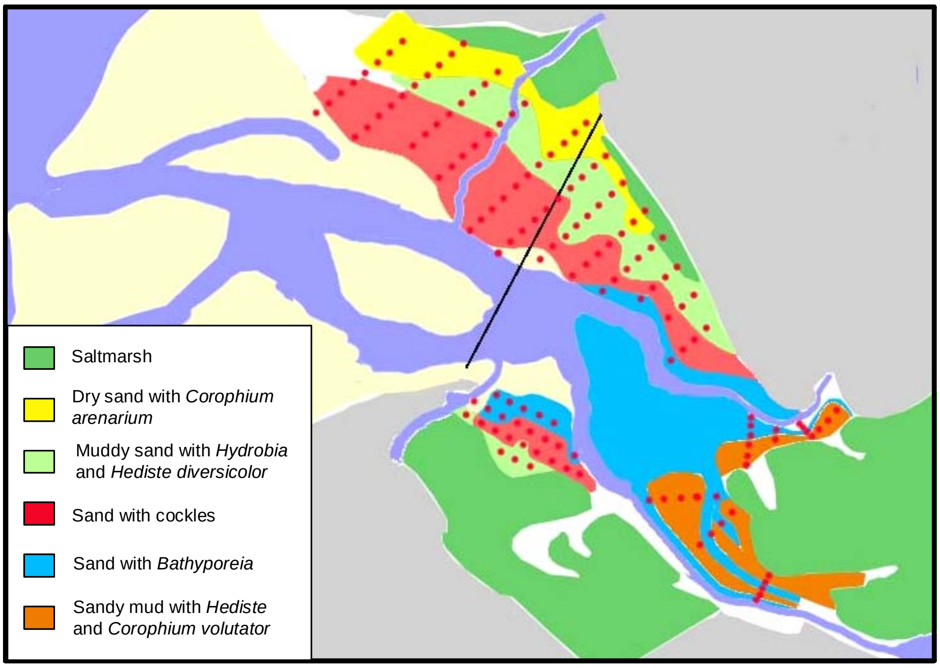


Figure 7.2 Invertebrate sampling stations and habitat types in the Baie de Somme

In the laboratory, all specimens were identified to species and most species were measured to 0.1mm, apart from small and/or easily broken worm species (nemerteans, nematodes, spionids, cirratulids, capitellids, oligochaetes), which were counted but not measured. Measurement of *Hediste diversicolor* was of the width of the first segment.

7.3.3 COMPONENTS

Separate samples of invertebrates were taken during each survey from a wide range of sites and frozen prior to ash-free-dry-mass (AFDM) analysis. After partial defrosting, head width was measured in worm species, body length in crustacean species, shell length for bivalves and spire height for gastropods. All molluscs, apart from *Hydrobia ulvae*, were removed from their shells before processing. Samples were dried to constant weight at 56 ^{o}C and burnt to constant weight in a muffle furnace at 460 ^{o}C. The loss of weight on burning (dry weight – ash weight) is the AFDM.

7.3.4 FORAGERS

Low tide counts of shorebirds in the Baie de Somme were made at 10 day intervals from September 2001 until March 2002. Numbers of birds feeding or resting were recorded and also the number and source of disturbances that took place during each recording period.

High water counts of total bird numbers present on the Baie de Somme each month were available for the period 1975-2002.

7.4 Data analysis

7.4.1 PATCHES

Sediment type and invertebrate communities sampled were used to identify habitat types within the estuary (Fig. 7.2).

7.4.2 RESOURCES

Resources used in the model were invertebrate prey size classes. Invertebrate data were combined for all sampling sites within each habitat patch and mean densities calculated for each prey size class.

Differences in invertebrate densities between the October and March surveys were used to calculate non-bird overwinter prey mortality.

7.4.3 COMPONENTS

The only resource component included in this model was AFDM. The AFDM for each prey size class was calculated using ($\log_e$) AFDM to ($\log_e$) body length relationships.

Differences in prey AFDM between the October and March surveys were used to calculate overwinter changes in AFDM.

7.4.4 FORAGERS

High water count data for the period 1993-2002 were used to calculate the mean number of each shorebird species present on the Baie de Somme during the winter and the time that these birds arrive from the breeding grounds.

7.5 Model variables

7.5.1 GLOBAL

Global variables used in the model are shown in Table 7.1. The variable weekend was included so that certain variables, such as disturbance, could differ in intensity between weekdays and weekends. An equation predicting day length was included in order to calculate hours of daylight so that variables could differ between day and night-time. Hourly tidal heights at Cayeux (just outside the estuary) for the winter 2000/2001 were obtained using TideWizard software (Marine Computing International 2000-2002). Tidal stage was calculated from this data so that bird distribution data could be extracted for three different stages of the tide: low tide, high tide and tide receding/advancing. Mean daily temperatures were obtained for Le Hourdel, situated on the south side of the Baie de Somme.

Table 7.1 Global variables used in the Baie de Somme model

Global variables	Value
Duration of time step	1 h
Day	Day 1 = 1 September
Weekend	
Time	
DayLength	21 June 18.11h, 21 December 9.25h
Daylight	
TideHeight	Tide heights at Cayeux for 2000-2001
TidalStage	Low = 3h, High = 3h
Temperature	Mean daily temperature (^{o}C) at Le Hourdel 2001-2002

7.5.2 PATCHES

Intertidal habitat patches in the Baie de Somme were divided into those that were within the Nature Reserve and those that were not. This resulted in nine different feeding patches within the model (Fig. 7.3).

Patch variables included in the model, and the baseline values used, are shown in Table 7.2. The area of each patch was measured off maps. The mean height of each patch was calculated by geostatistical Surfer © software from grid files using kriging as a gridding method. This enabled us to compute for each patch the mean time of coverage by sea water from the different available tide curves for three standard tide conditions: mean neap tide, mean tide and mean spring tide.

Disturbers were considered to be any human source of disturbance which affected the birds but which had no impact on their prey. Levels of disturbance were calculated from data collected during the bird surveys and from previous work (Triplet *et al.*, 1999; Triplet *et al.*, 2003). Fishers were not only potential sources of disturbance, but could also have an impact on prey densities. Hunters and raptors were a source of disturbance and also a potential mortality risk. Data on hunters and fishers was obtained from a literature search (P.Triplet unpublished information). Data on raptors was not available, so raptor frequencies were estimations.

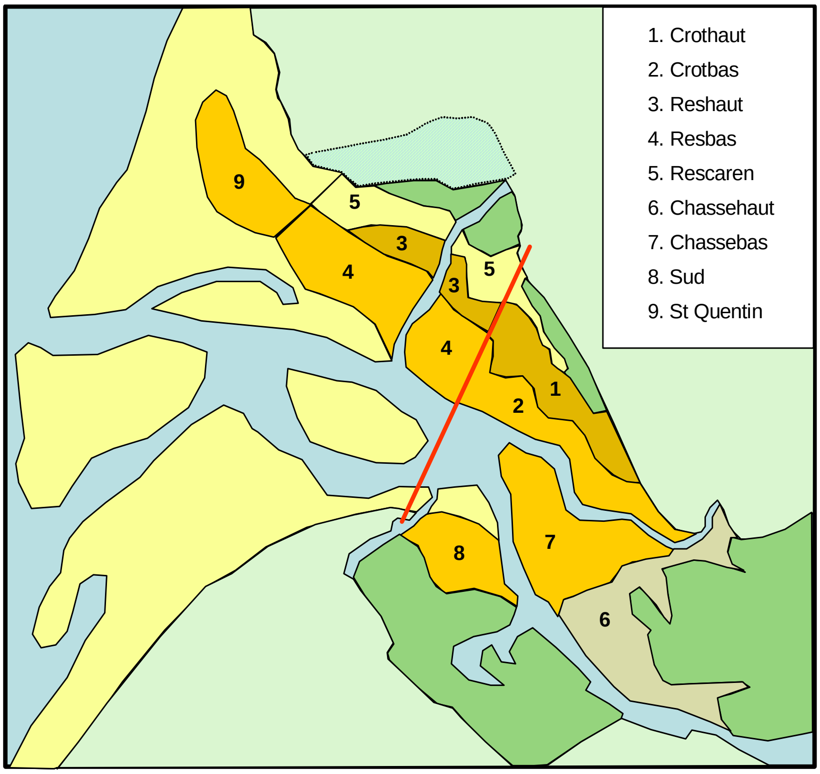


Figure 7.3 Feeding patches in the Baie de Somme model

Table 7.2 Patch variables used in the Baie de Somme model

Patch variables		Patch name								
		Crothaut	**Crotbas**	**Reshaut**	**Resbas**	**Rescaren**	**Chassehaut**	**Chassebas**	**Sud**	**St Quentin**
Patch area (m^2)		2110000	1070000	940000	2750000	1570000	1590000	3200000	1540000	1300000
Exposure tide ht (m)		7.5	7.1	8	7.3	8.6	7.1	6	6.4	5.6
Disturbers (h^{-1})	weekend day	0 - 2	0 - 2	0.3 - 1.8	0.3 - 1.8	0.3 - 1.8	0 - 2	0 - 2	0 - 2	0 - 2
	weekend night	0	0	0	0	0	0	0	0	0
	weekday day	0 - 1	0 - 1	0.2 - 0.8	0.2 - 0.8	0.2 - 0.8	0 - 1	0 - 1	0 - 1	0
	weekday night	0	0	0	0	0	0	0	0	0
Hunters (h^{-1})	weekend day	3 - 6	1.5 - 3	0	0	0	1.5 - 3	6 - 12	3 - 6	0
(1 Sep - 31 Jan)	weekend night	0 - 2	0 - 1	0	0	0	0 - 1	0 - 4	0 - 2	0
	weekday day	2 - 3	1 - 1.5	0	0	0	1 - 1.5	4 - 6	2 - 3	0
	weekday night	0 - 1	0 - 0.5	0	0	0	0 - 0.5	0 - 2	0 - 1	0
Fishers (h^{-1})	weekend day	0	0	0	0	0	0	0	0	0
	weekend night	0	0	0	0	0	0	0	0	0
	weekday day	0	0	0 - 5	51 - 88	0	0	0	0	24 - 42
	weekday night	0	0	0	0	0	0	0	0	0
Raptors (h^{-1})	weekend day	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7
	weekend night	0	0	0	0	0	0	0	0	0
	weekday day	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7
	weekday night	0	0	0	0	0	0	0	0	0

Table 7.3 Resource variables used in the Baie de Somme model

Resource		Initial density (n m^{-2})									Winter mortality (%)	Fishing loss (n fisher-1 d-1)	Resource component	
Species	Size class (mm)	Crothaut	Crotbas	Reshaut	Resbas	Rescaren	Chassehaut	Chassebas	Sud	St Quentin			Initial AFDM (g)	Overwinter change (%)
Cockles	5 - 9.99	1568.72	41	462	3471	0	0	0	1817	113	79	0	0.003945	-11
Cockles	10 - 14.99	1515.88	1126	1062	7455	0	0	0	3133	559	51	0	0.018061	-15
Cockles	15 - 19.99	103.55	337	336	376	0	0	0	50	260	10	0	0.049196	-17
Cockles	20 - 24.99	66.67	32	87	39	0	0	0	200	32.4	10	0	0.103988	-19
Cockles	25 - 29.99	25.36	8	36	61	0	0	0	33	81.8	25	433	0.189032	-21
Cockles	30 - 34.99	0	0	19	11	0	0	0	0	58.1	25	433	0.310886	-22
Cockles	35 - 39.99	0	0	0	0	0	0	0	0	15.2	25	433	0.476089	-23
Macoma	5 - 9.99	1149	88	29	382	0	0	4383	4383	0	58	0	0.005162	-3
Macoma	10 - 14.99	395	217	117	72	0	0	83	83	0	22	0	0.021927	-26
Macoma	15 - 19.99	871	244	213	427	0	0	350	350	0	22	0	0.056847	-38
Macoma	20 - 24.99	123	0	0	17	0	0	83	83	0	22	0	0.115805	-45
Macoma	25 - 29.99	24	0	0	0	0	0	0	0	0	22	0	0.204397	-51
Hydrobia	3+	30407	0	7307	20083	0	0	0	42213	0	87	0	0.001263	0
Worms	2 - 3.99	60.82	0	0	38.6	0	100	0	34	0	20	0	0.000136	0
Worms	4 - 5.99	196.28	0	23.93	221.4	0	450	0	167	0	20	0	0.001061	0
Worms	6 - 7.99	625.9	0	194.5	566.1	0	250	0	500	0	20	0	0.006274	0
Worms	8 - 9.99	226.77	0	156.38	544.8	0	50	0	333	0	20	0	0.023080	0
Worms	10 - 11.99	168.08	0	103.9	261.2	0	700	0	83	0	0	0	0.070963	0
Worms	12 - 13.99	86.88	0	50.88	22.18	0	350	0	34	0	0	0	0.175007	0
Worms	14 - 15.99	0	0	0	0	0	150	0	0	0	0	0	0.379800	0
Corophium	3+	0	0	0	0	8107	16017	0	0	0	0	0	0.000400	0

7.5.3 RESOURCES

Prey types and size classes used in the model, and their initial densities on each patch, are shown in Table 7.3. Worms were all *Hediste diversicolor*. Non-bird winter prey mortality was calculated from the difference in prey densities at the end of a model run compared with densities found in March. Fishing loss was based on the fact that fishermen are licensed to take 100kg of cockles a day each.

7.5.4 COMPONENTS

Initial values of AFDM for each resource, and any overwinter change, are shown in Table 7.3.

7.4.5 FORAGERS

Three species of shorebirds were included in the model: oystercatcher *Haematopus ostralegus*, dunlin *Calidris alpina*, and curlew *Numenius arquata*. Forager numbers, diets, constants and variables are shown in Table 7.4.

Forager diets were determined from literature searches (J.D. Goss-Custard unpublished data). Forager constants were arrival date, feeding efficiency and dominance. Arrival day was Day 1 for a certain number of birds (based on numbers present in August) whilst the arrival day of the rest of the population was drawn from a uniform distribution between Day 2 and Day 62 (October 31). The foraging efficiency of each individual within the population was drawn from a normal distribution, with a mean of one and a standard deviation of 0.125. The dominance score for each individual was drawn from a uniform distribution between 0 and 1.

Forager variables used were the area available for feeding, night-time feeding efficiency, lower critical temperature and three different types of interference: mobile prey interference, weak kleptoparasitism and large cockle kleptoparasitism (see Chapter 2). The area available for feeding was patch area minus any area affected by disturbers. This area was then used to calculate the degree of interference from conspecifics. Night-time feeding efficiency was expressed as a proportion of daytime efficiency and was the main parameter used to calibrate the model. The lower critical temperature (LCT: below which thermostatic energy costs are incurred) for each species was calculated from the relationship between known values for various wader species (from a literature search) and body mass. Mobile prey interference affected the intake rates of birds feeding on worms and *Corophium*, weak kleptoparasitism affected the intake rates of birds other than oystercatchers feeding on cockles, whilst large cockle kleptoparasitism affected the intake rate of oystercatchers feeding on cockles.

The rate at which shorebirds were able to feed depended on the abundance of food in a patch and the strength of interference from other competitors. The influence of the food supply on a bird's intake rate was calculated using a functional response (see Chapter 2).

The maximum amount of food that can be eaten at any one time is limited by a bird's gut processing rate and its crop capacity. This was expressed in the model as the maximum rate of consumption in kJ d^{-1} and was related to body mass using the following equation (Kirkwood, 1983):

$$C = 61.718tM^{0.7902} \tag{7.1}$$

Where c = consumption rate (J), t = time (s) and M = body mass (g). However, values calculated using this equation resulted in mass starvation amongst most birds in the model, probably because shorebirds can only feed for a certain amount of time each day. Model calibration, therefore, necessitated increasing this value until most or all birds survived the winter.

The energy assimilated from consumed food depended on the energy density of the food and the efficiency with which the energy from the food could be assimilated. Energy density was assumed to be 22KJg^{-1} for all prey species. Assimilation efficiency was assumed to be 0.75 for most birds consuming most diets (Table 7.4). However, higher assimilation efficiencies were used for dunlin consuming *Corophium* and oystercatchers consuming cockles. The reason for this is that Crustacea are thought to be more easily assimilated prey and oystercatchers have higher assimilation efficiencies when consuming cockles because they remove the shell before consuming the prey, whilst other species consume the shell.

Assimilated energy was converted into increased mass by assuming that 33KJ of energy was stored in each g of storage tissues (Kersten & Piersma, 1987). The thermoneutral energy requirements for each bird species were set at 2.5*BMR (Kersten *et al.*, 1987). The thermostatic costs below LCT were calculated using the relationship between published values (Kersten *et al.*, 1987) and species' body mass. Body mass data for all species were taken from the Wash, east England (Johnson, 1985).

Any disturbance event made part of a feeding patch unavailable for feeding. The area affected by disturbance was calculated from disturbance distances for each species obtained on the Baie de Somme and the Baie de Seine (Triplet *et al.*, 1998; Triplet, Sueur & Urban, 2001). The energy cost of disturbance was calculated using the following equation (Nudds & Bryant, 2000):

$$C = 61.718tM^{0.7902} \tag{7.2}$$

Where C = energetic cost in J, t = duration of flight and M = mean body mass in kg. The duration of flight following a disturbance was assumed to be two minutes.

Three sources of forager mortality were included in the model: starvation, predation and being shot. A forager died (or emigrated) if it failed to maintain any fat reserves i.e. body mass ≤ starvation mass. The starvation mass of each species was measured from previous studies or predicted from the basal body mass for species with no direct measurement. Dunlin were the only species to have a risk of being predated should any raptors be present, but, being a protected species, had no risk of being shot. Oystercatchers and curlew had a risk of being shot if there were any hunters present. The probability of being shot was calculated from the numbers of birds recorded as being shot each winter (P.Triplet unpublished information). Birds new to the estuary in autumn took one day to learn that they were at risk of being shot in a hunted area. Subsequently, they avoided hunted areas unless they were close to starving (reserves ≤ 8% of total body mass), in which case they risked feeding within the hunted area and the chance of being shot.

Table 7.4 Forager variables used in the Baie de Somme model

Forager variables	**Oystercatcher**	**Dunlin**	**Curlew**
Initial numbers	7000	6500	1000
Arrival dates	1 Sep - 31 Oct	1 Sep - 31 Oct	1 Sep - 31 Oct
Departure dates	14 Feb - 31 Mar	14 Feb - 31 Mar	14 Feb - 31 Mar
Diets eaten:			
Small molluscs (5 - 10mm + Hydrobia)		x	
Medium cockles (5 - 19.99mm)			x
Large cockles (15 - 39.99mm)	x		
Large Macoma (10 - 29.99mm)	x		x
Small worms (2 -7.99mm)		x	
Large worms (4 - 15.99mm)	x		x
Corophium		x	
Range of foraging efficiencies (coef. of variation)	0.125	0.125	0.125
Range of dominance values	0 - 1	0 - 1	0 - 1
Nighttime feeding efficiency	0.70	0.90	0.70
Lower critical temperature (LCT) (^{o}C)	10.0	23.0	4.0
Mobile prey interference:			
Aggregation factor	10	10	10
Threshold density (n ha^{-1})	100	100	100
Coefficients	0.48,0,0	0.48,0,0	0.48,0,0
Weak kleptoparasitism:			
Aggregation factor	10	10	10
Threshold density (n ha^{-1})	100	100	100
Coefficients	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0
Large cockle kleptoparasitism:			
Aggregation factor	10		
Threshold density (n ha^{-1})	100		
Coefficients	0.50,-0.50,0		
Functional response:			
B_{50} (g AFDM m^{-2})	0.761	0.761	0.761
Forager coefficient	-1.141162	-1.712318	-1.039356
Prey coefficient	0.36542	0.36542	0.36542
Maximum rate of consumption (kJ d^{-1})	1300	265	1952
Prey assimilaton efficiency:			
Cockles and Macoma	0.85	0.75	0.75
Worms	0.75	0.75	0.75
Corophium		0.85	
Energy density of fat reserves (kJ g^{-1})	33.4	33.4	33.4
Thermoneutral energy requirements (kJ d^{-1})	757	132	997
Thermostatic costs below LCT (kJ deg^{-1} d^{-1})	31.8	1.5	42.1
Area affected by disturbance (m^{2}):			
Disturbers	25447	9503	80425
Hunters	125664	125664	125664
Fishers	85530	85530	85530
Energy cost of disturbance (kJ)	4.52	0.74	6.54
Time cost of diturbance (h)	0.5	0.25	0.5
Probability of being shot (hunter^{-1})	0.005	0	0.005
Probability of predation (raptor^{-1})	0	0.00001	0
Basal mass (g)	500	48.8	757
Mean arrival weight (g)	484.2	47.3	881
Target weight (g)	484.2+(0.5971*Day)	47.3+(0.1376*Day)	881
		- (0.00068*Day^{2})	
Starvation weight (g)	350	39	489

7.6 Results

7.6.1. MODEL CALIBRATION

Two parameters were used to calibrate the model, the maximum daily consumption rate and night-time feeding efficiency. Calculated values of maximum daily consumption using Kirkwood (1983) resulted in mass starvation of all three forager species. This value was, therefore, increased in increments of 5% of the original value until most birds of all species survived the winter. The final value for all species, for both this model and the model of the Exe estuary, was 25% higher than the original value.

Although forager overwinter mortality rates on the Baie de Somme were unknown, it was assumed that they were above zero. We therefore used night-time feeding efficiency, about which little is known, to calibrate the model such that overwinter starvation rates for all three species were above zero. We did this by systematically reducing night-time feeding efficiency for each species until some birds had starved by the end of the winter.

7.6.2 MODEL VALIDATION

7.6.2.1 Bird distribution

One test of the model is to see how well it predicts the birds' distribution around the estuary at low tide. We compared the distribution of birds in the model between October and January with mean low water and tide receding/advancing counts made during the winter of 2001/2002. The model predicted well the distribution of birds around the estuary at both low water (Fig. 7.4a) and tide receding/advancing (Fig. 7.4b). The main discrepancies were that more oystercatchers and curlew were predicted to feed in the higher part of the Reserve (ResHaut) than were observed and more dunlin were predicted to feed in the patch near Le Crotoy (CrotHaut) than were observed.

7.6.2.2 Proportion of time spent feeding

Another test of the model is to compare the proportion of time that birds spend feeding during the tidal cycle. Data on bird feeding activity was available throughout the winter. We compared these data with model outputs for the low tide period during daylight for each month (Fig. 7.5). Bird feeding activity in the model was very close to that observed for all three species throughout the winter.

7.6.2.3 Population response to environmental change

A further test of the model was to investigate the effect of environmental change on bird mortality. The two tests we used were reducing mean daily temperature and reducing invertebrate densities. A reduction in the mean daily temperature of three to four degrees throughout the winter resulted in an increase in mortality in all three bird species (Fig. 7.6). Oystercatcher mortality was particularly sensitive to a lowering of winter temperatures. Reducing invertebrate densities caused a steady increase in mortality in oystercatchers and dunlin (Fig. 7.7). The effect on curlew was less clear, probably because of the confounding effect of increased oystercatcher mortality removing competition for their main prey species. However, these two tests did demonstrate that a deterioration in the environment invoked an appropriate response in the model populations.

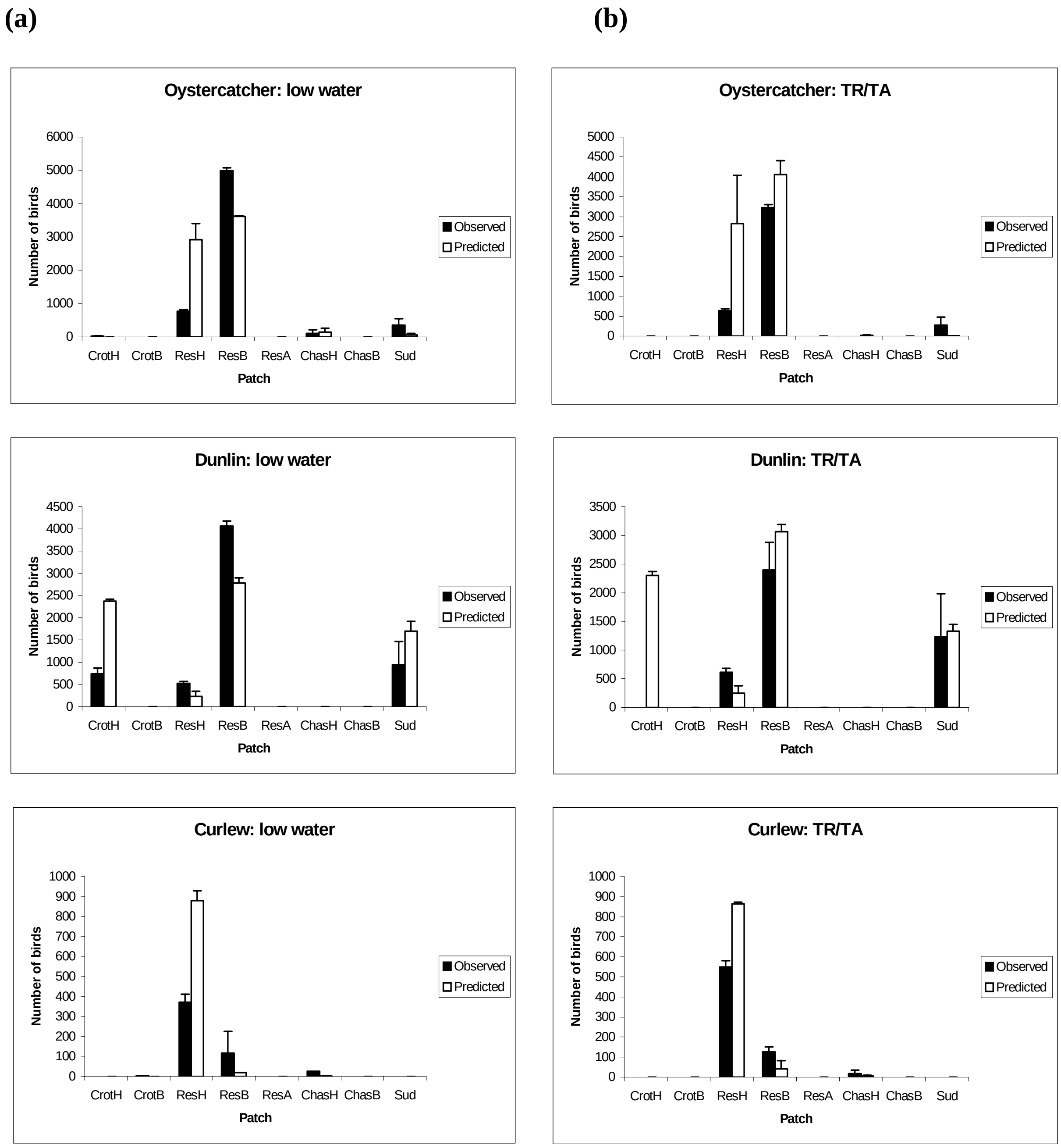


Figure 7.4 Observed and predicted bird distributions in the Baie de Somme during a) low water and b) tide receding/tide advancing. Bars show means ± 1 se.

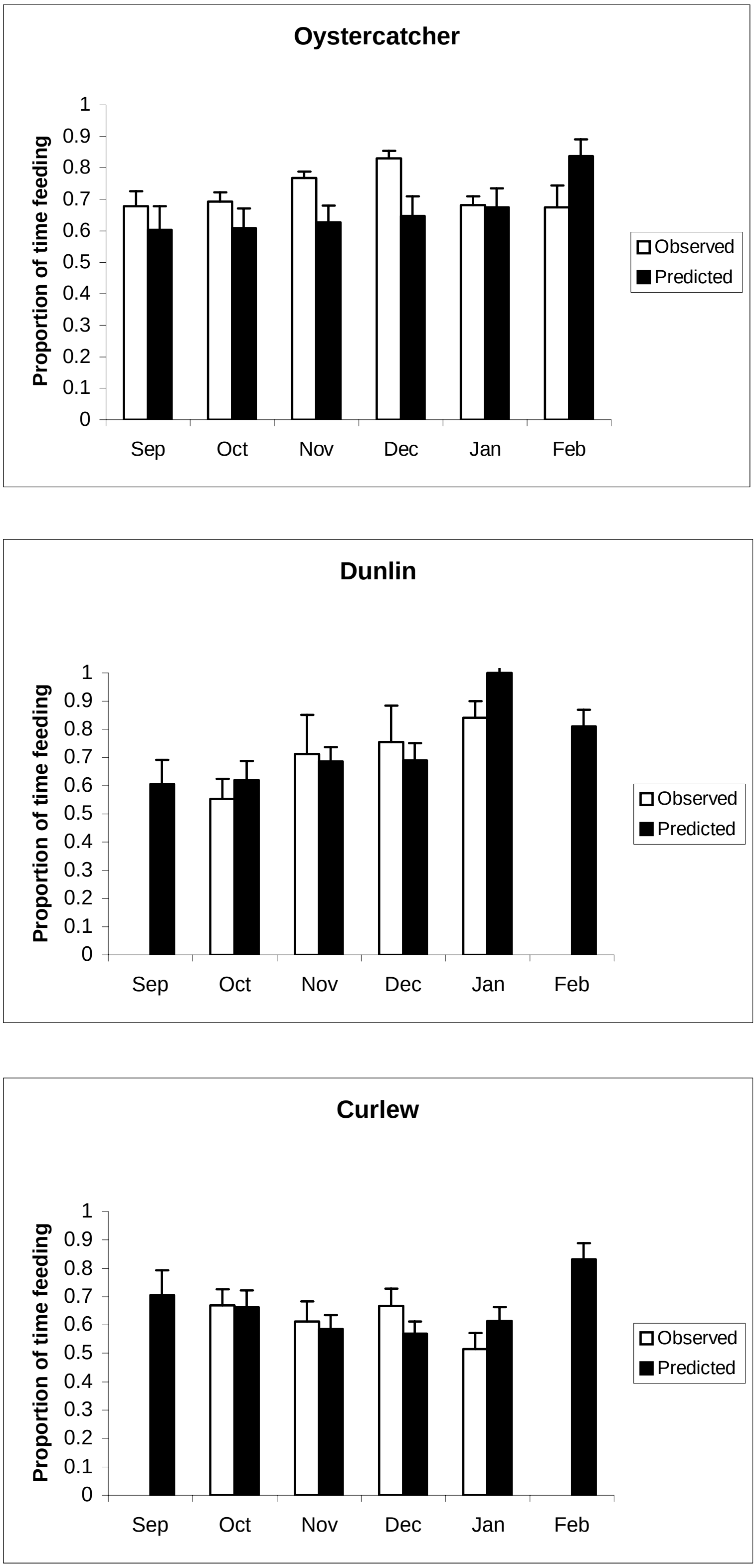


Figure 7.5 Observed and predicted values for the proportion of time spent feeding by shorebirds through the winter. Bars show means ± 1 se.

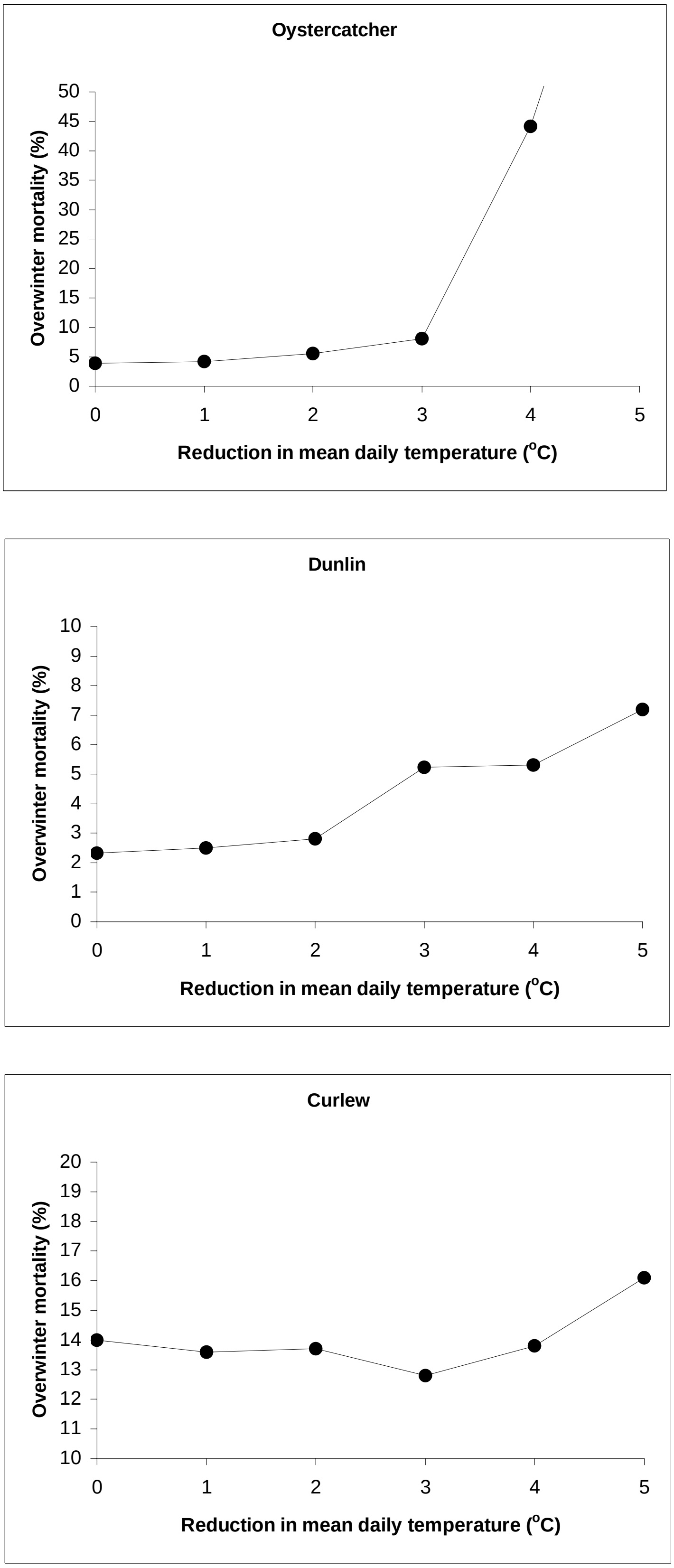


Figure 7.6 The effect of lowering mean daily temperatures on shorebird mortality.

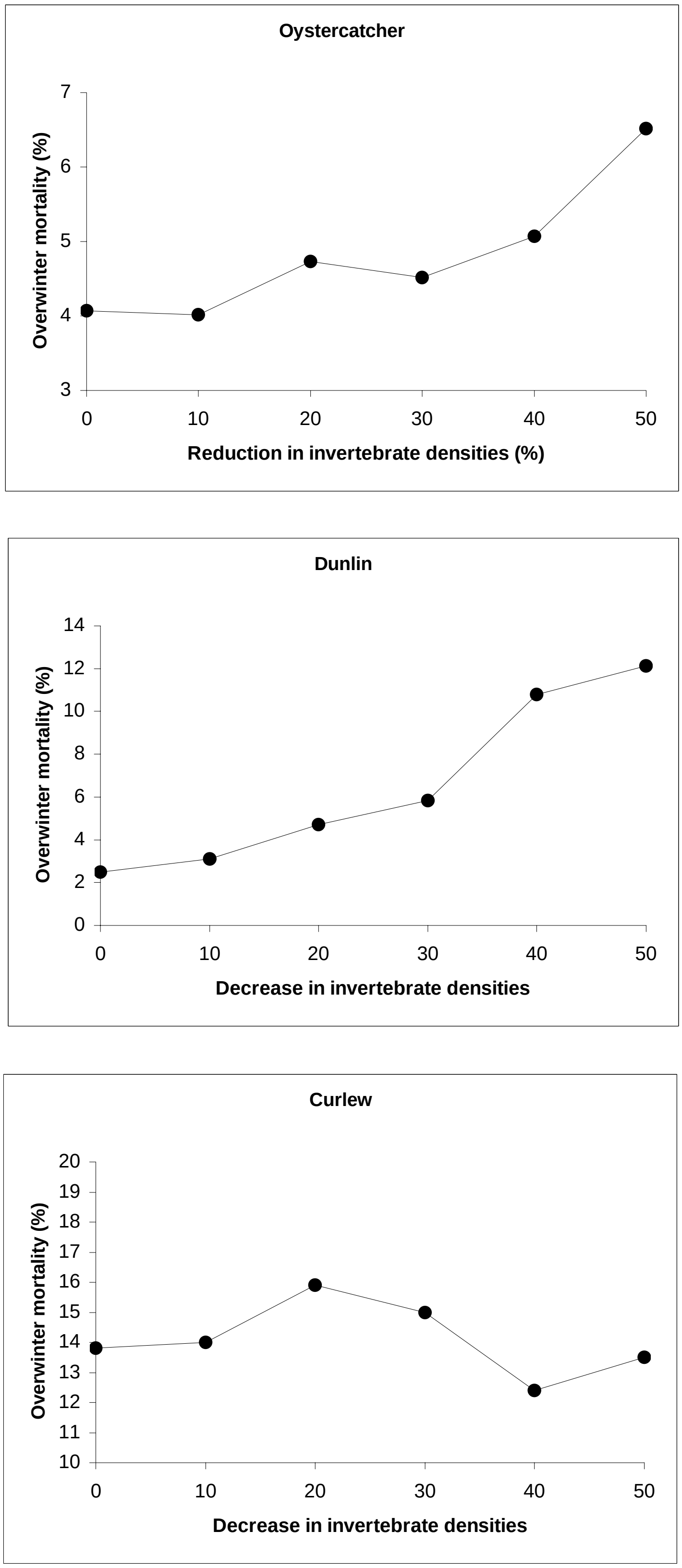


Figure 7.7 The effect of reducing invertebrate densities on shorebird mortality.

7.6.3 ISSUES

7.6.3.1 Hunting

We simulated the effect of reducing the area hunted in the Baie de Somme by removing hunting from either the north side of the estuary (Crothaut & Crotbas), the central part of the estuary (Chassehaut & Chassebas) or from the south of the estuary (Sud). Removing hunting from the north side of the estuary decreased mortality in oystercatchers, but not in dunlin and curlew (Fig. 7.8a). Removing hunting from the south of the estuary decreased mortality in oystercatchers and dunlin, but not in curlew. However, removing hunting from the central part of the estuary significantly reduced mortality in all three species. Curlew mortality, in particular, was reduced to less than 1% if curlew could feed in the central part of the estuary without being shot.

We simulated the effect of reducing the hunting season by stopping hunting earlier in the winter. Reducing the hunting season had little effect on dunlin or curlew mortality (Fig. 7.8a). However, reducing the hunting season by four weeks or more did result in a decrease in oystercatcher mortality.

We repeated these simulations with overwinter temperatures lowered by three degrees to explore the effect of hunting during cold weather. The pattern of the effect of reducing the hunted area was the same as before, although the magnitude of the decrease in shorebird mortality was greater (Fig. 7.8b). Reducing the length of the hunting season still had no effect on curlew mortality, but oystercatcher mortality was lowered with a reduction of only two weeks and dunlin mortality was reduced if the hunting season was shortened by 6 weeks.

7.6.3.2 Spartina Encroachment

Between 1995 and 2000, *Spartina* marsh in the Baie de Somme increased downshore by 100 - 200m (P. Triplet unpublished data), giving an encroachment rate of between 20 and 40 m y^{-1}. *Spartina* marsh extends for approximately 5 km along the shore above patches Crothaut and Rescaren (Fig. 7.3). An encroachment rate of 20m y^{-1} would therefore result in a loss of habitat of 10 ha y^{-1}, and an encroachment rate of 40m y^{-1} a habitat loss of 20ha y^{-1}. In our simulations we removed habitat from Crothaut and Rescaren, until all of Rescaren had been removed, when habitat loss started to affect Reshaut.

Spartina encroachment had little effect on oystercatcher and curlew mortality except, perhaps, when habitat loss reached 200 ha, which is when Reshaut, where many oystercatchers and curlew feed, started to be affected by the encroachment (Fig. 7.9). Dunlin mortality, however, increased steadily with *Spartina* encroachment, particularly when habitat loss exceeded 100ha. At present rates of encroachment, this level of habitat loss is likely to be reached in 5 to 10 years’ time.

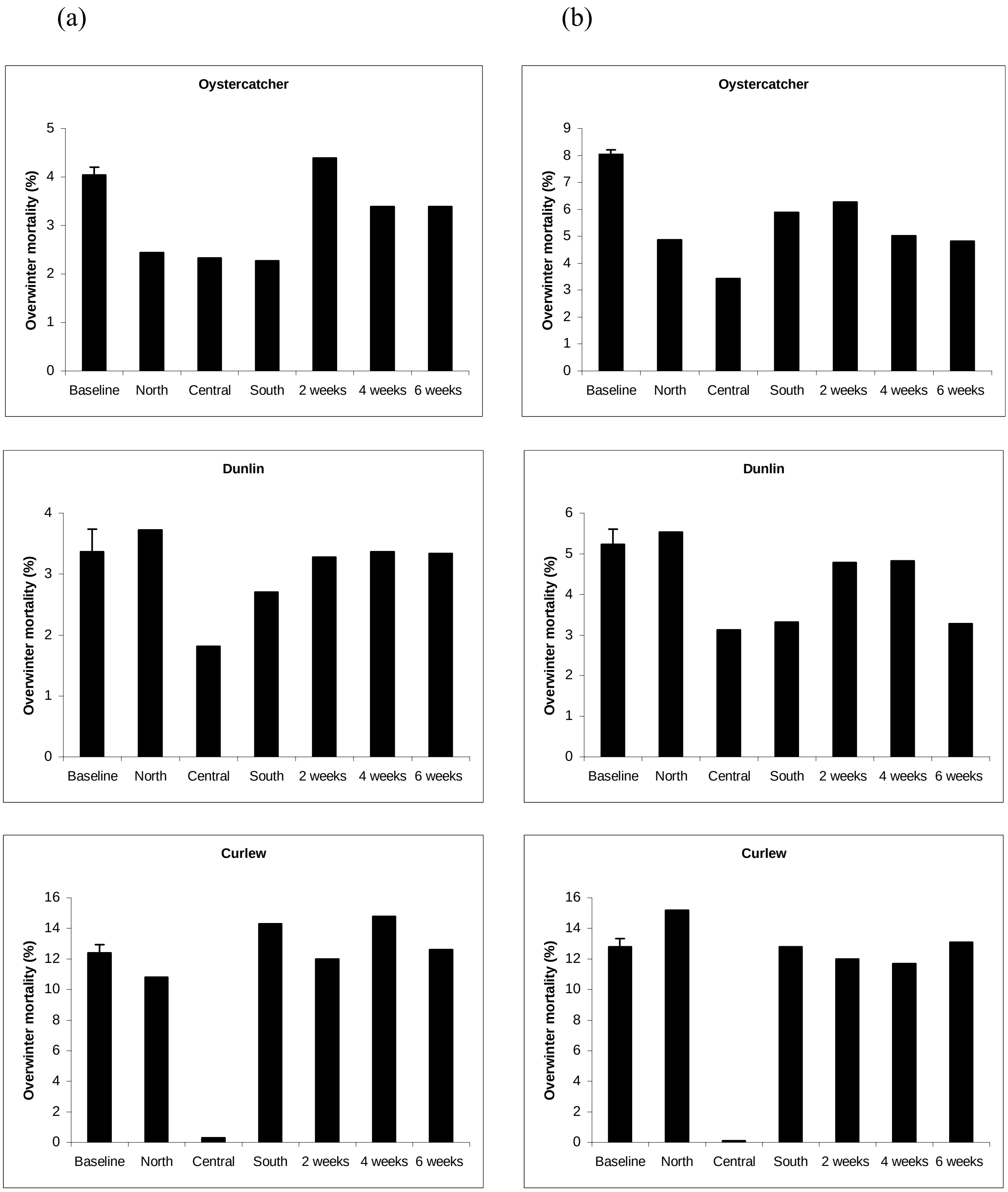


Figure 7.8 The effect on shorebird mortality of reducing the hunted area and the hunting season in the Baie de Somme with a) baseline mean daily temperatures and b) temperatures reduced by 3 ^{o}C. Baseline = present-day situation, North = no hunting allowed on the north side of the estuary, Central = no hunting allowed in the central part of the estuary, South = no hunting allowed in the South. 2 weeks = hunting season finished two weeks earlier, 4 weeks = hunting season finished 4 weeks earlier, 6 weeks = hunting season finished 6 weeks earlier.

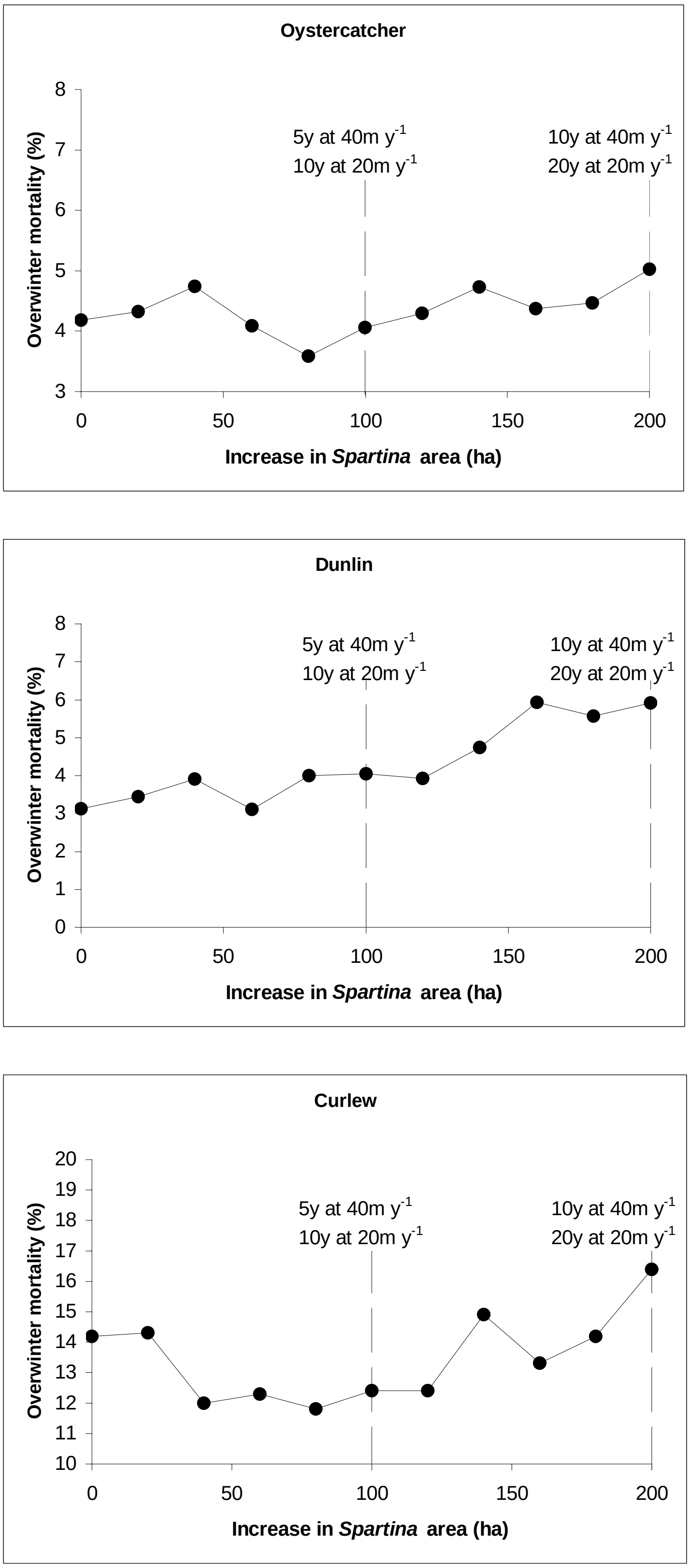


Figure 7.9 The effect of *Spartina* encroachment on shorebird mortality. For explanation, see text.

7.6.3.3 Disturbance

Disturbance was simulated by varying the number of disturbers per hour within the Reserve, with the disturbance rate being the same in the four feeding patches: ResHaut, ResBas, ResCaren and StQuentin. These disturbance events were in addition to any disturbances by fishermen and raptors. Disturbances only took place during daylight and when the patch was exposed. We ran three sets of simulations: a) with weekday disturbance half that at the weekends, b) with weekday disturbance the same as at weekends and c) with mean temperatures reduced by 3^{o}C.

There was only a slight difference in the results between weekday disturbance being half that at weekends and being the same (Fig. 7.10). This was probably because patches within the Reserve were already highly disturbed during the week by fishermen. Varying the number of disturbances within the Reserve had little effect on dunlin mortality. This is understandable as dunlin could feed outside the Reserve without the risk of being shot. Under baseline conditions, disturbance also had little effect on curlew mortality, except, perhaps, when disturbance levels every day exceeded 7 h^{-1} (Fig. 7.10b). Oystercatcher mortality, however, clearly increased when disturbance events exceeded 2.5 h^{-1} (everyday) or 3 h^{-1} (weekends higher).

When mean temperatures were lowered, dunlin mortality appeared to rise and return to baseline levels as the number of disturbances increased (Fig. 7.11). This may be an artifice of natural variation in dunlin mortality, or else be the result of dunlin no longer feeding in the Reserve once disturbance reached a certain level. In cold weather, curlew mortality increased noticeably when the number of disturbances exceeded 5 h^{-1}. For oystercatchers, the threshold value for disturbance remained the same as before, with mortality increasing when disturbance events exceeded 2.5 h^{-1}.

7.6.3.4 Fishing

We ran two sets of fishing simulations: a) varying the cockle stocks whilst keeping the number of fishermen at baseline levels and b) varying the number of fishermen whilst keeping cockle stocks at baseline levels.

Neither varying cockle stocks nor increasing the number of fishermen had any effect on dunlin or curlew mortality (Fig. 7.12). Oystercatcher mortality increased markedly when the density of large cockles (>15mm) at the start of the winter fell below 250 m^{-2}. However, increasing cockle stocks above present day levels did not result in any decrease in oystercatcher mortality. Decreasing the number of fishermen also had no effect on oystercatcher mortality, but increasing the number of fishermen did. However, oystercatcher mortality only started to increase when the daily number of fishermen exceeded 200, which is around double the current average of 105 fishermen d^{-1}.

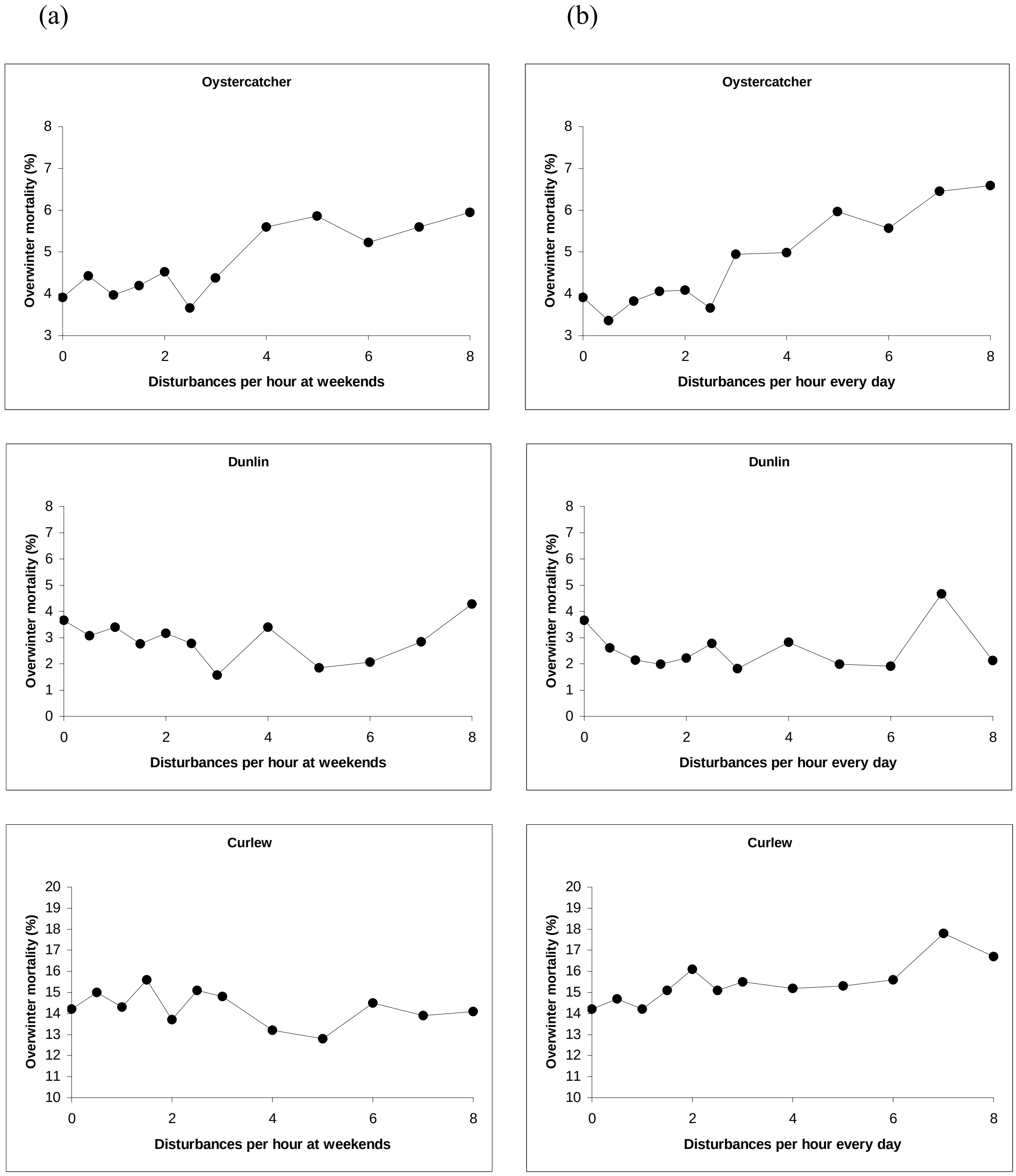
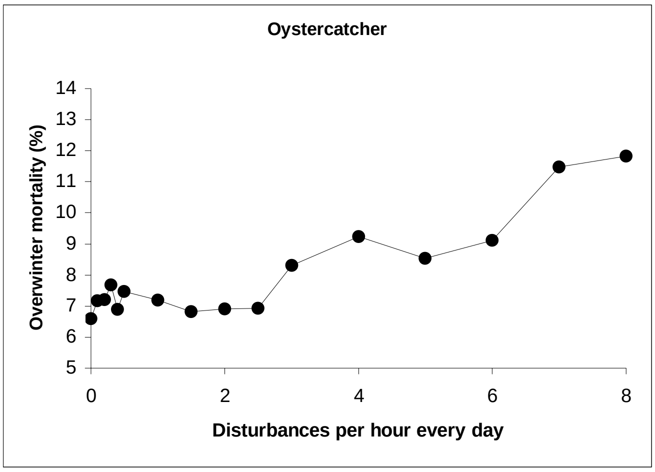
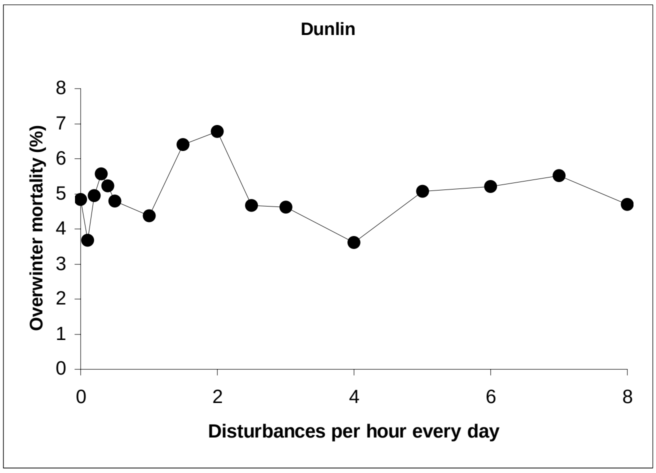


Figure 7.10 The effect of increasing the rate of disturbances within the Reserve with a) weekday disturbances half the weekend rate and b) weekday disturbance rates the same as the weekend.





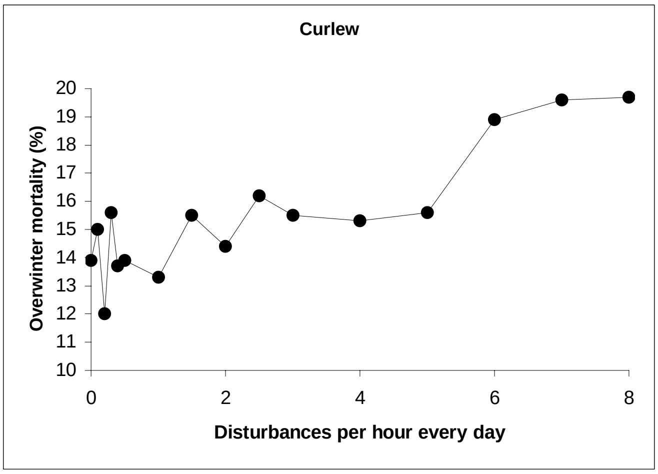


Figure 7.11 As Figure 7.10b, but with mean daily temperatures reduced by 3°C.

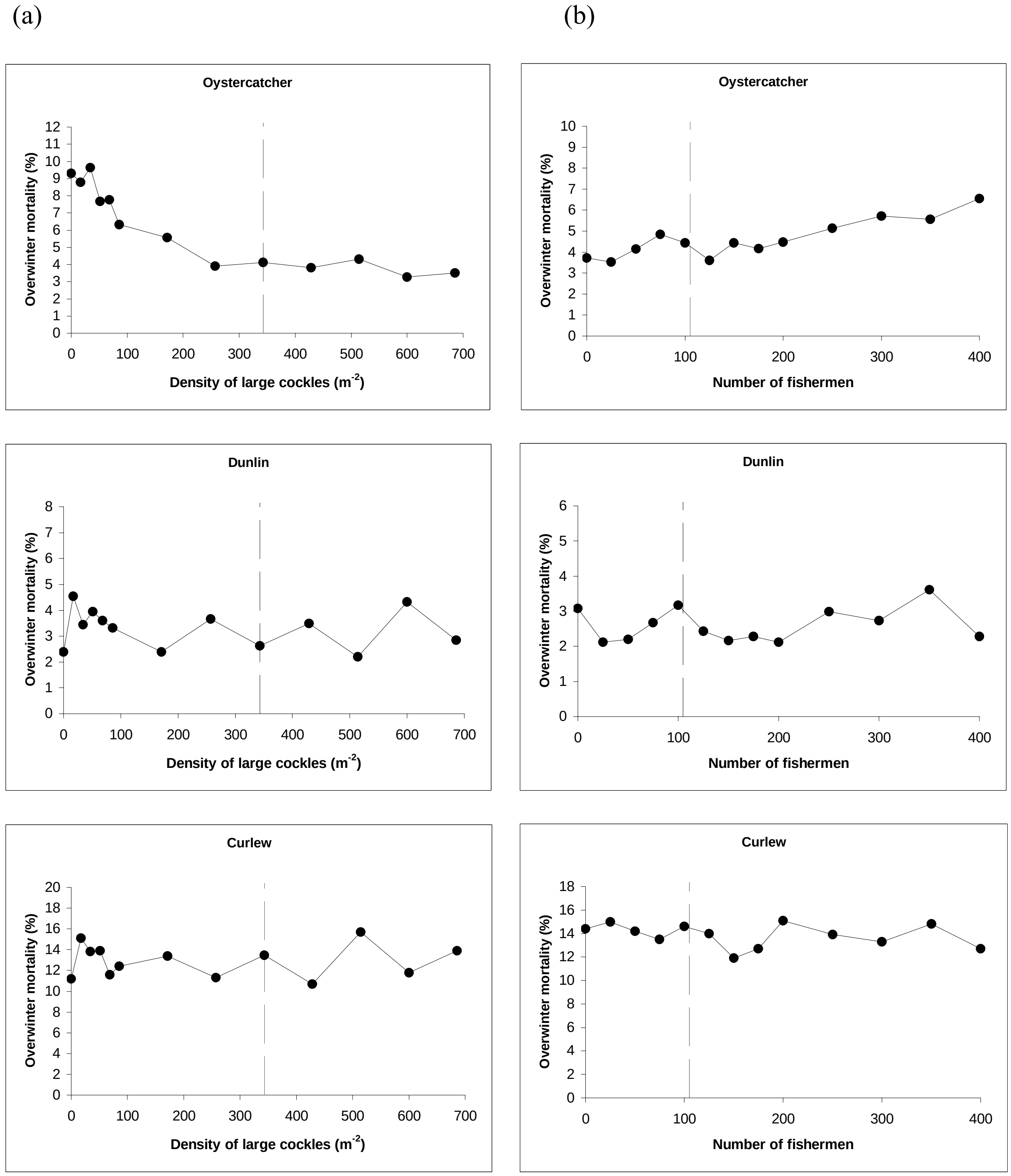


Figure 7.12 The effect of a) reducing the density of large cockles (>15mm) at the start of the winter and b) increasing the daily number of fishermen on shorebird mortality. Dashed lines show present day levels.

7.6.3.5 Accretion

Between 1993 and 2001, accretion in the Baie de Somme resulted in an average increase in sediment levels of 30cm, or 3.75 cm y^{-1} (N. Loquet, unpublished data). Previous work has shown that cockle stocks only occur between 6.7 and 8.4m SLWL, with an optimum sediment height of 7.7m (N. Loquet, unpublished data). This means that cockle stocks are likely to disappear from areas which are raised above 8.4m. If accretion continued at the current rate, cockle stocks may be lost from ResHaut in 11 years' time, from ResBas in 29 years' time and St Quentin in 75 years' time. This means that the upper part of the Reserve, ResHaut, will be the first area to be affected by accretion.

We simulated the effect of accretion in two ways. Firstly, we had accretion affecting cockle stocks alone by removed half and then all of the cockle stocks within ResHaut, without reducing the area of the habitat or removing the other invertebrates present. Secondly, we had accretion affecting all the invertebrates present by removing half and then the entire patch from the model.

Removing just the cockle population from ResHaut had no effect at all on shorebird mortality, presumably because the birds could switch to other prey items (Fig. 7.13a). However, removing just half of ResHaut increased mortality in all three shorebird species and removing the entire patch had a catastrophic effect on oystercatcher and curlew populations (Fig. 7.13b).

7.6.3.6 Population change

In our final simulations, we explored the effect of population increases on shorebird mortality. Increasing numbers of oystercatchers and dunlin resulted in a steady increase in overwinter mortality (Fig. 7.14). This suggests that no increase in these species' numbers could occur in the Baie de Somme without an increase in their mortality rates. However, increasing curlew numbers by up to 50% had no effect on curlew mortality. This suggests that higher numbers of curlew could overwinter in the Baie de Somme without any increase in mortality.

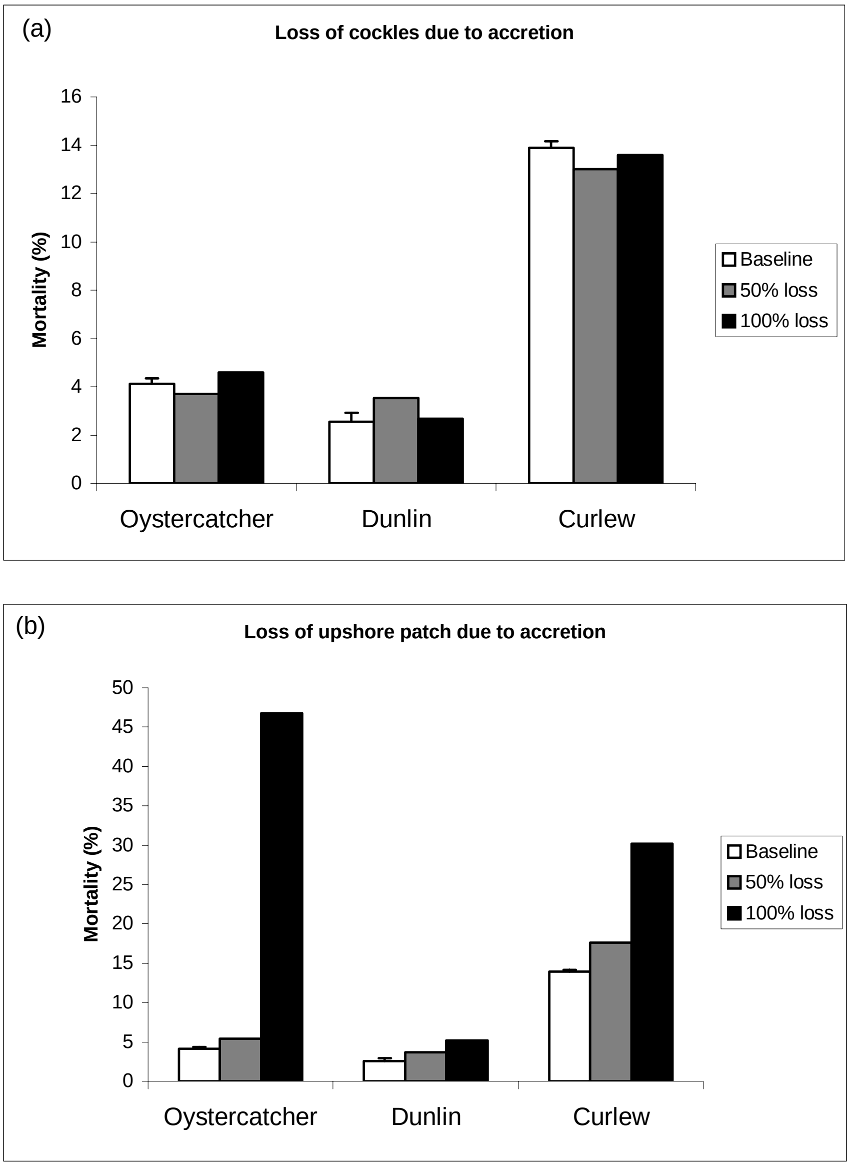


Figure 7.13 The effect of accretion on shorebird mortality through a) removal of 50% and 100% of cockle stocks from affected area and b) removal of 50% and 100% of the total habitat affected.

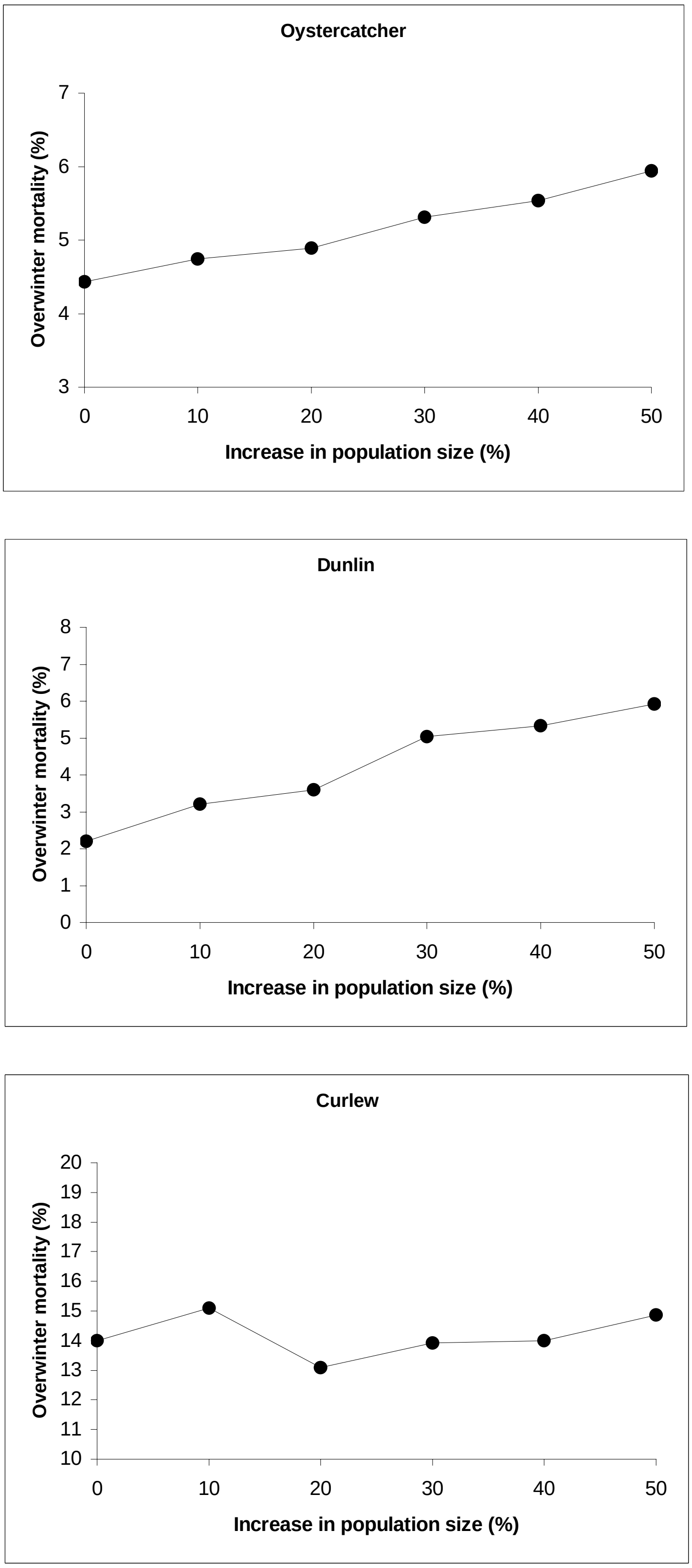


Figure 7.14 The effect of increasing population size on shorebird mortality.

7.7 Conclusions

Using data collected for this Report, we have built a behaviour-based model of three shorebird species overwintering in the Baie de Somme. The model predicted well the present-day distribution of these shorebirds around the estuary, and the proportion of time that they spend feeding during the tidal cycle. The model bird populations also responded in an appropriate way to reductions in winter temperatures and reductions in their food supply. Although we do not know whether shorebird overwinter mortalities in the model are the same as those in the Baie de Somme, we do know that they are within a realistic range. We also feel confident about model predictions of the effect of change on levels of shorebird mortality.

Time constraints, and the length of time taken for each model run, meant that no repeat runs were done for any of the simulations done for this Report. As a result, variation included in the model parameters is reflected in the figures presented here. It also meant that no statistical analyses could be made of the results. Future work will involve repeat simulations and statistical analysis of our results.

In this Report, we used the model to address several issues in the Baie de Somme. One of the most interesting features of the Baie de Somme results was the buffering effect of hunting on oystercatcher and curlew mortality. This was because, if birds were starving, there was a plentiful supply of food outside the Reserve which they could exploit at the risk of being shot. This meant that the principal source of mortality for oystercatchers and curlew was being shot, and that more birds were shot when they were starving. However, it also meant that starving birds had a chance, albeit a risky one, of replenishing their reserves. Needless to say, reducing the area hunted had a marked effect on oystercatcher and curlew mortality.

A previous version of the model has already been used to explore the effect of disturbance on oystercatchers within the Reserve in the Baie de Somme (Goss Custard *et al.*, submitted). In the present study, oystercatcher mortality was affected by increased levels of disturbance within the Reserve, but the threshold level of disturbance, above which mortality increased, was much higher than in Goss-Custard's study. However, in the present model, more alternative feeding patches and prey types were available to the birds. In particular, oystercatchers disturbed within the Reserve could feed outside the Reserve with the risk of being shot. Thus, the hunted area probably buffered the effect of disturbance, or, indeed, other deteriorations in feeding conditions within the Reserve.

As we expected, dunlin were most likely to be affected by *Spartina* encroachment and oystercatchers most likely to be affected by cockle stocks and fishing. However, we were slightly surprised what little effect increasing the number of fishermen had on shorebird mortality and assume that this was because of the long exposure times in the Baie de Somme, allowing the birds plenty of time to make up for lost feeding time at night and during the weekend. It is also true, however, that disturbance due to fishing did not incur increased energetic costs. This suggests that short-term disturbances (incurring energetic costs of flight) are more deleterious to shorebird survival than long-term disturbances (where birds merely avoid feeding in a certain area).

Finally, we explored the effect of accretion on shorebird survival. Our results suggest that, if accretion only affected cockle stocks, then shorebird mortality is unlikely to increase in the near future. However, if other invertebrates are also removed from the affected patch, fewer birds are likely to survive the winter. This was because the upshore patches, which are the most likely to be affected by accretion, were important feeding areas for all three species of shorebird.

7.8 References

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8 SINGLE-SITE MODELS: EXE ESTUARY WADERS

Sarah Durell, Richard Stillman, Selwyn McGrorty, Andy West and John Goss-Custard

8.1 Study site

The Exe estuary is situated in the south-west U.K. It is designated an SSSI for its habitats and the species they support, a Ramsar Waterfowl Habitat site, and an SPA European marine site under the EU Birds Directive. It is a relatively small (10km long and around 2km wide), sheltered estuary protected from the sea by the sand bar at Dawlish Warren (Fig. 8.1). The main sources of freshwater are the River Exe and the smaller River Clyst which both enter the estuary near Topsham. The mean tidal range is 3.72m at spring tides and 1.46m at neap tides. The tidal stream is strong, particularly at the estuary mouth, where a speed of 9.25 km hr^{-1} may be reached on spring tides (Holme, 1949). At high spring tides, the estuary is completely covered by water, but at low tide extensive mud- and sand-flats are uncovered either side of the shallow main channel. In the lower reaches of the estuary there are several mussel *Mytilus edulis* beds (Goss-Custard *et al.*, 1980; McGrorty *et al.*, 1990; McGrorty & Goss-Custard, 1991, 1995) and extensive *Zostera* beds (Fox, 1996).

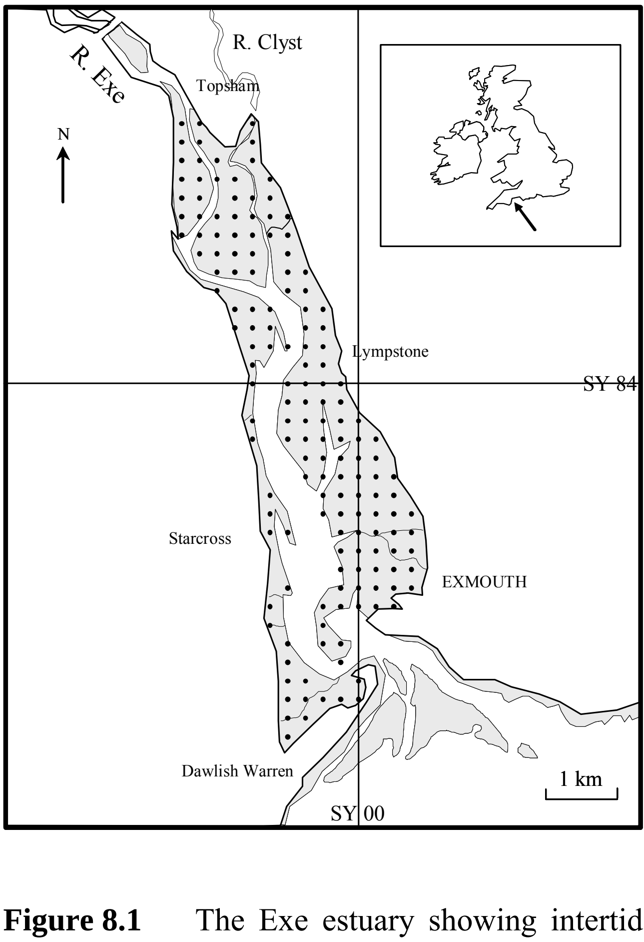

Figure 8.1 The Exe estuary showing intertidal sampling points based on the Ordnance Survey National Grid

8.2 Issues

8.2.1 SHELLFISHING

Shellfishing is an important issue on the Exe estuary, particularly with reference to mussel fishing and oystercatchers. However, the issue of shellfishing and shorebirds on the Exe estuary has already been addressed, using earlier versions of the model (Stillman *et al.*, 1996). Shellfishing, therefore, was not an issue that was considered in the present simulations.

8.2.2 DISTURBANCE

The main issue on the Exe estuary at present is disturbance, both from fishermen and from various types of recreational usage such as dog walkers and cyclists. In our simulations, we considered the effect on shorebird survival of increasing levels of disturbance in various parts of the estuary. Sources of disturbance simulated included the effect of the creation of a cycle path along the sea wall, and the effect of increasing levels of disturbance on the high water roost at Dawlish Warren.

8.3 Data collection

8.3.1 PATCHES

The Exe estuary was surveyed in September and October 2001. We needed a systematic and repeatable coverage of the whole estuary at a scale that would yield sufficient invertebrate samples for analysis but not too many samples to collect within the time available. We therefore chose a 250m x 250m sampling grid which was located on the Ordnance Survey National Grid (Fig. 8.1). Samples were taken at every intersection of this grid situated in the intertidal area, giving 158 sampling points. Each sampling point was located on the ground by using a compass and a 1m A-frame pacing stick.

At each sampling point, several environmental variables were measured for inclusion in an analysis to define resource patches. These were:

1. Sediment type: Surface sediment samples were taken to a depth of 1cm, placed in labelled polythene zip bags and kept frozen until required for analysis. A Coulter LS 130 particle size analyser was used to determine the size distribution of sediment particles in the range 0.1 – 900 microns (µm). Sediment samples were defrosted, thoroughly mixed and passed through a 1mm sieve before a subsample was placed in the analyser. Any particles ≥ 1mm were dried and weighed. Sediments were classified using the proportion of fine particles (= fines = < 63 µm) as sand (< 10% fines), muddy sand (10 – 29% fines), sandy mud (30 – 80% fines) and mud (>80% fines). Mean particle size was used in our analyses.

2. Sediment organic content: To measure sediment organic content, samples were passed through a 0.5mm mesh to remove the macrofauna, dried to constant weight at 90 ^{o}C, weighed, burnt in a muffle furnace to constant weight at 550 ^{o}C and reweighed. The difference in weight, or loss on ignition (LOI), of the burned sample from the dried one was expressed as a percentage of the dry weight.

3. Shear strength: Consolidation of surface sediments was measured in the field, using a 5cm deep Pilcon shear vane. Three measurements of shear strength (k Pa) were taken and the mean calculated for each sampling point.

4. Exposure time: We measured the proportion of the tidal cycle for which each sampling point was uncovered by the tide at low water by marking all the sampling points with bamboo canes and watching them from above HWM with a telescope. The amount of time for which each point was exposed was measured on both a neap and a spring tide with the mean of these two values being used in analyses. Mean exposure time was used as a measure of any upshore gradient in invertebrate distribution.

5. Distance up-estuary: As a measure of any up-estuary gradient in invertebrate distribution, the shortest distance in kilometres from each site to a point midway between the end of Dawlish Warren and Exmouth Dock was measured on a 1:25000 Ordnance Survey map.

6. Zostera: The presence or absence of *Zostera* within a square metre around each sampling point was noted in the field and included in our analyses as a binary variable.

8.3.2 RESOURCES

A full survey of benthic invertebrates was made in September and October 2001 and a repeat survey of a subsample of sites in March 2002. At each of the sampling sites mentioned above, smaller invertebrates were sampled by taking a 10cm diameter by 30cm deep core which was sieved through a 0.5mm mesh. Lugworm *Arenicola marina* were sampled by counting the number of worm casts in a randomly placed 1x 1m quadrat and larger shellfish were sampled by hand raking a 0.25 m^2 quadrat.

The sieved core contents were fixed in 4% formalin (formaldehyde) in seawater for a period of approximately two weeks and then washed and stored in 70% alcohol. Samples were washed in the laboratory through a 0.5mm sieve to remove residual sediment and sorted under a low power binocular microscope. Hand-raked shellfish were frozen on return to the laboratory.

If possible, all specimens were identified to species. Most species were measured to 0.1mm, apart from small and/or easily broken worm species (nemerteans, nematodes, spionids, cirratulids, capitellids, oligochaetes), which were counted but not measured. In addition, mandible length was measured in a subsample of 135 whole ragworm *Hediste diversicolor* to calculate the relationship between mandible length and preserved worm length. This relationship was used to calculate the length of broken worms (heads only).

8.3.3 COMPONENTS

Separate samples of invertebrates were taken during both the autumn and spring surveys from a wide range of sites and frozen prior to ash-free-dry-mass (AFDM) analysis. After partial defrosting, body length was measured for most worm and all crustacean species, shell length for bivalves and spire height for gastropods. Body length was not measured in the smaller worm species: these were ashed in bulk (25 -100 worms per crucible) and the mean AFDM calculated for one worm. Mandible length was measured for *Hediste diversicolor*. All molluscs, apart from *Hydrobia ulvae*, were removed from their shells before processing. Samples were dried to constant weight at 90 ^{o}C and burnt to constant weight in a muffle furnace at 550 ^{o}C. The loss of weight on burning (dry weight – ash weight) is the AFDM.

8.3.4 FORAGERS

Low tide shorebird count data for the Exe estuary were obtained from the British Trust for Ornithology's (BTO) Wetland Bird Survey (WeBS), the latest low tide survey having taken place in 1993/94. Data on total bird numbers throughout the winter were obtained from data published by the Birds of Estuaries Enquiry (BoEE) (BTO/RSPB/WT, 1978) and WeBS (Musgrove *et al.*, 2000; Pollitt *et al.*, 2003).

8.4 Data analysis

8.4.1 PATCHES

Cluster and non-metric multidimensional scaling (MDS) techniques were used to determine patch types, based on a Bray-Curtis similarity matrix calculated from fourth root transformed invertebrate biomass density data (Clarke & Warwick, 1994).

Stepwise discrimination on the invertebrate groups was used to determine the key environmental variables describing these groups. These environmental variables were then used to derive discriminant functions to assign each site to an invertebrate group. The percentage of sites predicted to the correct group was estimated by two methods: the 're-substitution' method, where all sites were used to classify all sites, and the more rigorous 'cross-validation' method, where each site was left out in turn, a model fitted to the remaining sites and the group predicted for the missing site (Krzanowski, 1988). Using both observed and predicted site classifications, we grouped sites geographically into habitat patches (Durell *et al.*, 2005).

8.4.2 RESOURCES

Resources used in the model were invertebrate prey size classes. Invertebrate data were combined for all sampling sites within each habitat patch and mean densities calculated for each prey size class. Worm species were combined into three prey types: small worms (oligochaetes and polychaete species <10mm), large worms (all other polychaete species) and earthworms. Crustacea were also combined into one prey type. All mollusc species were kept as separate prey types.

Differences in invertebrate densities between the autumn and spring survey were used to calculate non-bird overwinter prey mortality.

8.4.3 COMPONENTS

The only resource component included in this model was AFDM. For most species, the AFDM for each prey size class was calculated using ($\log_e$) AFDM to ($\log_e$) body length relationships. In the case of *H. diversicolor*, ($\log_e$) AFDM to ($\log_e$) mandible length and ($\log_e$) mandible length to ($\log_e$) preserved worm length relationships were used to calculate the AFDM of a preserved worm. For several small worm species, no size categories were used and biomass densities were based on the mean AFDM for one worm.

Differences in prey AFDM between the autumn and spring surveys were used to calculate any overwinter decline in AFDM.

8.4.4 FORAGERS

WeBS data were used to estimate the mean number of each shorebird species present on the Exe estuary during the winter and the time that these birds arrive from the breeding grounds.

8.5 Model variables

8.5.1 GLOBAL

Global variables used in the model are shown in Table 8.1. The variable weekend was included so that certain variables, such as disturbance, could differ in intensity between weekdays and weekends. An equation predicting day length was included in order to calculate hours of daylight so that variables could differ between day and night-time. Hourly tidal heights at Starcross for the winter 2000/2001 were obtained using TideWizard software (Marine Computing International 2000-2002). Tidal stage was calculated from this data so that bird distribution data could be extracted for three different stages of the tide: low tide, high tide and tide receding/advancing. Mean daily temperatures for Exmouth for 1998/99 were obtained from the British Atmospheric Data Centre (BADC).

Table 8.1 Global variables used in the Exe estuary model

Global variables	Value
Duration of time step	1 h
Day	Day 1 = 1 September
Weekend	
Time	
DayLength	21 June 18.11h, 21 December 9.25h
Daylight	
TideHeight	Tide heights at Starcross for 2000-2001
TidalStage	Low = 3h, High = 3h
Temperature	Mean daily temperature (^{o}C) at Exmouth 1998-1999

8.5.2 PATCHES

Seven intertidal habitat patches were defined by cluster analysis of invertebrate biomass densities and are described in Durell et al. (2005). With surrounding fields, this gave eight different feeding patches in the model (Fig. 8.2). Patch variables included in the model, and the baseline values used, are shown in Table 8.2. The area of each patch was measured off an OS map. The mean tide height at which each patch was uncovered by the tide was calculated from comparison of hourly tide heights at Starcross with the mean exposure time of each patch on spring and neap tides.

Disturbers were considered to be any human source of disturbance which affected the birds but which had no impact on their prey. Fishers were not only potential sources of disturbance, but could also have an impact on prey densities. Raptors were a source of disturbance and also a potential mortality risk.

8.5.3 RESOURCES

Prey types and size classes used in the model, and their initial densities on each patch, are shown in Table 8.3. Apart from mussels, non-bird winter prey mortality was calculated from the difference in prey densities at the end of a model run compared with densities found in the spring survey. Values for overwinter mussel mortality were taken from previous experimental work (McGrorty *et al.*, 1990). No fishing loss was included in any of the present runs, largely because the interaction of shellfishing and oystercatchers has already been explored in previous models (Stillman *et al.*, 1996).

8.5.4 COMPONENTS

Initial values of AFDM for each resource, and any overwinter change, are shown in Table 8.3.

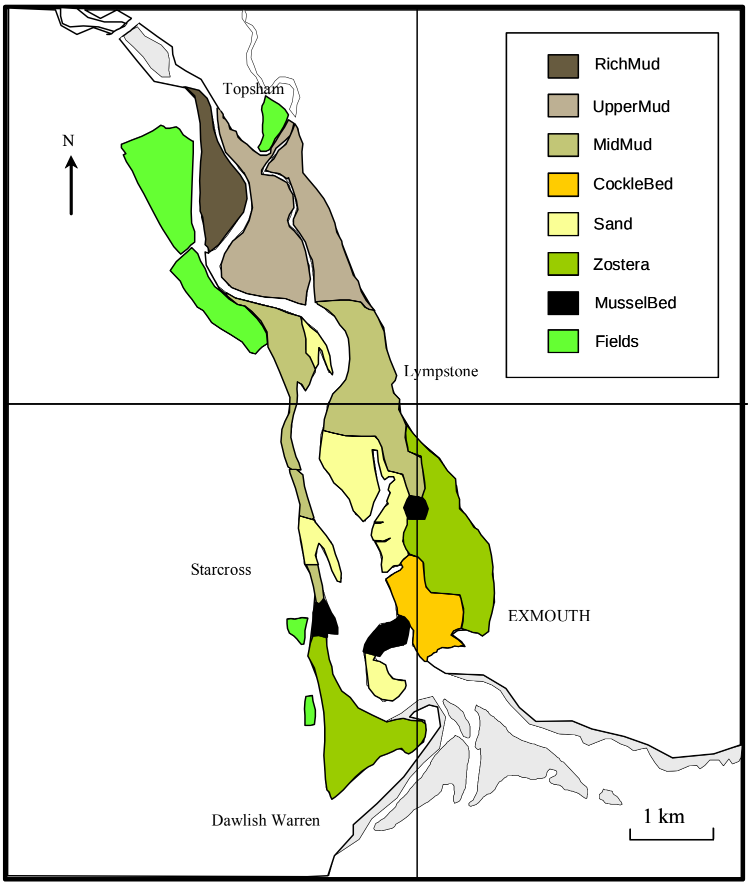

Figure 8.2 Feeding patches used in the Exe estuary model

Table 8.2 Patch variables used in the Exe estuary model

Patch variables		Patch name							
		RichMud	**UpperMud**	**MidMud**	**CockleBed**	**Sand**	**Zostera**	**MusselBed**	**Fields**
Patch area (m^2)		660000	2250000	2060000	660000	1330000	2420000	390000	2000000
Exposure tide ht (m)		2.70	2.65	1.8	2.18	1.66	2.36	1.63	n/a
Disturbers (h^{-1})	weekend day	0	0	0	1 - 10	0	1 - 2	1 - 2	0 - 10
	weekend night	0	0	0	0	0	0	0	0
	weekday day	0	0	0	1 - 5	0	1 - 2	1 - 2	0 - 5
	weekday night	0	0	0	0	0	0	0	0
Fishers (h^{-1})	weekend day	0	0	0	0	0	0	0	0
	weekend night	0	0	0	0	0	0	0	0
	weekday day	0	0	0	0	0	0	0	0
	weekday night	0	0	0	0	0	0	0	0
Raptors (h^{-1})	weekend day	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 1
	weekend night	0	0	0	0	0	0	0	0
	weekday day	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 0.7	0 - 1
	weekday night	0	0	0	0	0	0	0	0

Table 8.3 Resource variables used in the Exe estuary model

Resource		Initial density (n m^{-2})								Winter	Fishing loss	Resource Component	
Species	Size class (mm)	RichMud	UpperMud	MidMud	CockleBed	Sand	Zostera	MusselBed	Fields	mortality (%)	(n fisher-1 d-1)	Initial AFDM (g)	Change (%)
LittleWorms	all	2124.36	6203.76	16317.69	5270.5	4122.62	7358.53	5600.7	0	20	0	0.0015	0
Worms	5 - 14.99	2205.182	927.484	188.686	11.54	14.65	272.68	127	0	25	0	0.0007299	0
Worms	15 - 29.99	669.636	431.03	232.22	115.45	190.5	265.21	1765.3	0	25	0	0.0043352	0
Worms	30 - 44.99	611.91	157.79	112.49	5.77	75.71	41.09	0	0	40	0	0.0136016	0
Worms	45 - 59.99	323.27	130.85	83.46	5.77	43.96	26.15	0	0	40	0	0.0293882	0
Worms	60 - 74.99	184.73	69.27	56.24	0	17.1	18.68	0	0	50	0	0.0525037	0
Worms	75 - 89.99	23.09	46.18	27.21	5.77	9.77	0	0	0	85	0	0.0836142	0
Worms	90 - 104.99	34.64	26.94	32.66	0	9.77	3.74	0	0	85	0	0.123292	0
Worms	105+	11.55	15.39	16.33	11.55	17.1	3.74	25.4	0	85	0	0.2336498	0
Crustacea	3+	1685.64	846.67	364.67	271.32	928.08	56.03	101.6	0	0	0	0.0006	0
Scrobicularia	5 - 9.99	46.18	50.03	78.01	0	0	0	0	0	65	0	0.0034	0
Scrobicularia	10 - 14.99	34.63	42.33	21.77	0	0	0	0	0	65	0	0.0098	0
Scrobicularia	15 - 19.99	34.63	23.09	23.58	0	0	0	0	0	65	0	0.023	0
Scrobicularia	20 - 24.99	34.63	42.33	3.62	0	0	0	0	0	65	0	0.0478	-4
Scrobicularia	25 - 29.99	11.54	23.09	10.88	0	0	0	0	0	65	0	0.0903	-9
Scrobicularia	30 - 34.99	0	38.48	18.14	0	0	0	0	0	65	0	0.159	-13
Scrobicularia	35 - 39.99	57.72	19.24	10.88	0	0	0	0	0	65	0	0.2649	-17
Scrobicularia	40 - 44.99	11.54	15.39	10.88	0	0	0	0	0	65	0	0.4224	-20
Cockles	5 - 9.99	0	0	0	22.45	0	16.97	0	0	94	0	0.0034	-15
Cockles	10 - 14.99	0	0	0	9.45	0	12.71	0	0	45	0	0.0171	-25
Cockles	15 - 19.99	0	0	0	8	0	10.94	0	0	30	0	0.0494	-30
Cockles	20 - 24.99	0	0	0	8.73	0	19.76	0	0	22	0	0.1095	-34
Cockles	25 - 29.99	0	0	0	2.55	0	11.88	0	0	22	0	0.2064	-37
Cockles	30 - 34.99	0	0	0	0	0	2	0	0	0	0	0.3497	-39
Cockles	35 - 39.99	0	0	0	0	0	0.82	0	0	0	0	0.549	-41
Cockles	40 - 44.99	0	0	0	0	0	0	0	0	0	0	0.8143	-43
Hydrobia	3+	0	61.58	18.14	744.68	0	8382	63.5	0	53	0	0.001	0
Winkles	5 - 9.99	0	0	0	0	0	25.56	122.4	0	75	0	0.0046	-15
Winkles	10 - 14.99	0	0	0	0	0	17.65	65.6	0	60	0	0.0282	-15
Winkles	15 - 19.99	0	0	0	0	0	36.47	164	0	45	0	0.0956	-15
Winkles	20 - 24.99	0	0	0	0	0	5.53	12.8	0	45	0	0.2384	-15
Mussels	5 - 9.99	0	0	0	0	0	22.41	50.8	0	6	0	0.0042	-33
Mussels	10 - 14.99	0	0	0	0	0	3.74	266.7	0	6	0	0.0171	-31
Mussels	15 - 19.99	0	0	0	0	0	0	190.5	0	6	0	0.0432	-30
Mussels	20 - 24.99	0	0	0	0	0	3.74	101.6	0	6	0	0.0862	-30
Mussels	25 - 29.99	0	0	0	0	0	0	165.1	0	6	0	0.1496	-29
Mussels	30 - 34.99	0	0	0	0	0	3.74	139.7	0	6	0	0.2365	-28
Mussels	35 - 39.99	0	0	0	0	0	3.74	165.1	0	6	0	0.3499	-28
Mussels	40 - 44.99	0	0	0	0	0	7.47	241.3	0	6	0	0.4927	-27
Mussels	45 - 49.99	0	0	0	0	0	3.74	241.3	0	6	0	0.6677	-27
Mussels	50 - 54.99	0	0	0	0	0	0	177.8	0	6	0	0.8774	-26
Mussels	55 - 59.99	0	0	0	0	0	0	50.8	0	6	0	1.1246	-26
Earthworms	5 - 14.99	0	0	0	0	0	0	0	0	0	0	0.0009	0
Earthworms	15 - 29.99	0	0	0	0	0	0	0	7.45	0	0	0.0054	0
Earthworms	30 - 44.99	0	0	0	0	0	0	0	35.40	0	0	0.0165	0
Earthworms	45 - 59.99	0	0	0	0	0	0	0	62.73	0	0	0.0346	0
Earthworms	60 - 74.99	0	0	0	0	0	0	0	42.86	0	0	0.0601	0
Earthworms	75 - 89.99	0	0	0	0	0	0	0	26.71	0	0	0.0935	0
Earthworms	90 - 104.99	0	0	0	0	0	0	0	17.39	0	0	0.135	0
Earthworms	105+	0	0	0	0	0	0	0	7.45	0	0	0.194	0

8.4.5 FORAGERS

Six species of shorebirds were included in the model: dunlin *Calidris alpina*, grey plover *Pluvialis squatarola*, black-tailed godwit *Limosa limosa*, bar-tailed godwit *Limosa lapponica*, oystercatcher *Haematopus ostralegus* and curlew *Numenius arquata*. Two types of oystercatchers were included in the model: shellfish specialists and worm specialists. These two types of oystercatchers varied only in their feeding efficiencies on different types of prey. Forager numbers, diets, constants and variables are shown in Table 8.4.

Forager diets were determined from literature searches (J.D. Goss-Custard unpublished data). Feeding efficiencies on certain diets, such as earthworms, were set lower than those on the preferred diets for each species. Forager constants were arrival date, feeding efficiency and dominance. Arrival day was Day 1 for all oystercatcher and curlew. For the other four species, a certain number of birds (based on numbers present in August) were present on Day 1, whilst the arrival day of the rest of the population was drawn from a uniform distribution between Day 2 and Day 62 (October 31). The foraging efficiency of each individual within the population was drawn from a normal distribution, with a mean of one and a standard deviation of 0.125. The dominance score for each individual was drawn from a uniform distribution between 0 and 1.

Forager variables used were the area available for feeding, night-time feeding efficiency, lower critical temperature and three different types of interference: mobile prey interference, weak kleptoparasitism and strong kleptoparasitism (see Chapter 2). The area available for feeding was patch area minus any area affected by disturbers. This area was then used to calculate the degree of interference from conspecifics. Night-time feeding efficiency was expressed as a proportion of daytime efficiency and was the main parameter used to calibrate the model. The lower critical temperature (LCT: below which thermostatic energy costs are incurred) for each species was calculated from the relationship between known values for various wader species (from a literature search) and body mass. Mobile prey interference affected the intake rates of birds feeding on worms and *Crustacea*, weak kleptoparasitism affected the intake rates of birds other than oystercatchers feeding on molluscs, whilst strong kleptoparasitism affected the intake rate of oystercatchers feeding on molluscs.

The rate at which shorebirds were able to feed depended on the abundance of food in a patch and the strength of interference from other competitors. The influence of the food supply on a bird's intake rate was calculated using a functional response (see Chapter 2).

The maximum amount of food that can be eaten at any one time is limited by a bird's gut processing rate and its crop capacity. This was expressed in the model as the maximum rate of consumption in kJ d^{-1} and was related to body mass using the following equation (Kirkwood, 1983):

$$C = 61.718tM^{0.7902} \tag{8.1}$$

Where c = consumption rate (J), t = time (s) and M = body mass (g). However, values calculated using this equation resulted in mass starvation amongst most birds in the model, probably because shorebirds can only feed for a certain amount of time each day. Model calibration, therefore, necessitated increasing this value until most or all birds survived the winter.

The energy assimilated from consumed food depended on the energy density of the food and the efficiency with which the energy from the food could be assimilated. Energy density was assumed to be 22 kJ g^{-1} for all prey species. Assimilation efficiency was assumed to be 0.75 for most birds consuming most diets. However, higher assimilation efficiencies were used for birds consuming crustacea and oystercatchers consuming molluscs. Crustacea are thought to be more easily assimilated prey and oystercatchers have higher assimilation efficiencies when consuming molluscs because they remove the shell before consuming the prey, whilst other species consume the shell.

Assimilated energy was converted into increased mass by assuming that 33 kJ of energy was stored in each g of storage tissues (Kersten & Piersma, 1987). The thermoneutral energy requirements for each bird species were set at 2.5*BMR (Kersten *et al.*, 1987). The thermostatic costs below LCT were calculated using the relationship between published values (Kersten *et al.*, 1987) and species' body mass. Oystercatcher body mass data were those from the Exe estuary (Goss-Custard *et al.*, 1982). Body mass data for other species were taken from the Wash, east England (Johnson, 1985).

Any disturbance event made part of a feeding patch unavailable for feeding. The area affected by disturbance was calculated from disturbance distances for each species obtained on the Exe and the Wash (J.D. Goss-Custard and M. G. Yates unpublished information). The energy cost of disturbance was calculated using the following equation (Nudds & Bryant, 2000):

$$C = 61.718tM^{0.7902} \tag{8.2}$$

Where C = energetic cost in J, t = duration of flight and M = mean body mass in kg. The duration of flight following a disturbance was assumed to be two minutes.

Two sources of forager mortality were included in the model starvation and predation. A forager died if it failed to maintain any fat reserves i.e. body mass ≤ starvation mass. The starvation mass of each species was measured from previous studies or predicted from the basal body mass for species with no direct measurement. Dunlin were the only species to have a risk of being predated should any raptors be present.

Table 8.4 Forager variables used in the Exe estuary model

Forager variables	**Dunlin**	**Grey Plover**	**Black-tailed Godwit**	**Bar-tailed Godwit**	**Oystercatcher** (shellfish)	**Oystercatcher** (worms)	**Curlew**
Initial numbers	5600	400	600	360	1870	630	780
Arrival dates	1 Sep - 31 Oct	1 Sep - 31 Oct	1 Sep - 31 Oct	1 Sep - 31 Oct	1 Sep	1 Sep	1 Sep
Diet & feeding efficiency:							
Small worms (<30mm)	0.90						
Medium worms (30 - 59.99mm)	0.90	1.00					
Large worms (60-104.99mm)		1.00	1.00	1.00	0.50	1.00	1.00
Mega worms (105mm+)				1.00	0.50	1.00	1.00
Crustacea (3+mm)	1.00						
Small molluscs (5 - 9.99mm)	1.00	1.00					
Medium Scrobicularia (10-19.99mm)			1.00	1.00			1.00
Large Scrobicularia (20-44.99mm)					0.50	0.70	
Medium cockles (10 -19.99mm)			1.00	1.00			1.00
Large cockles (15- 44.99mm)					1.00	0.50	
Winkles (15+mm)					1.00	0.50	
Mussels (25+mm)					1.00	0.50	
Small earthworms (15 - 44.99mm)	0.50		0.50		0.50	0.50	0.60
Large earthworms (45+mm)			0.50		0.50	0.50	0.60
Range of foraging efficencies (coef. of variation)	0.125	0.125	0.125	0.125	0.125	0.125	0.125
Range of dominance values	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1
Night-time feeding efficiency	0.80	0.55	0.55	0.55	0.60	0.55	0.60
Lower critical temperature (LCT) (^{o}C)	23	18	18	16	10	10	4
Mobile prey interference:							
Aggregation factor	10	10	10	10	10	10	10
Threshold density (n ha^{-1})	100	100	100	100	100	100	100
Coefficients	0.48,0,0	0.48,0,0	0.48,0,0	0.48,0,0	0.48,0,0	0.48,0,0	0.48,0,0
Weak kleptoparasitism:							
Aggregation factor	10	10	10	10	10	10	10
Threshold density (n ha^{-1})	100	100	100	100	100	100	100
Coefficients	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0	0.08,-0.08,0
Strong kleptoparasitism:							
Aggregation factor					5	5	
Threshold density (n ha^{-1})					65.4	65.4	
Coefficients					0.50,-0.50,0	0.50,-0.50,0	
Functional response:							
B_{50} (g AFDM m^{-2})	0.761	0.761	0.761	0.761	0.761	0.761	0.761
Forager coefficient	-1.712318	-1.343798	-1.333913	-1.249942	-1.141162	-1.141162	-1.039356
Prey coefficient	0.36542	0.36542	0.36542	0.36542	0.36542	0.36542	0.36542
Maximum rate of consumption (kJ d^{-1})	265	856	960	958	1560	1300	1952
Prey assimilaton efficiency:							
Worms	0.75	0.75	0.75	0.75	0.75	0.75	0.75
Crustacea	0.85						
Scrobicularia, cockles and winkles	0.75	0.75	0.75	0.75	0.85	0.85	0.75
Mussels					0.854	0.854	
Energy density of fat reserves (kJ g^{-1})	33.4	33.4	33.4	33.4	33.4	33.4	33.4
Thermoneutral energy requirements (kJ d^{-1})	132	430	489	484	757	757	997
Thermostatic costs below LCT (kJ deg^{-1} d^{-1})	1.5	9.0	11.7	11.7	31.8	31.8	77.1
Area affected by disturbance (m^{2})	9503	11310	31420	31420	25447	25447	80425
Energy cost of disturbance (kJ disturbance^{-1})	0.74	2.66	2.3	3.02	4.52	4.52	6.54
Time cost of disturbance (h)	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Probability of predation (raptor^{-1})	0.00001	0	0	0	0	0	0
Basal mass (g)	48.8	219	228	321	500	500	757
Mean arrival mass (g)	47.3	225	216	304	486	486	881
Target mass(g)	47.3+(0.1376*Day)	278	232	327	486+(0.7185*Day)	486+(0.7185*Day)	881
	- (0.00068*Day2)						
Starvation mass (g)	39	127	161	227	350	350	489

8.6 Results

8.6.1. MODEL CALIBRATION

Two parameters were used to calibrate the model, the maximum daily consumption rate and night-time feeding efficiency. Calculated values of maximum daily consumption using Kirkwood (1983) resulted in mass starvation of most of the forager species. This value was, therefore, increased in increments of 5% of the original value until most birds of all species survived the winter. The final value for all species, except mussel-feeding oystercatchers, was 25% higher than the original value. The maximum consumption rate for mussel-feeding oystercatchers had to be increased still further, to 50% higher than the original value. We think this was necessary because mussel beds on the Exe estuary are only exposed for a relatively short time in the tidal cycle, so birds had to be able to feed at a very fast rate.

Apart from oystercatchers (Durell *et al.*, 2000; Goss-Custard & Durell, 1984), forager overwinter mortality rates on the Exe estuary were unknown. However, it was assumed that they were above zero. We used night-time feeding efficiency, about which little is known, to calibrate the model such that overwinter starvation rates for all species were above zero, and for oystercatchers was between 0.4 and 4%. We did this by systematically reducing night-time feeding efficiency for each species until some birds had starved by the end of the winter.

8.6.2 MODEL VALIDATION

8.6.2.1 Bird distribution

One test of the model is to see how well it predicts the birds' distribution around the estuary at low tide. We compared the mean distribution of birds in the model between October and January with WeBS counts for 1993/94. The model predicted well the distribution of birds at low water (Fig. 8.3). The main discrepancies were the distribution of bar-tailed godwit and curlew between mud and sand patches. However, in the model, the two species were seen to use both types of patch as the tide receded and advanced.

8.6.2.2 Use of fields at high water

Another test of the model was to see which birds moved to feed in nearby fields at high water. The main species seen feeding in fields around the Exe estuary are black-tailed godwit, oystercatcher and curlew (S.E.A. Durell unpublished information). Apart from a few dunlin early on in the year, these were the three species that were predicted to feed in the fields (Fig. 8.4). The model also predicted well the numbers of oystercatchers feeding in fields at high water throughout the winter (Goss-Custard & Durell, 1983).

8.6.2.3 Population response to environmental change

A further test of the model was to investigate the effect of environmental change on bird mortality. The two tests we used were reducing mean daily temperature and reducing invertebrate densities. A reduction in the mean daily temperature throughout the winter resulted in an increase in mortality in all six bird species (Fig. 8.5). Reducing invertebrate densities also caused a steady increase in mortality (Fig. 8.6). These two tests demonstrated that a deterioration in the environment invoked an appropriate response in the model populations.

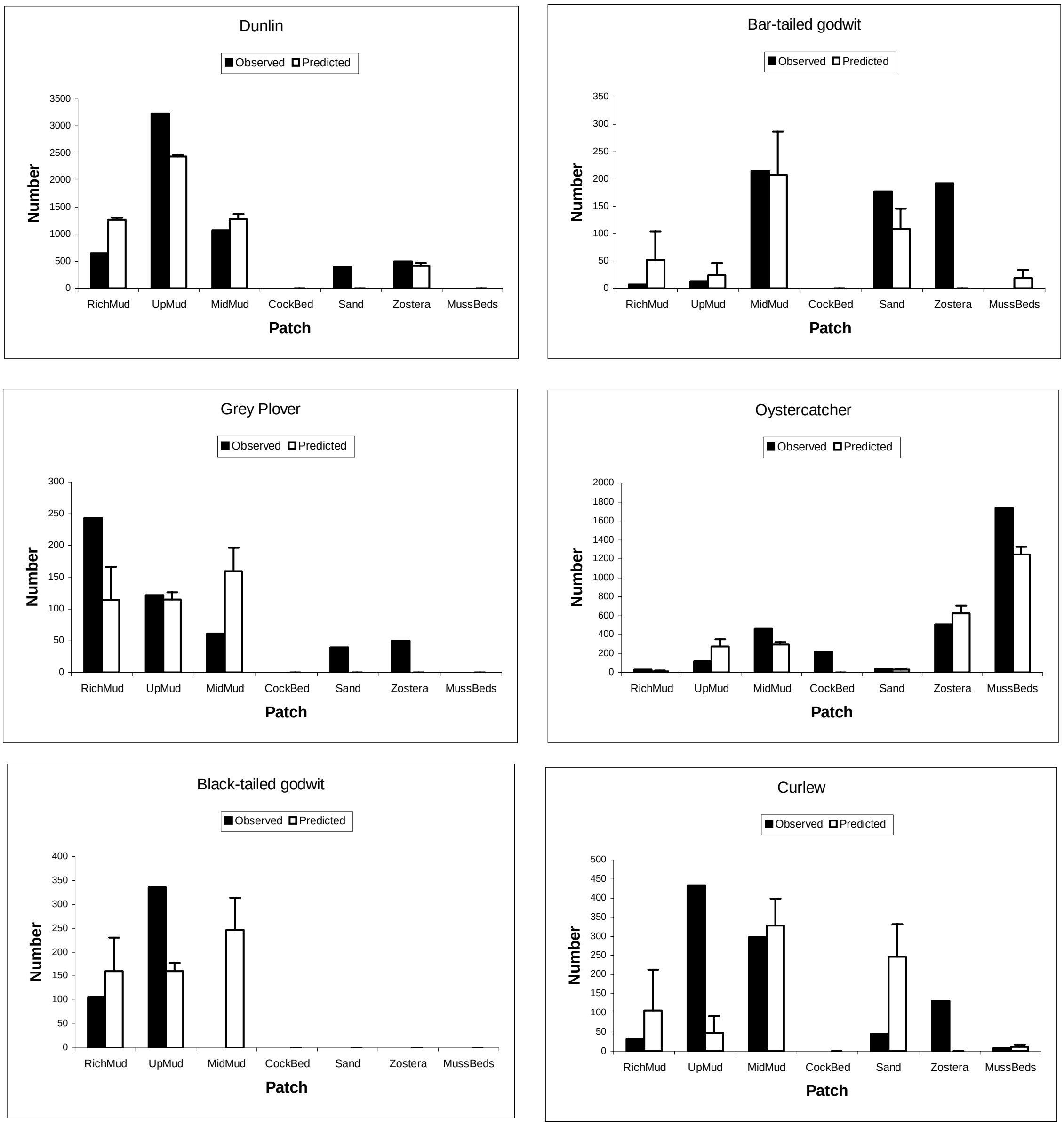

Figure 8.3 Observed and predicted distribution of shorebirds on the Exe estuary. Observed distributions are from WeBS low water counts for 1993/94. Predicted distributions are the mean numbers at low water from October to January.

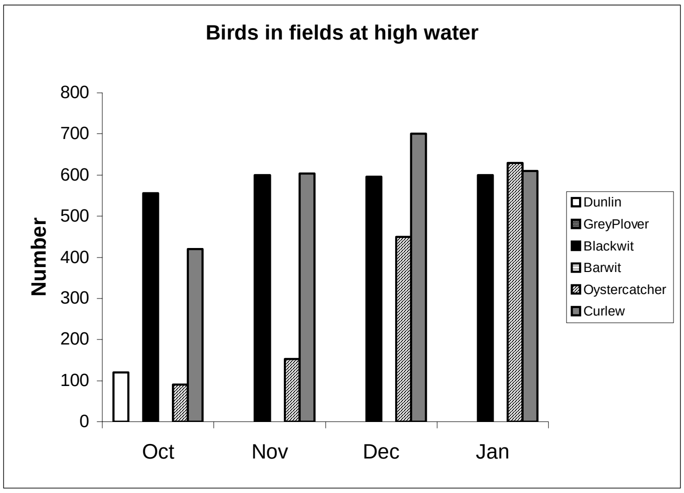

Figure 8.4 Number of birds predicted to feed in fields at high water through the winter

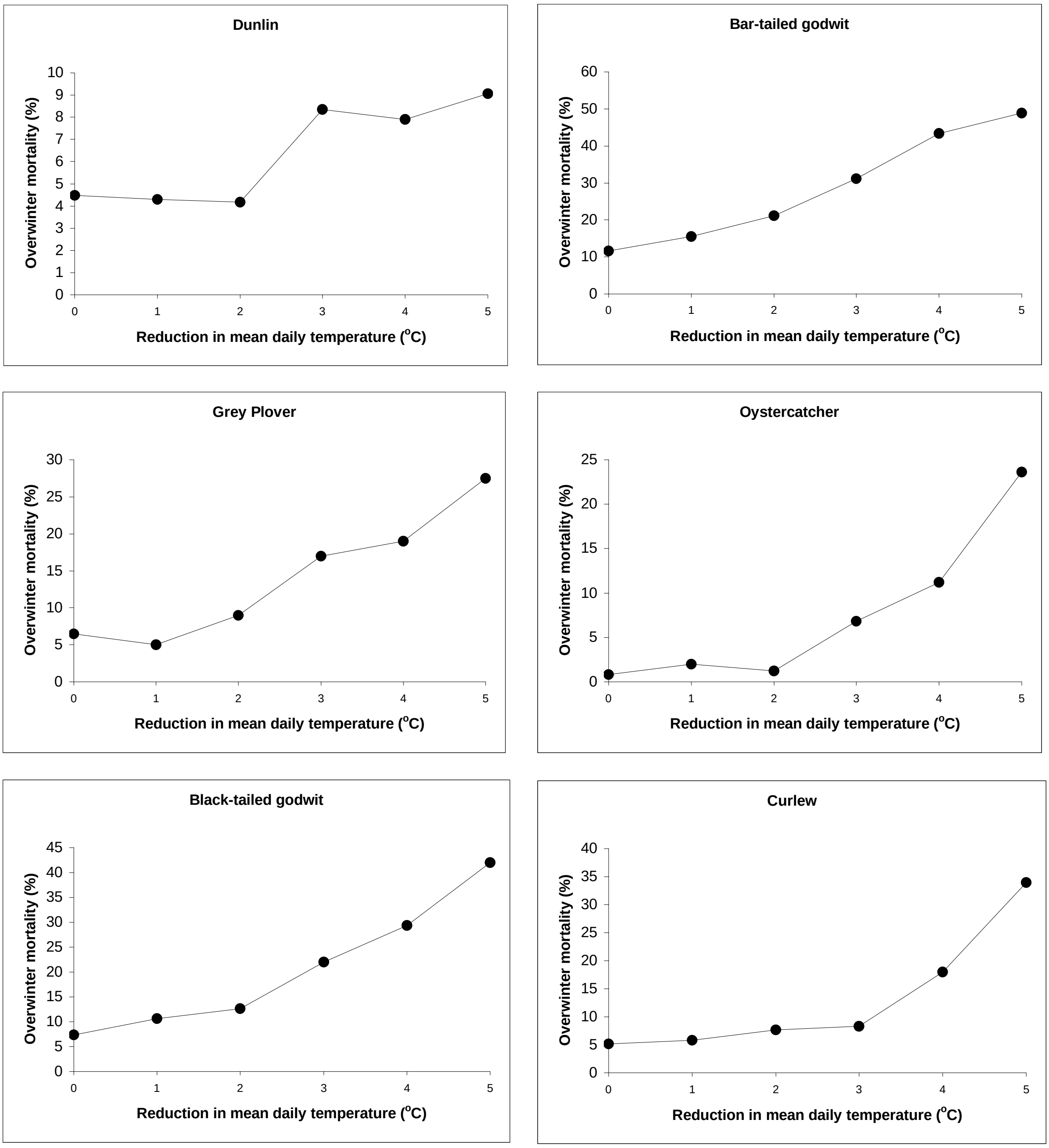

Figure 8.5 The effect of lowering mean daily temperatures on shorebird mortality.

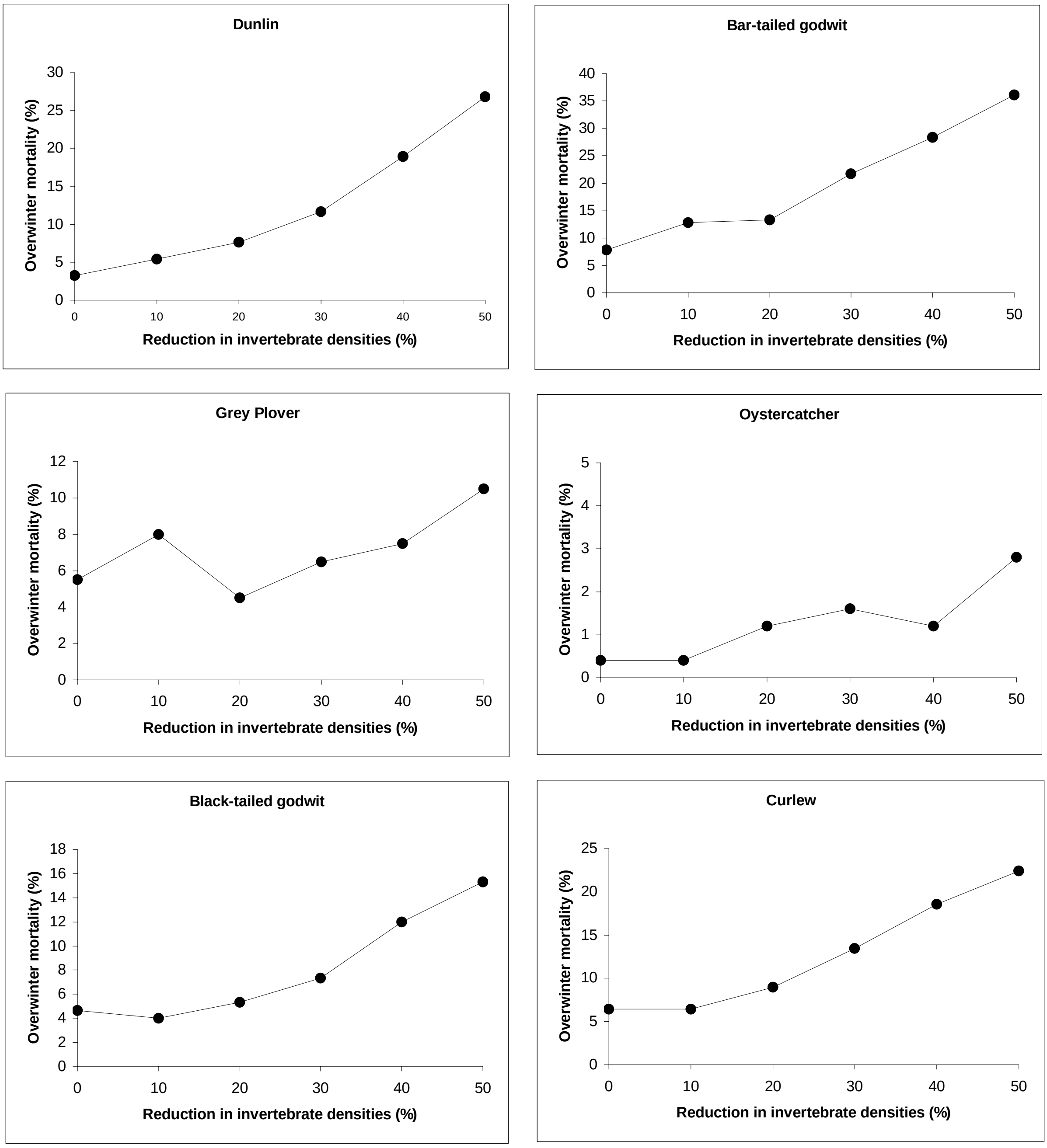

Figure 8.6 The effect of reducing invertebrate densities on shorebird mortality.

8.6.3 ISSUES

8.6.3.1 Disturbance associated with a cycle path

We simulated the effect of disturbance associated with a cycle path along the estuary near Powderham in two ways. Firstly, we simulated the effect of birds avoiding altogether an area of mudflat within 175 m of the sea wall (J.D. Goss-Custard unpublished data) in daylight hours. Secondly we simulated the effect of a range of disturbance events per hour on the birds feeding on this mudflat in daylight hours.

Removing an area of mudflat next to the sea wall at Powderham had no effect on the mortality of any of the shorebird species in the model (Fig. 8.7). Similarly, having up to ten walkers an hour disturbing shorebirds on this mudflat did not have any effect on shorebird mortality (Fig. 8.8).

However, it is also true that a cycle path along the sea wall at Powderham would also disturb birds feeding in the fields nearby. We therefore explored the effect of varying the amount of disturbance events affecting field-feeding birds. The species that feed most in these fields are black-tailed godwit and curlew. Black-tailed godwit did not appear to be affected by disturbance until the frequency was greater than eight disturbance events per hour (Fig. 8.9). Curlew mortality, on the other hand, appeared to increase steadily as disturbance events increased. No other species were affected by field disturbance.

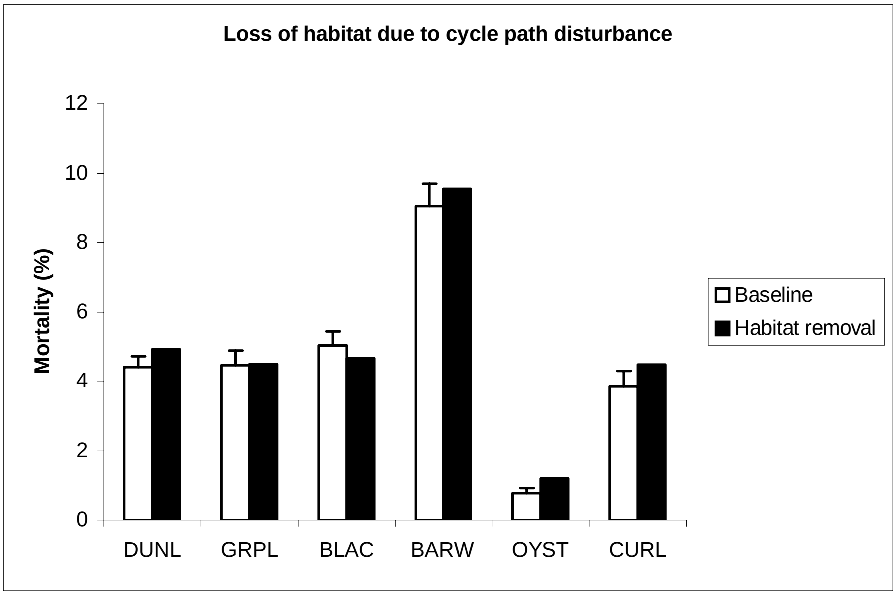

Figure 8.7 The effect on shorebird mortality of potential habitat loss from disturbance associated with a cycle path.

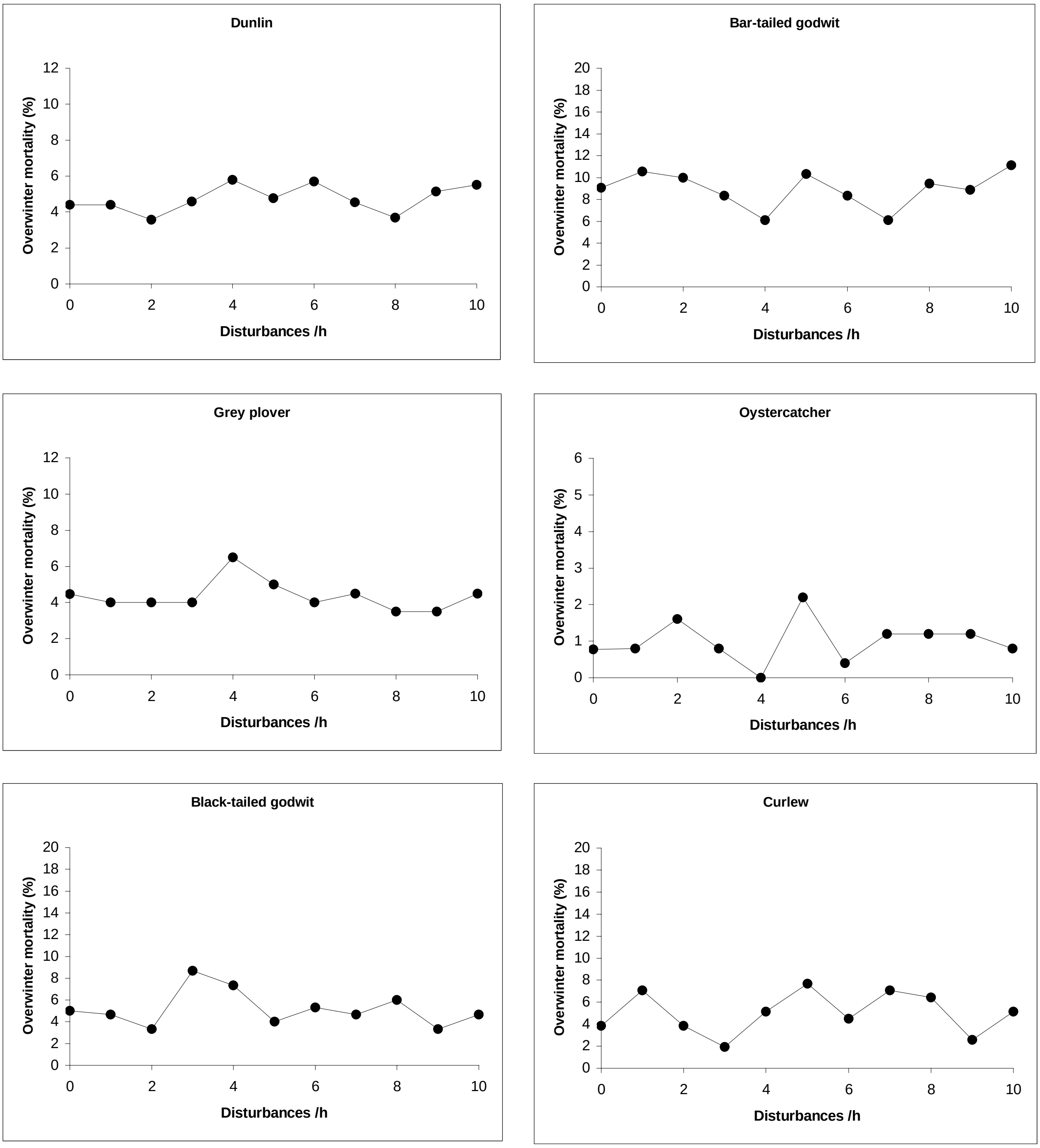

Figure 8.8 The effect on shorebird mortality of disturbance associated with a cycle path affecting birds feeding on the mudflats.

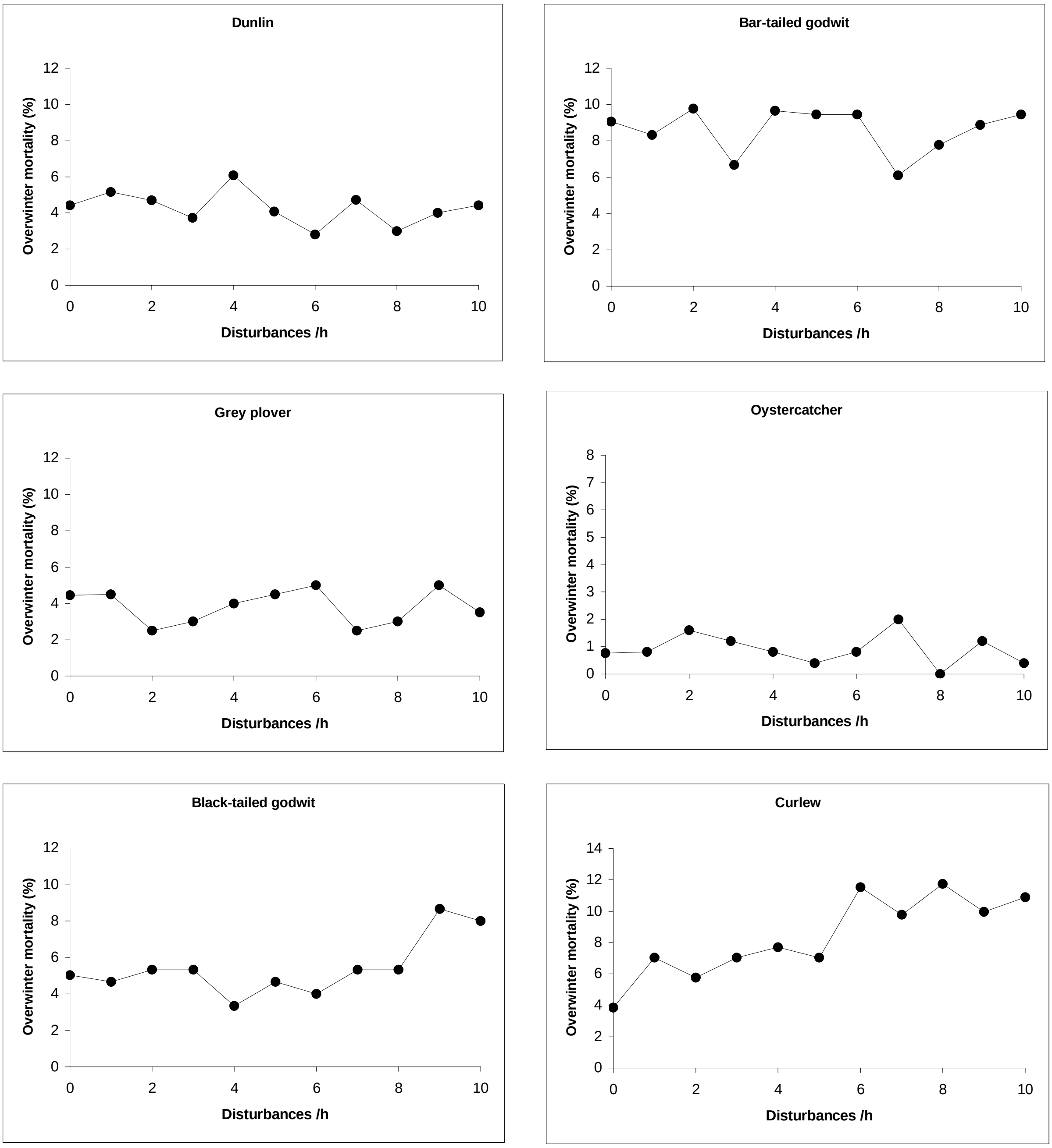

Figure 8.9 The effect on shorebird mortality of disturbance associated with a cycle path affecting birds feeding in nearby fields.

8.6.3.2 Roost disturbance

Roost disturbance was simulated by increasing the number of disturbance events per hour in daylight at Dawlish Warren. Disturbing the birds up to five times per hour over the high water period had little effect on their mortality (Fig. 8.10). We therefore repeated these simulations whilst decreasing mean daily temperatures by 3°C. In cold weather, there was still no discernable change in shorebird mortality resulting from increasing disturbances up to five per hour (Fig. 8.11).

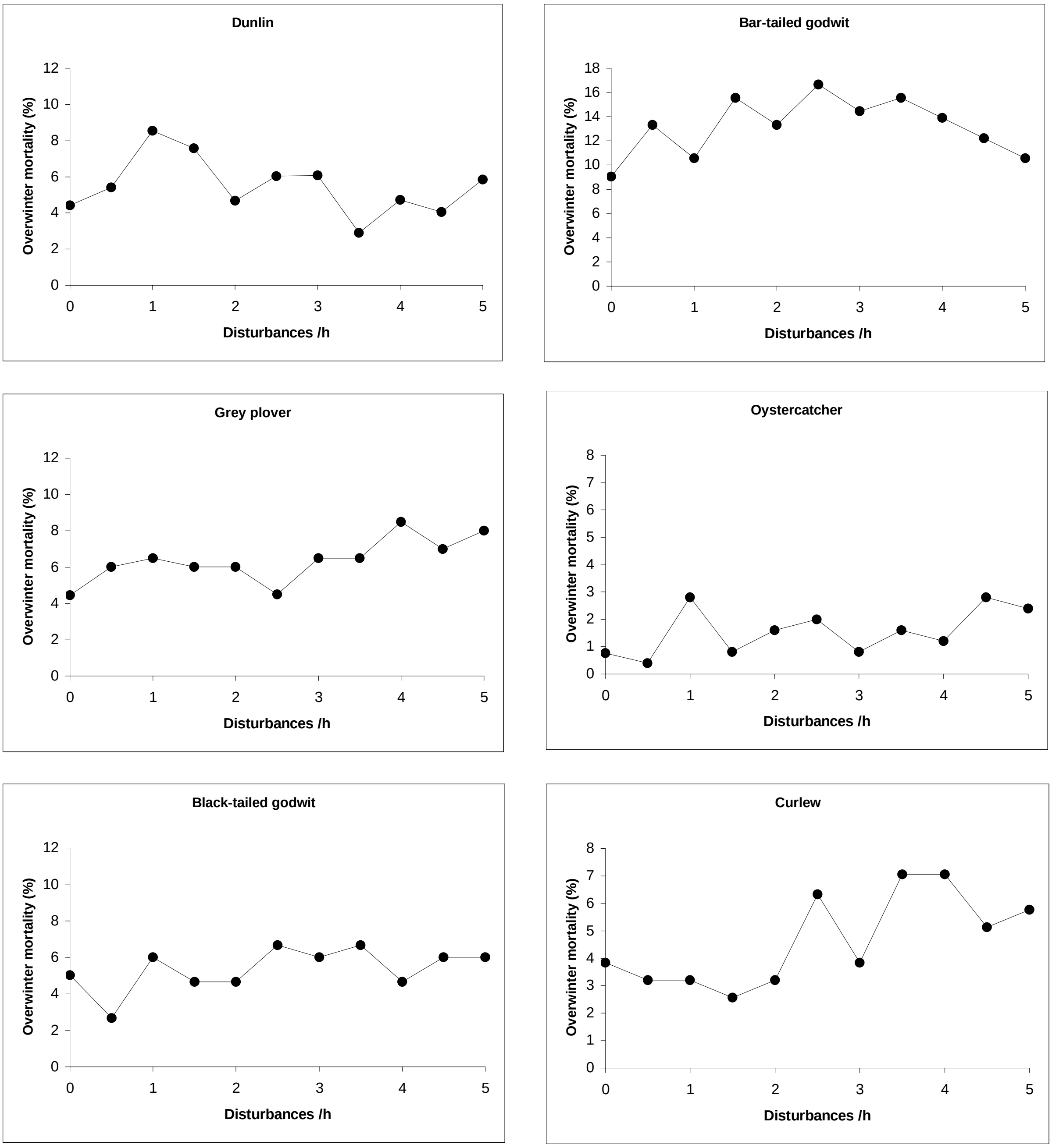

Figure 8.10 The effect on shorebird mortality of disturbance of the high water roost.

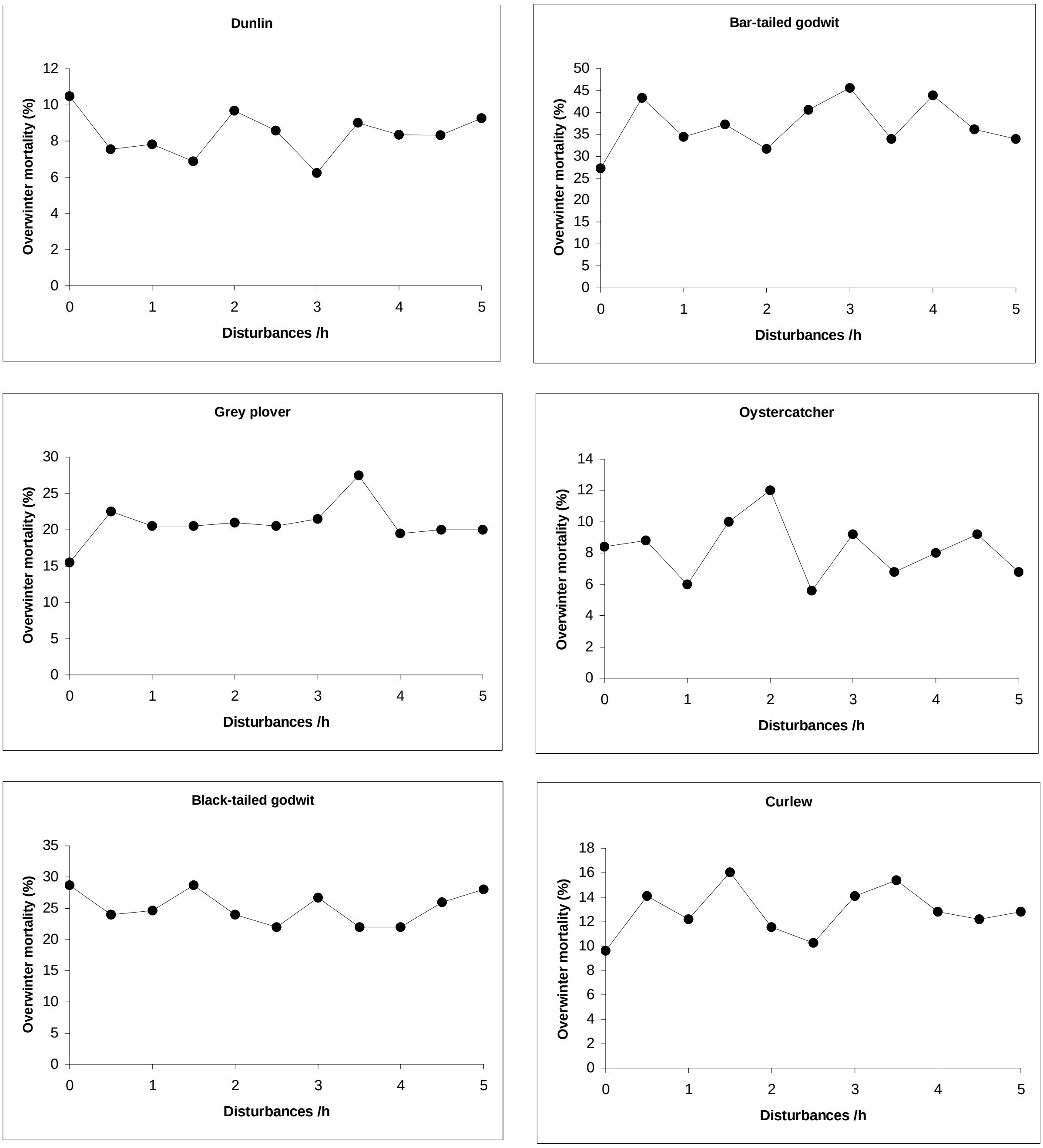

Figure 8.11 The effect on shorebird mortality of disturbance of the high water roost in cold weather.

8.7 Conclusions

Using data collected for this Report, we have built a behaviour-based model of six shorebird species overwintering on the Exe estuary. The model predicted well the present-day distribution of these shorebirds around the estuary. The model bird populations also responded in an appropriate way to reductions in winter temperatures and reductions in their food supply. Oystercatcher overwinter mortalities in the model were in the same range as those found in real life (Durell *et al.*, 2000; Goss-Custard *et al.*, 1982). Data were not available for mortality rates in the other five shorebird species modelled, but we feel that they were within a realistic range. We also feel confident about model predictions of the effect of environmental change on levels of shorebird mortality.

Time constraints, and the length of time taken for each model run, meant that no repeat runs were done for any of the simulations done for this Report. As a result, variation included in the model parameters is reflected in the figures presented here. It also meant that no statistical analyses could be made of the results. Future work will involve repeat simulations and statistical analysis of our results.

In this Report, we used the model to address two main issues in the Exe estuary. A previous version of the model has already been used to explore the effect of shellfishing on mussel-feeding oystercatchers (Stillman *et al.*, 1996). In this study we explored the effect of increased levels of disturbance. We found that disturbance resulting from a cycle path along the side of the estuary at Powderham was unlikely to have any effect on the mortality of shorebirds feeding on nearby mudflats. However, we found that disturbance affecting birds feeding in the fields at high water did result in raised mortality levels in curlew and black-tailed godwit.

Finally, we explored the effect of increasing levels of disturbance of the high water roost at Dawlish Warren. We were surprised to find that increasing disturbance levels up to five events per hour had no discernable effect on shorebird mortality. We assume, therefore, that birds in the model were able to make up for any increase in energy demands incurred by disturbance at the high water roost.

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9 MULTI-SITE MODELS: WADERS

Richard A. Stillman

9.1 Introduction

This chapter describes the work conducted in work package 6 of the project. The objective of this work package was to compare the predictions of single-site and multi-site wader models. In contrast to other work packages, the model was not parameterised for a particular system, but instead was developed in a more general way. It was developed for a system incorporating two sites, each comprised of a single patch, exposed by the tide for 12 hours in every 24 hours. Birds consume food when the patch is exposed and roost when the patch is not exposed. Two versions of the model were developed, one representing knot feeding on small bivalves, and the other representing oystercatchers feeding on large bivalves. The model predicted both local survival rates on one focal patch and global survival rates on the two sites (focal and buffer sites). The model also predicted how the influx of immigrants (i.e. those displaced from the focal site) to the buffer site influenced survival rates on that site. Different simulations investigate how local and global survival rates, are influence by conditions on one or both sites, the distance between sites and the relative size of the two sites.

9.2 Model parameters

This section describes the parameter values and assumptions used for each of the five elements of the model.

9.2.1 GLOBAL

Global variables used in the model are shown in Table 9.1. The model started on 1 September, ran for 200 days and had a time step length of 1 hour.

9.2.2 PATCHES

The purpose of the model was to understand when the predictions of single and multi-site models will differ. A *single-site* and *multi-site* version of the model were therefore developed for each species. The models were not intended to represent any particular site(s) in great detail and so were kept as simple as possible. The single site model was comprised of a single patch, the *focal site*. The multi-site model was comprised of two patches, the focal site and the *buffer site*. Default patch variables used in the models are shown in Table 9.2.

9.2.3 RESOURCES AND COMPONENTS

Prey types and size classes used in the model, and their initial densities on each patch, are shown in Table 9.3. The model simply included the bivalve food consumed by knot and oystercatchers. Knot were assumed to consume small bivalves (<15mm) and oystercatchers to consume large bivalves (>20mm). The initial densities of bivalves were typical values recorded for cockles *Cerastoderma edule* in the Baie de Somme survey (Chapter 8). For simplicity, over winter mortality due to factors other than the birds was assumed to be zero. The initial ash-free dry mass content was that measured for cockles in the Baie de Somme (Chapter 8). The season change of ash-free dry mass during winter was a typical value for bivalves (Zwarts 1991).

9.2.4 FORAGERS

Forager numbers, diets, constants and variables are shown in Table 9.4. Individuals were assumed to arrive on 1 September and remain in the system for 200 days. Forager constants were foraging efficiency and dominance. Individuals were assumed to vary in their foraging efficiency, which influences intake rate in the absence of competitors, and dominance, which influences the effect of competitors on intake rate. The foraging efficiency of each individual within the population was drawn from a normal distribution, with a mean of one and a standard deviation of 0.125. The dominance score for each individual was drawn from a uniform distribution between 0 and 1. The forager variables used determined the strength of interference, which was assumed to be stronger in oystercatchers than in knot. The rate at which shorebirds were able to feed depended on the abundance of food in a patch and the strength of interference from other competitors. The influence of the food supply on a bird's intake rate was calculated using a functional response (see Chapter 2). The energy assimilated from consumed food depended on the energy density of the food and the efficiency with which the energy from the food could be assimilated. Energy density was assumed to be 22 kJ g^{-1} for all prey species. Assimilation efficiency was assumed to be 0.75 for knot, which consume bivalves whole, and 0.85 for oystercatcher, which remove the flesh from bivalve shells. Assimilated energy was converted into increased mass by assuming that 33 kJ of energy was stored in each g of storage tissues (Kersten & Piersma 1987). The thermoneutral energy requirements for each bird species were calculated from body mass using the "all species" equation of Nagy, Girard & Brown (1999). Bird body masses were based on data for the Wash, east England (Johnson 1985).

Table 9.1 Global variable values used in the multi-site model.

Global variables	Value
Duration of time step	1 h
First day	1 September
Number of days	200

Table 9.2 Patch variable values used in the multi-site model.

Bird species	Patch variables	Value
Knot	Focal site area	20.6 ha
	Buffer site area	20.6 ha
Oystercatcher	Focal site area	44.4 ha
	Buffer site area	44.4 ha

Table 9.3 Resource and component parameter values used in the multi-site model.

Bird species	Resource	Initial density (n m^{-2})			Component		
		Focal patch	Buffer patch	Winter mortality	Initial AFDM	Change	Energy density
Knot	Small bivalves	2000	2000	0%	0.01 g	-28%	22 KJg^{-1}
Oystercatcher	Large bivalves	250	250	0%	0.08 g	-28%	22 KJg^{-1}

Table 9.4 Forager parameter values used in the multi-site model.

Forager variables	Knot	Oystercatcher
Initial numbers	1000	1000
Arrival date	1 Sep	1 Sep
Diets eaten	Small bivalves	Large bivalves
Range of foraging efficiencies (coefficient of variation)	0.125	0.125
Range of dominance values	0 - 1	0 - 1
Kleptoparasitism:		
Aggregation factor	10	10
Threshold density (n ha^{-1})	100	100
Coefficient for least dominant bird	-0.08	-0.5
Coefficient for most dominant bird	0	0
Functional response:		
B_{50} (g AFDM m^{-2})	0.761	0.761
Forager coefficient	-1.712318	-1.141162
Prey coefficient	0.36542	0.36542
Prey assimilation efficiency:	0.75	0.85
Energy density of fat reserves (kJ g^{-1})	33.4	33.4
Non-thermoregulatory energy requirements (kJ d^{-1})	283	724
Mean arrival mass (g)	75	500
Target mass(g)	75	500
Starvation mass (g)	50	350

9.3 Results

9.3.1 SINGLE-SITE MODEL

This section describes the predictions of the single-site model. This single-site is termed the *focal site* in the multi-site model. Birds are assumed to die if they cannot survive in the single-site model, but to emigrate to the *buffer site* in the multi-site model.

9.3.1.1 Density-dependence

Figure 9.1 shows the effect of bird density on the survival, body condition and spare feeding time of oystercatchers and knots in the single site model. Each of these are measures of site quality. High site quality is indicated by high survival and body condition, and more spare feeding time. Increased bird density increases the difficulty birds have in surviving (i.e. it decreases site quality). In both species, the following changes occur as bird population density increases.

- *High site quality* - When population density is low, all individuals survival in good condition.
- *Intermediate site quality* - As population density increases, survival and body condition remain high, but the amount of spare feeding time decreases. This happens because the increased depletion and interference competition at higher population densities reduce the feeding rate of birds, and hence birds need to spend a higher proportion of the time feeding to meet their requirements.
- *Low site quality* - As population density decreases further, survival remains at 100% but the body condition of some individuals starts to decrease. These individuals are unable to meet their requirements even by feeding continuously.
- *Lowest site quality* - With further increases in population density, both body condition and survival are decreased.

The purpose of this chapter is to show when the predictions of single and multi-site models will differ. This will happen when birds displaced from a site are able to find and survive on an alternative site. In this case, a single-site model would predict less than 100% survival, but a multi-site model would predict 100% survival. In order to compare single and multi-site models, it was important that survival rates were relatively low in the single-site model. This was because predictions will inevitably be the same or very close if survival is very high in the single-site model. For this reason, the default single-site survival rate was assumed to be 85% in all subsequent simulations (i.e. 15% of individuals will either die in the single site model, or emigrate in the multi-site model). Figure 9.1 shows the knot and oystercatcher population densities leading to 85% survival in the single-site model.

9.3.1.2 Characteristics of the individuals which die / emigrate

The predictions of a multi-site model are likely to depend on when individuals decide to emigrate. Two extreme assumptions are that individuals will emigrate at the start of winter (anticipating that their reserves will decease later in winter), or that they will emigrate just before their body reserves are exhausted. We assumed that the second condition would arise when a birds fat reserves comprised 8% of its total body mass. Figure 9.2 shows the characteristics of the 15% of birds which emigrated / died in the single-site model. In knot, foraging efficiency was the major determinant of whether or not a bird emigrated / died. In oystercatchers, both foraging efficiency and dominance determined whether or not a bird emigrated / died. Dominance was relatively more important in oystercatchers because interference competition was stronger in this species. Figure 9.2 shows linear equations which can be used to discriminate between those birds which will survive on the site and those which will emigrate / die. In subsequent simulations, the following emigration rules were used.

- *Late emigration* – a bird emigrates, *near the end of winter*, when its fat reserves comprise less than 8% of its total body mass.

- *Early emigration* – a bird emigrates, *at the start of winter*, if it expects that its reserves would comprise less than 8% of its total body mass by the end of winter (predicted using the relationships in Figure 9.2).

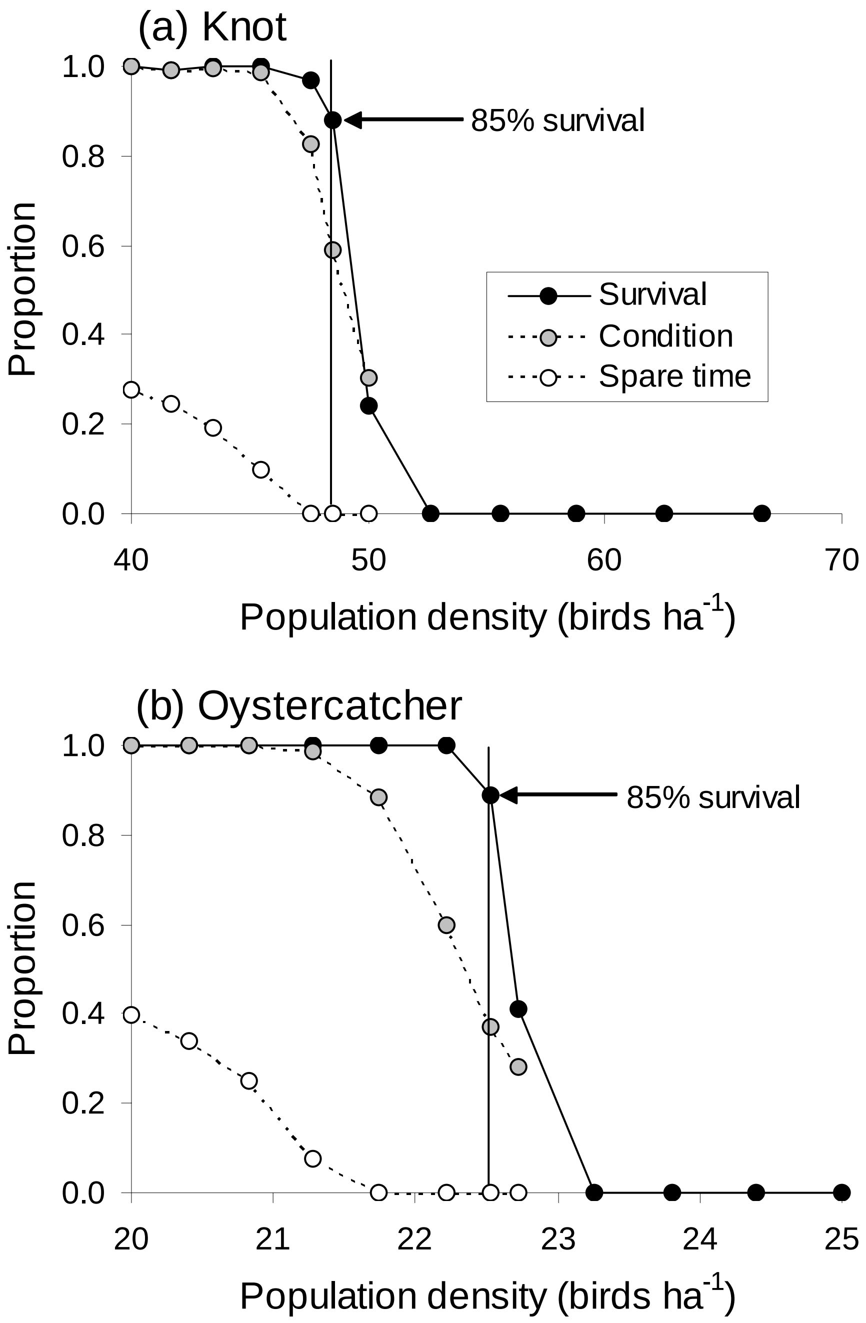
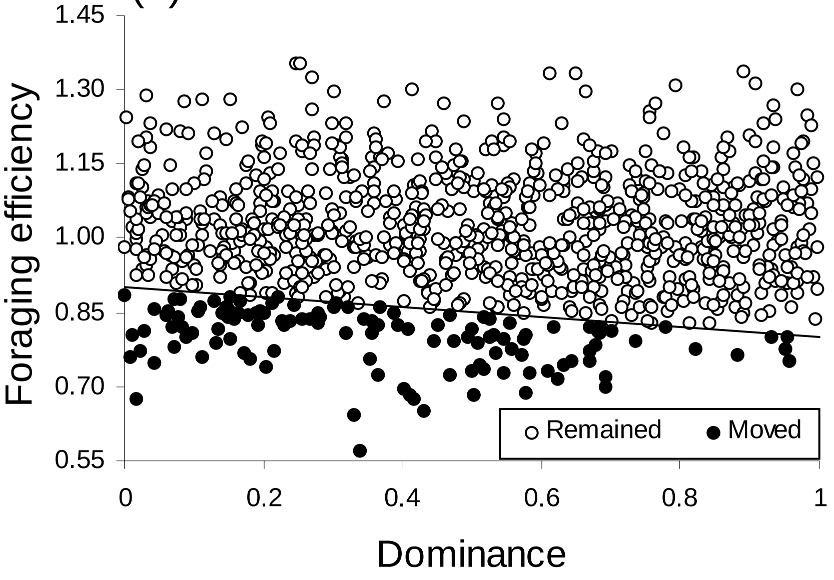
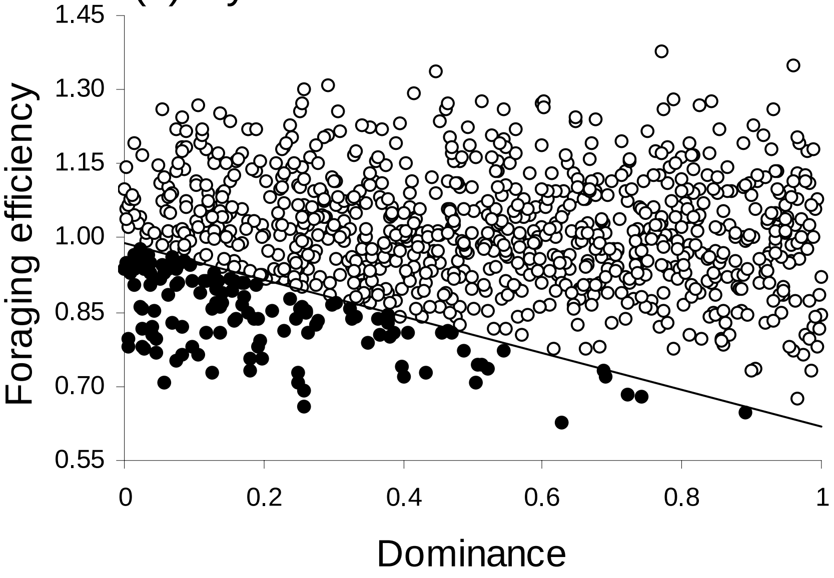


Figure 9.1 The effect of knot (a) and oystercatcher (b) population density on the proportion of birds surviving on the focal site (solid circles), the body condition of the birds remaining on the focal site (proportion of fat reserves remaining at the end of winter) (grey circles) and the amount of spare feeding time of the birds remaining on the focal site at the end of winter (proportion of the time not spent feeding) (open circles). The vertical lines show the population densities resulting in 85% survival which are used in subsequent simulations.



(a) Knot



(b) Oystercatcher

Figure 9.2 Characteristics of the individual knot (a) and oystercatchers (b) which either remained on the focal site throughout winter (open circles) or died / emigrated to the buffer site before the end of winter (closed circles). The lines discriminate between birds which either remained on the focal site or died / moved to the buffer site (knot move if foraging efficiency ≤ 0.9 - 0.1 x dominance; oystercatcher move if foraging efficiency ≤ 0.99 - 0.37 x dominance).

9.3.2 MULTI-SITE MODEL

This section describes the predictions of the multi-site model. Predictions are made for both *local* survival (i.e. assuming that all birds that emigrate die) or *global* survival (i.e. including the fate of the birds emigrating to the buffer site).

9.3.2.1 Distance between sites

The predictions of single and multi-site models can only differ if birds in a multi-site model are able to emigrate to and survive on the buffer site. This cannot happen if the buffer site is too distant to be reached by birds after they leave the focal site. Figure 9.3 shows the effect of the distance between sites on local and global survival For simplicity, we assumed that enough food was present on the buffer site to ensure the survival of all birds that successfully emigrated to the site, and that no birds were on the buffer site at the start of winter. Local survival was unaffected by whether early or late emigration was assumed, being 85% in both cases. However, both local body condition and spare feeding time were higher with early emigration. When birds emigrated early, they reduced the depletion and interference competition suffered by the remaining birds, which were therefore more easily able to survive winter. Global survival was influenced by both the distance between sites and the time at which birds emigrated. When birds emigrated early, they had the fat reserves to successfully emigrate to the buffer site, irrespective of the time to move to the site. When birds emigrated late, they had less fat reserves and so could only successfully emigrate to relatively close buffer sites. In summary, a multi-site model is more likely to produce different predictions to a single-site model if the multiple sites are relatively close together.

9.3.2.2 Relative bird density on sites

The previous simulations assumed that no birds were on the buffer site at the start of winter, whereas this is unlikely to be the case in reality. Simulations were therefore run assuming that the buffer site initially contained a range of bird densities (Figures 9.4 and 9.5), but contained the same amount of food as the focal site. We assumed that the buffer site could be reached within one hour and so could always be reached by emigrating birds. For simplicity, we assumed that starving birds did not emigrate from the buffer to the focal site, but instead died. Local survival was not influenced by the initial density of birds on the buffer site. Global survival was higher than local survival if the initial bird densities on the buffer site were lower than those on the focal site. When initial bird density on the buffer site was similar to, or higher than the bird density on the focal site, global survival decreased. With early emigration, all emigrants died if initial bird density on the buffer site was 90% or more of that on the focal site, and hence global survival equalled local survival. With late emigration, global survival decreased more gradually as initial bird density on the buffer site rose above that on the focal site. This happened because birds emigrated from the focal site very close to the end of winter and so only needed to survive for a short time on the buffer site before the end of winter. However, although they survived, these individuals were in very poor condition (i.e. their body reserves were very low). Early emigration had a potentially more detrimental effect of the populations of birds initially starting on the buffer site (Figure 9.5). This happened because early emigrants competed with those on the buffer site for more time than late emigrants. This caused increased mortality of the birds initially starting on the buffer site. In summary, a multi-site model is more likely to produce different predictions to a single-site model if the buffer site has a lower initial bird density than the focal site.

9.3.2.3 Relative size of sites

The previous simulations assumed that both the focal and buffer sites were the same size, whereas this may not be the case in reality. Simulations were therefore run assuming that the buffer site initially contained the same density of birds and same amount of food as the focal site, but that the buffer site was either smaller or larger than the focal site (Figure 9.6). We assumed that the buffer site could be reached within one hour and so could always be reached by emigrating birds. For simplicity, we assumed that starving birds did not emigrate from the buffer to the focal site, but instead died. Local survival was not influenced by the size of the buffer site. With early emigration, all emigrants died if the buffer site was smaller than the focal site, and hence global survival equalled local survival. Early emigration also had a potentially detrimental effect on the population of birds starting on the buffer site, causing increased mortality of these birds if the buffer site was smaller than the buffer site. With late emigration, global survival was not influenced by the initial size of the buffer site. This happened because birds emigrated from the focal site very close to the end of winter and so only needed to survive for a short time on the buffer site before the end of winter. However, although they survived, the body condition of the emigrating birds increased as the size of the buffer site increased. In summary, a multi-site model is more likely to produce different predictions to a single-site model if the buffer site is larger than the focal site.

9.3.2.4 Relative quality of sites

The previous simulations assumed that both the focal and buffer sites contained the same biomass of food at the start of winter, whereas this may not be the case in reality. Simulations were therefore run assuming that the buffer site initially contained the either more or less food than the focal site (Figure 9.7). For simplicity, we assumed that both sites were the same size and contained the same density of birds. We assumed that the buffer site could be reached within one hour and so could always be reached by emigrating birds. For simplicity, we assumed that starving birds did not emigrate from the buffer to the focal site, but instead died. Local survival was not influenced by the quality of the buffer site. Global survival was greater than local survival if the buffer site contained more food than the focal site. This happened because surplus food was available in the buffer site to feed the immigrating birds. In summary, a multi-site model is more likely to produce different predictions to a single-site model if the buffer site is of higher quality than the focal site.

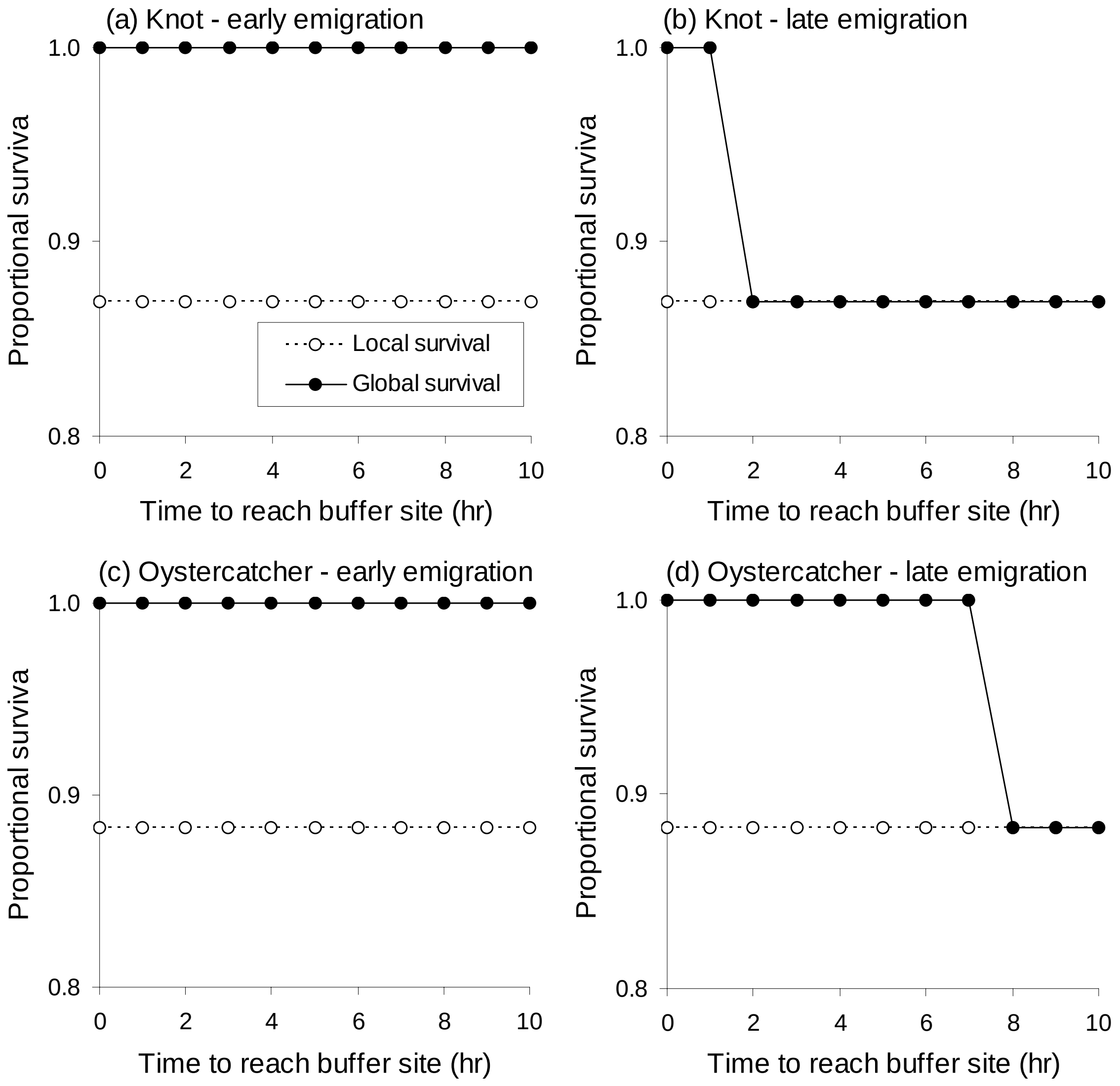


Figure 9.3 The effect of the distance between focal and buffer sites on local and global survival of knots (a, b) and oystercatchers (c, d). Individuals either emigrated from the focal site at the start (a, c) or near the end (b, d) of winter. Both sites were of the same size and contained the same amount of food at the start of winter. No birds were present on the buffer site at the start of winter.

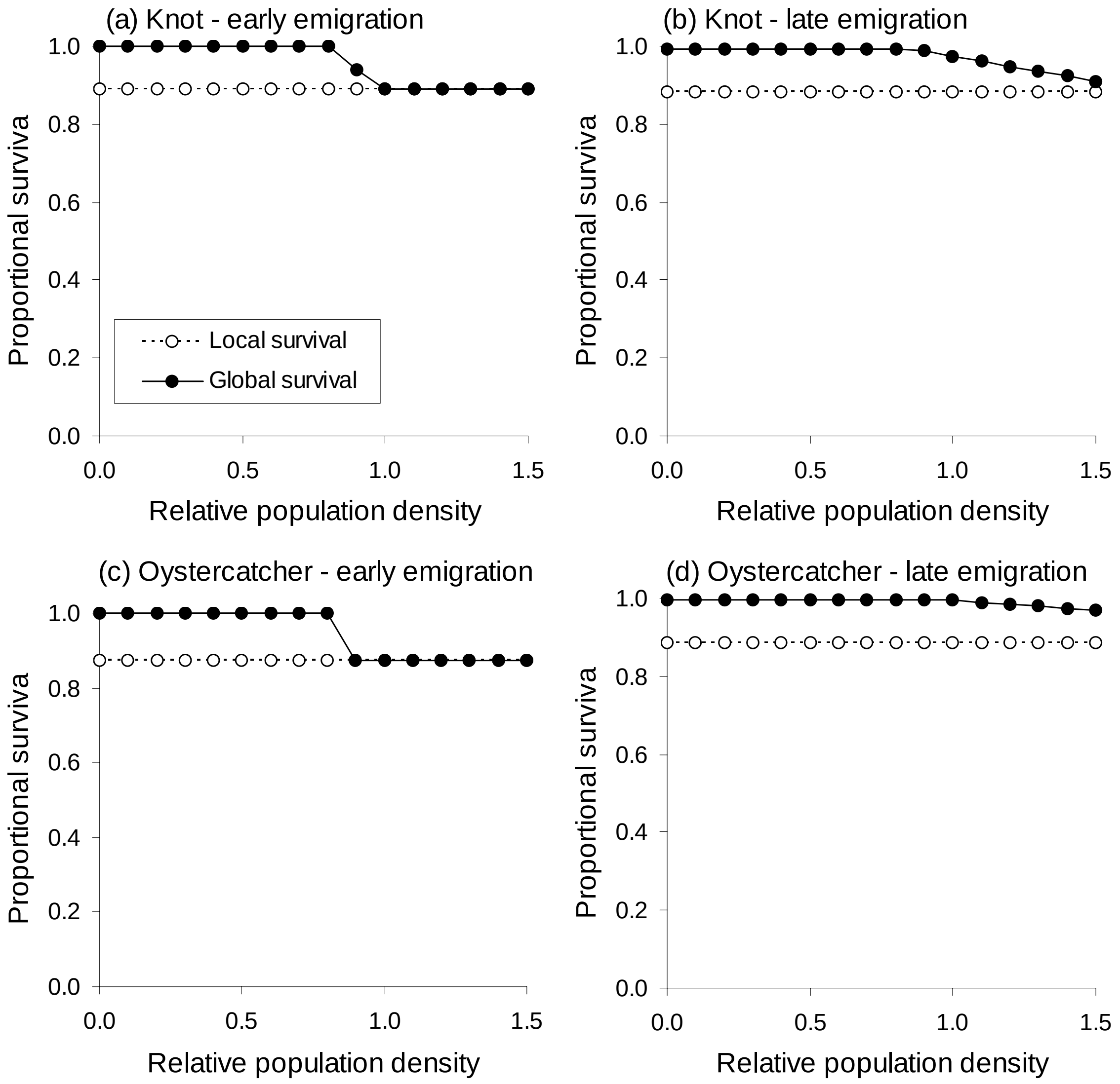


Figure 9.4 The effect of the density of birds on the focal and buffer sites on local and global survival of knots (a, b) and oystercatchers (c, d). Individuals either emigrated from the focal site at the start (a, c) or near the end (b, d) of winter. Both sites were of the same size and contained the same amount of food at the start of winter. Birds took one hour to emigrate from the focal to the buffer site.

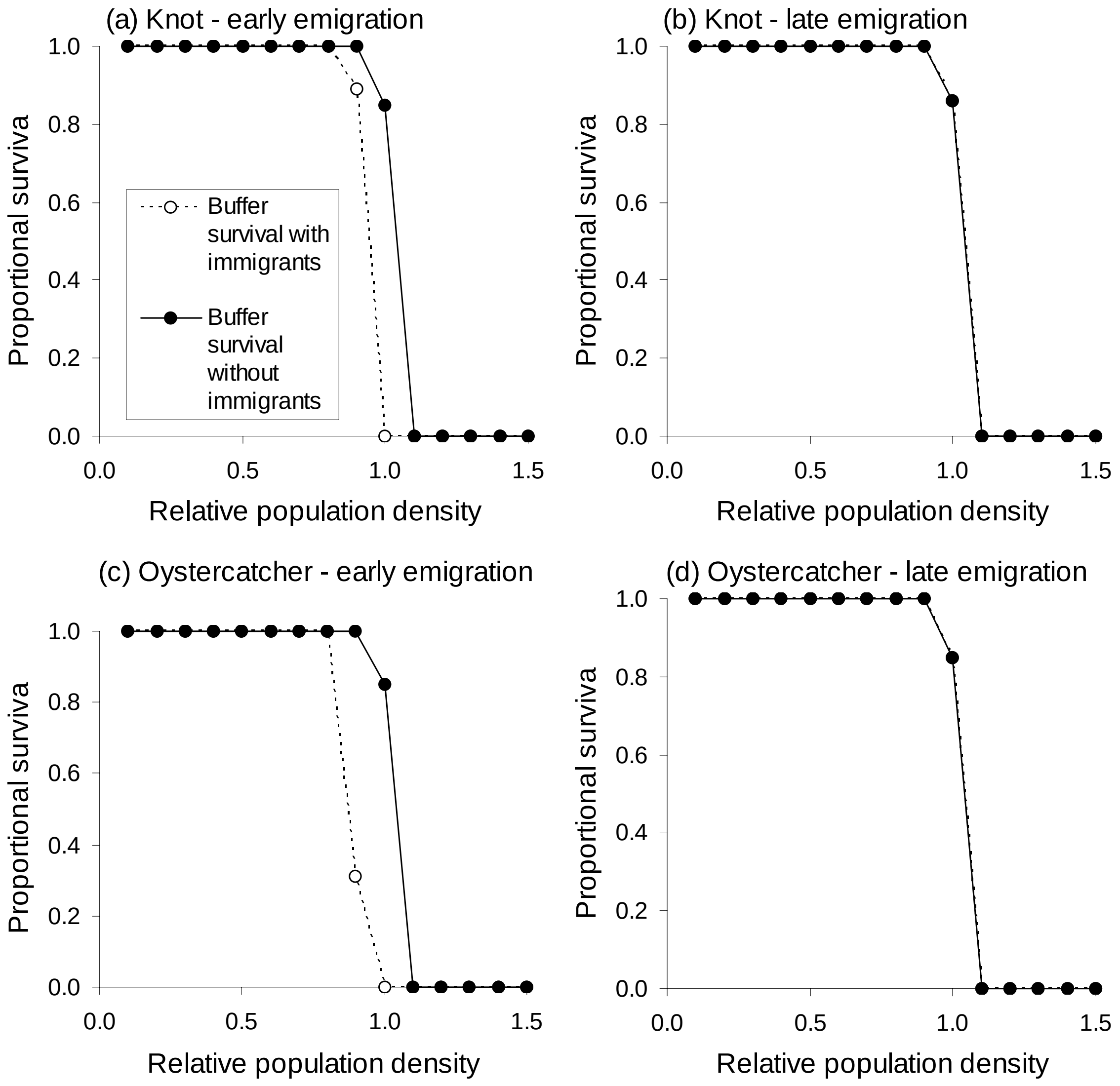


Figure 9.5 The effect of immigrants from the focal site on the survival rates of knots (a, b) and oystercatchers (c, d) initially starting on the buffer site. Individuals either emigrated from the focal site at the start (a, c) or near the end (b, d) of winter. The relationships show the survival rates of birds starting on the buffer site in the absence (solid circles) or presence (open circles) of emigrants from the focal site. Both sites were of the same size and contained the same amount of food at the start of winter. Birds took one hour to emigrate from the focal to the buffer site.

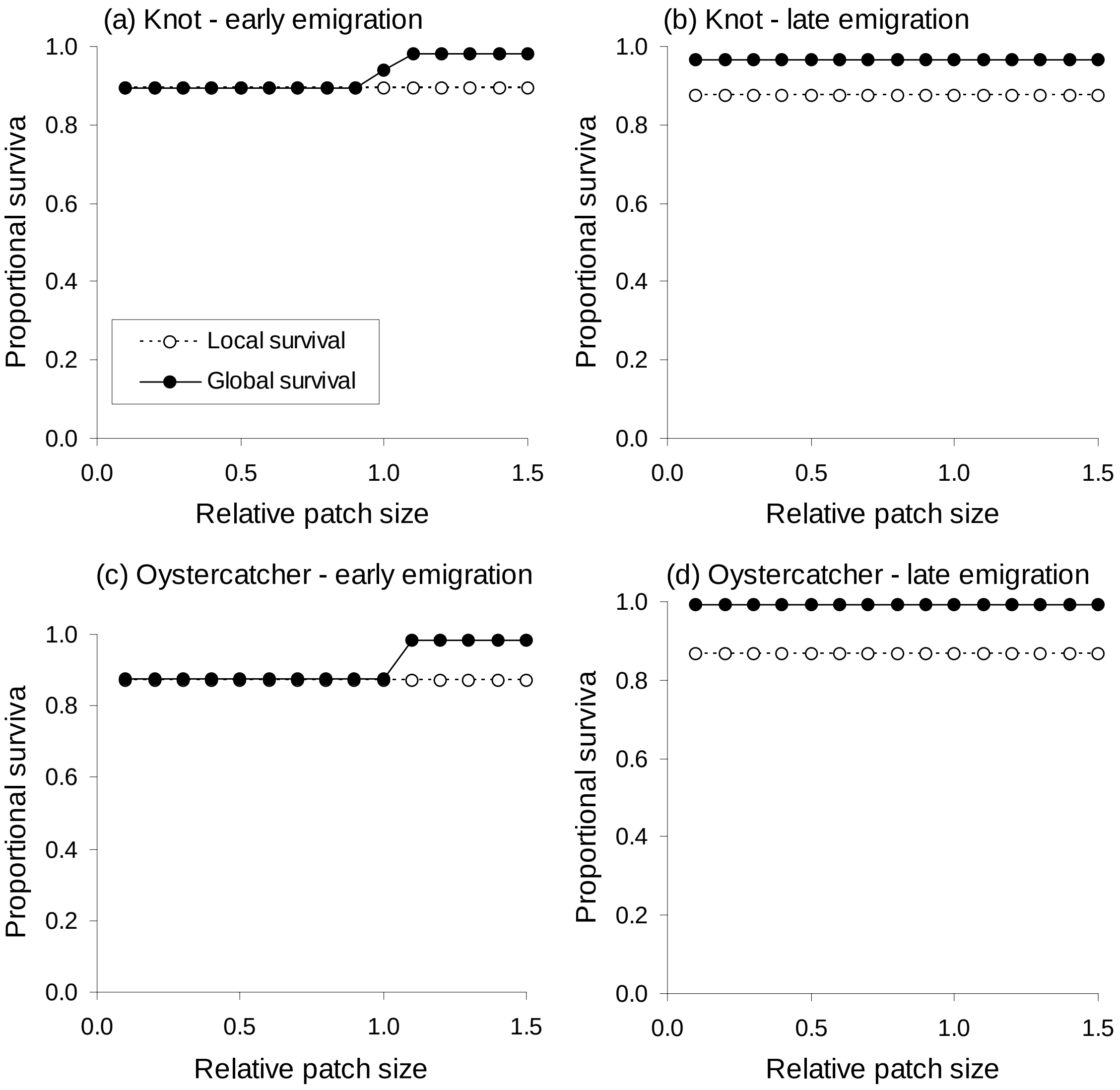


Figure 9.6 The effect of the relative size of the focal and buffer sites on local and global survival of knots (a, b) and oystercatchers (c, d). Individuals either emigrated from the focal site at the start (a, c) or near the end (b, d) of winter. Both sites contained the same density of birds and food at the start of winter. Birds took one hour to emigrate from the focal to the buffer site.

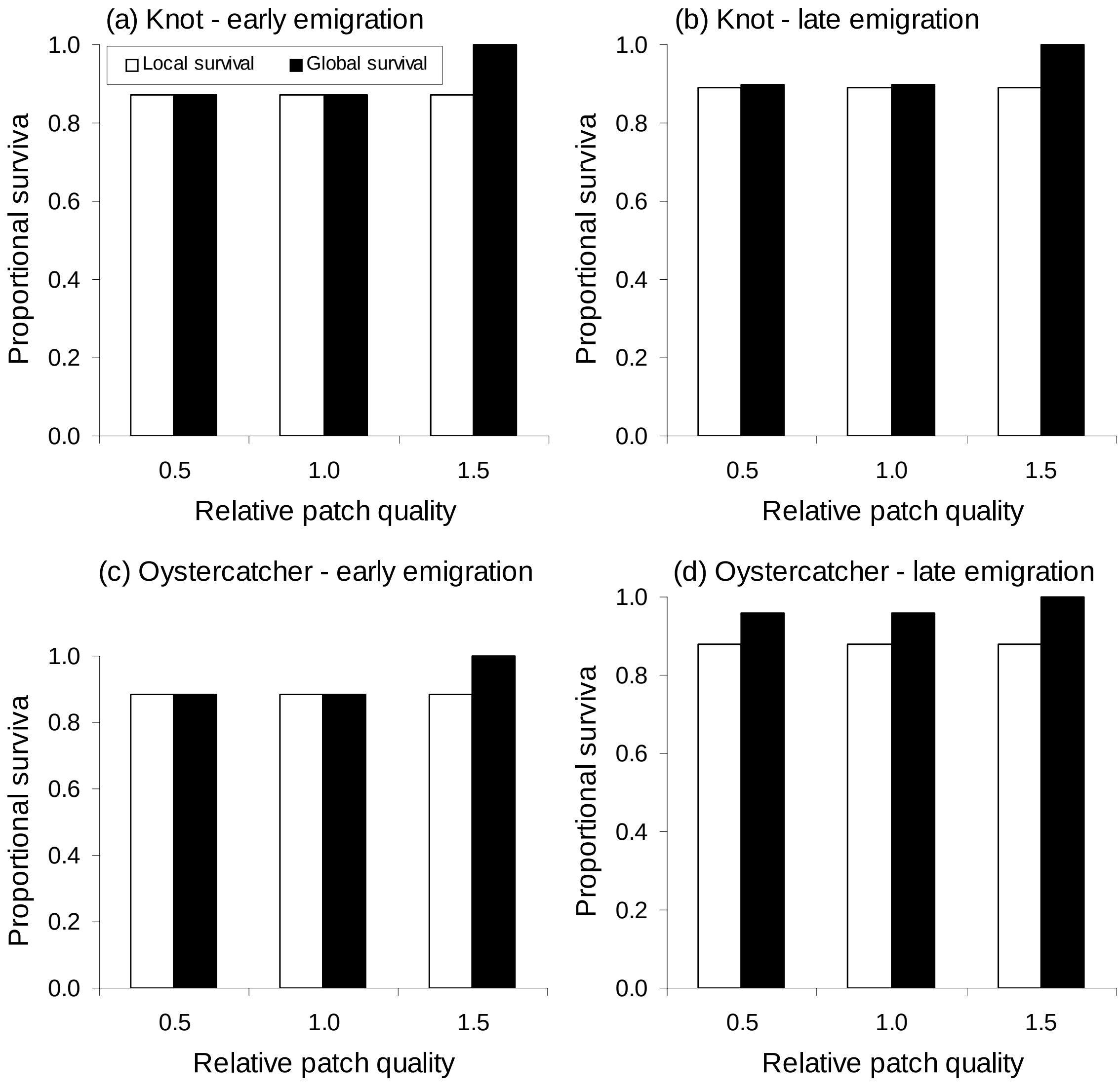


Figure 9.7 The effect of the relative quality (food biomass density) of the focal and buffer sites on local and global survival of knots (a, b) and oystercatchers (c, d). Individuals either emigrated from the focal site at the start (a, c) or near the end (b, d) of winter. Both sites were of the same area and contained the same density of birds at the start of winter. Birds took one hour to emigrate from the focal to the buffer site.

9.4 Summary

This chapter compared single and multi-site models developed for knot and oystercatcher feeding on bivalves. General model predictions were the same for both species and are summarised as follows.

Local survival on the focal patch was the same in all simulations because it was assumed that no birds emigrated from the buffer site to the focal site. The multi-site model predicted that global survival (of birds starting on a focal site) was higher than local survival when:

- Sites were close enough together so that the buffer site could be reached by birds emigrating from the focal site.
- The buffer site could support the emigrating birds because it (i) had a lower initial density of birds, (ii) was larger than the focal site and / or (iii) had a higher food density than the focal site.

The survival of birds initially starting on the buffer site was decreased when:

- The buffer site could not support the resident and immigrating birds because it (i) had a high initial density of birds and / or (ii) was smaller than the focal site.

The results show that the presence of a buffer site can either have no effect on global survival or increase global survival of birds starting on a focal site. They also show that the influx of immigrants to a buffer site can either have no effect or decrease the survival of birds initially starting on the buffer site.

9.5 References

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10 MULTI-SITE MODELS: BRENT GEESE

Richard Caldow, Hervé Fritz, Preben Clausen, Bart Ebbinge and Richard Stillman

10.1 Introduction

This chapter describes the work conducted in work package 5 of the project. The objective of this work package was to parameterize and test a multi-site, year-round model for one exemplary, herbivorous wildfowl species, the brent goose, which is currently the focus of much debate as to how best to limit its conflict with various human activities, including agriculture, while protecting its most important sites. As explained in Chapter 1 the model MORPH was used in this work package. This model has been developed during the project, and replaces the multi-site model which existed at the start of the project, and which was originally planned to be used during the project. The model was parameterised using a combination of literature review within each of the partner countries and new fieldwork, conducted largely in France.

10.2 Study region

Dark-bellied brent geese *Branta bernicla bernicla* (hereafter referred to as brent geese) breed along the Arctic coasts of the Yamal, Gydan and Taimyr peninsulas and on the islands of the Kara Sea including Severnaya Zemlya (van Nugteren 1997). They migrate to and from these breeding grounds along the northern coast of Siberia and through the Baltic Sea. They spend the late-autumn - late spring wholly in western Europe. Their ‘wintering’ distribution extends along the coast of mainland Europe from the Danish Wadden Sea in the north to the Bassin d’Arcachon in south-west France, and also includes many sites on the eastern and southern coasts of England (Fig. 10.1). The modelling exercise described here deals only with the habitat selection, between site distribution, and survival of brent geese between October and May i.e. while in their western European ‘wintering’ grounds.

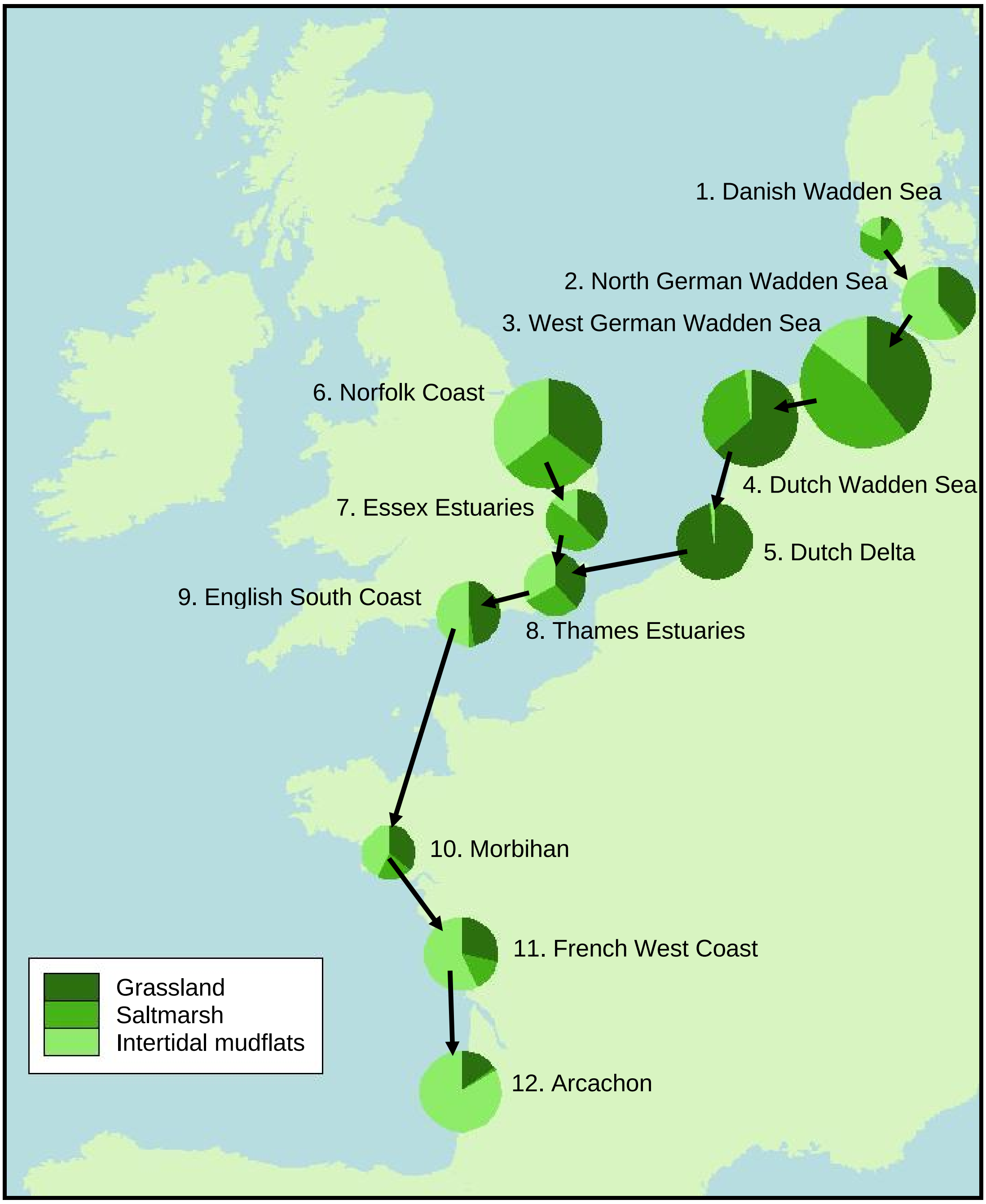


Figure 10.1 Distribution of the 'super-sites' used in the multi-site brent goose model. The area of each symbol is proportional to the combined area of grassland, saltmarsh and vegetated mudflats at a site, and the area of each segment is proportional to the relative area of each habitat within a site. The arrows show the routes brent geese are assumed to follow when forced to leave a site during winter. In spring geese are assumed to migrate directly from their wintering site to sites 1 to 5.

10.3 Issues

10.3.1 CHANGE OF AGRICULTURAL PRACTICES

Until the second half of the 20th century brent geese foraged entirely on natural, intertidal and saltmarsh resources during their stay in western Europe. Following the Europe wide die-back of *Zostera spp.* in the 1930s brent geese have exhibited an increasing tendency to feed on farmland habitats, principally grasslands but also arable crops. A large proportion of the population now rely on such habitats between November and March. In spite of this fact, large areas of farmland habitat utilised by brent geese in England still fall outside the boundaries of coastal Special Protection Areas. The usage of agricultural land by brent geese depends heavily upon the way in which it is managed e.g. grazing intensity and rates of fertiliser application, because this influences the quantity and quality of the vegetation available to them. Abandonment of management and more subtle changes to the way in which land is managed (e.g. following revisions to the CAP) may, therefore, have affects on brent geese. Thus, the model is used to explore the consequences of reducing the areas of both salt marsh habitats (as the most suitable marshes tend to be those that are grazed by livestock) and of suitable farmland habitat. Simulations in which geese are prevented from feeding on farmland in the England, the Netherlands, Germany and Denmark (geese in France currently make very little use of such resources) reveal how the survival of the geese would be affected if they were restricted solely to their natural intertidal and salt marsh habitats.

10.3.2 LOSS OF INTERTIDAL RESOURCES

Amongst all geese, the brent goose is the most reliant upon food resources that grow intertidally namely *Zostera spp.* and green algae e.g. *Enteromorpha* spp and *Ulva* spp.. These are the main traditional foods of brent geese in winter. *Zostera* spp. suffered a wide-spread dieback in the 1930's due, it is thought, to fungal infection. Recovery from this die-back is still far for complete. Although the die-back in the 1930s was particularly severe the fungal agent is still present in many populations and it is not inconceivable that another mass mortality of *Zostera* spp. could occur. Thus, the model is used to explore the consequences of the gradual and ultimately complete loss of traditional intertidal resources at a Europe-wide scale. These simulations reveal the importance of these traditional intertidal food resources for a population of geese that now routinely feeds on other resources for most of the winter.

10.3.3 DISTURBANCE

Brent geese, as herbivores, have to feed for a large proportion of the day in order to meet their daily energy intake requirements. Thus, they are potentially very susceptible to disturbance that prevents them from feeding and necessitates additional energetic expenditure associated with flying from sources of disturbance. Most forms of human disturbance occur during daylight, and birds are able to compensate for excessive daytime disturbance by feeding undisturbed at night. Thus, the model is used to explore the consequences of varying frequencies of daytime disturbance in farmland, saltmarsh and intertidal habitats.

10.3.4 HUNTING

In the past, brent geese were a major quarry species throughout western Europe. However, since the 1950s each of the key western European countries has imposed hunting bans which in most countries are complete. In some countries there are nonetheless conditions under which licences to shoot brent geese can be issued to prevent severe damage to agricultural crops. The last European country to introduce a ban on hunting brent geese (in 1971) was Denmark. Prior to then, on average c2200 geese were shot annually in Denmark, the majority of which were dark-bellied birds. As the population of this race has increased dramatically since 1971 there has been increasing pressure to re-instate hunting of brent geese in Denmark. Accordingly, the consequences of renewed hunting in Denmark are explored.

10.4 Data collection

The majority of the data used to parameterise the model, and to validate it, were gathered from reviews of published and unpublished material within the UK, Denmark, Netherlands, Germany, and France. Some additional material was derived from Irish and American studies.

10.4.1 SITES

National datasets of brent goose counts within each of the partner countries were collated. Data from the early-mid 1990s were used to determine the important sites to be retained in the model.

10.4.2 PATCHES

Each of the partners was responsible for sourcing information from within their own country regarding the recent presence/absence and extent (hectares) of the principal habitats exploited by brent geese i.e. farmland, saltmarsh, *Zostera* beds and green algal beds. In spite of the conservation status of brent geese, such data were seldom held by a single national body. Thus, collation of these data required a wide variety of sources to be explored. In England some 49 different offices/organisations were contacted in order to source the necessary information. In addition, new surveys of the *Zostera* beds in the Danish Wadden Sea were conducted.

10.4.3 RESOURCES

Data concerning the biomass density of the plants in each of the principal habitats were collated from the same sources described previously. Additional work was conducted at French sites to measure the biomass densities of intertidal resources through the over-wintering period.

10.4.4 COMPONENTS

Two resource components which birds may consider in formulating their patch choices are considered in the model i.e. energy and nitrogen. Data concerning the seasonal variation in the nutritional quality of the plants in the various principal habitats were collated from the literature as were data concerning the efficiency with which these components can be digested from various plant types by the geese.

10.4.5 FORAGERS

Brent geese have been counted regularly throughout the winter and spring in all relevant European countries over many years. Some of these data were collated by each of the partners and used to define the sites for inclusion in the model, to establish the initial distribution of birds between sites, to define the total population used in the model, and to validate the model’s predictions of mid-winter and late spring distribution.

10.5 Data analysis

10.5.1 SITES

In the early-mid 1990s brent geese were counted at about 140 main sites in western Europe. Analyses of these data revealed that in each month between October and May, 75% or more of the population was held across only 36 sites. Of these, two were only important in one month, were geographically isolated from the others in the country concerned, and at most held <2% of the population. This left 34 discrete sites (2 in Denmark, 7 in Germany, 8 in the Netherlands, 12 in England and 5 in France) to be considered in the model as holding the bulk of the population in every month. For the purposes of running the model these 34 sites were amalgamated on the basis of geographic proximity, similarity of goose seasonal usage patterns, and similarity of tidal characteristics into 12 'super-sites' (Fig. 10.1).

10.5.2 PATCHES

Across the whole of western Europe, the habitats exploited by brent geese comprise arable crops, grasslands, high saltmarsh, low saltmarsh, pioneer saltmarsh, intertidal algal beds, intertidal *Zostera* beds, sub tidal *Zostera* beds and sub tidal *Ruppia* beds. Data on the extent of all of these were collated. Due to the lack of a functional response for brent geese feeding on arable crops this habitat could not be modelled explicitly. Thus, farmland in the model is considered to consist purely of grassland but to include the area of arable land utilised by the birds at each 'super-site' in the total farmland area at each. Due to a lack of a functional response for *Salicornia* feeding birds, pioneer saltmarsh, where *Salicornia* is a major component of the resources available, could also not be modelled explicitly. For, simplicity high and mid-level salt marshes were combined into one habitat and their areas summed at each site. The sizes of intertidal patches were calculated by summing the extent of intertidal *Zostera* beds and intertidal algal beds at each super-site. For simplicity, the sub-tidal beds of *Zostera marina* at French sites were added to the intertidal resources at these sites. Due to the virtual absence of *Ruppia* throughout the sites considered in the model, the few patches of this habitat were excluded from the model. Thus, each super-site in the model comprised three patches representing, farmland, saltmarsh and intertidal habitats, the area of each having been derived by summing the areas of each habitat across each of its constituent sites.

10.5.3 RESOURCES

Farmland habitats were assumed to contain one resource i.e. grassland plant species (e.g. *Lolium perenne*, *Agrostis stolonifera*, *Poa spp*. etc.). Saltmarsh habitat was assumed to contain two principal resources i.e. halophytic plants (e.g. *Aster tripolium*, *Plantago maritima*, *Triglochin maritima* and *Spergularia spp.*) and non-halophytic plants (e.g. *Puccinellia maritima*). Intertidal beds also contained two resources i.e. green algae (*Enteromorpha spp* and *Ulva spp*) and eelgrass (*Zostera spp.*). Thus, in the model the birds had access to five dietary resources. The dataset collating information on the seasonal variation in the biomass densities of these various plant species was examined to determine the early autumn values that were used to define the starting conditions in the model. Due to a lack of detailed data on all plant species in all countries it was necessary to apply average initial biomass densities across all 12 super-sites.

Whenever sufficient data were available, sequential values of plant biomass density (ideally derived from exclosure experiments to remove the effects of goose depletion) were analysed to yield daily proportionate survival rates of the vegetation between successive sampling occasions. These values were regressed against date to yield equations predicting the seasonal changes in vegetation survival rates between October and May. These equations were used to incorporate non-goose induced changes to the biomass density of the birds' resources. Sufficient data were available to enable more than one survival function to be generated for each of the grassland, intertidal *Zostera* and algal resources. This allowed the geographic variation in the dynamics of these vegetation types to be included in the model.

10.5.4 COMPONENTS

The data collated concerning the energy density of each plant species was analysed to yield estimates of the energy density of each of the principal resources in the model. Due to a lack of geographic range in the dataset it was necessary, for each resource type, to apply an average energy density across all super-sites. Again due to a paucity of data it was not possible to estimate seasonal variation in the energy density of the various plant species at any site.

The data collated concerning the % nitrogen content of each plant species was analysed to yield estimates of the % nitrogen content of each of the principal resources in the model. In the case of pasture grasses, saltmarsh non-halophytes (i.e. *Puccinellia maritima*), green algae and *Zostera* there were sufficient data to estimate the seasonal variation in the % nitrogen content of these resources. However, due to a lack of both spatial and temporal variation in the dataset it was again necessary, for each resource, to apply either an average over-winter value or an average seasonal equation across all super-sites.

Although water is not a resource component from which foraging geese gain any direct benefit, the model included a measure of the water content of the various resources because the gut capacity of the birds is dictated by the volume of fresh vegetation that they ingest, not be the volume of dry matter from which they extract energy and nutrients. Data collated concerning the % dry matter of various plant species was examined to yield the average % dry matter for each of the resources in the model. Due to a lack of data the average values for each resource had to be assumed to remain constant throughout the winter and to be the same across all 12 super sites.

10.5.5 FORAGERS

The brent goose population has varied widely in size over the last half century. The population increased markedly from c 34,000 in 1971 to reach a peak of c 314,000 in 1991. Since then the population has begun to decline (Ebbinge *et al*. 2002). The average population size over the last twenty years is around 230,000 and this was chosen as a representative population size with which to run the model. Count data from the early-mid 1990s were analysed to establish the autumn arrival pattern at each of the 12 super-sites and to establish the stable mid-winter distribution of birds under current circumstances. This information was used to control the arrival time and winter destination of each bird in the model. In spring, all brent geese congregate along the Dutch, German and Danish North Sea coasts. The count data were analysed to determine the distribution of birds between these areas in the spring and thus to determine the target spring staging site for each bird in the model.

10.6 Model variables

10.6.1 GLOBAL

Only two global variables were used in the model: Day and Time. Day 1 was taken to be the 1st of October and a model simulation covered the period from then until 31st May by when all brent geese have departed from western Europe on spring migration to the Arctic. Each day was divided into 24 one hour time steps. Other variables that were treated as global variables in the models described in Chapters 6 7 and 8 e.g. day length, were treated here as patch variables due to the geographic variation in these parameters at the scale of western Europe addressed here. These are discussed below.

10.6.2 PATCHES

There were a total of 36 patches in the model (12 super-sites each containing three patches).

The location of each patch in the model was determined from the coordinates of the super-site to which it belonged. The latter were derived from the literature review. Site locations were used to determine the distance required to fly between each site.

The area of each model patch was derived as described above and can be calculated from the data presented in Table 10.1 which details (for completeness) the values for all of the principal habitat types at each of the 36 real world 'sites'

The annual maximum and minimum day length (sunrise to sunset) at each site was derived from data held on the website http://aa.usno.navy.mil/cgi-bin/aa_rstablew.pl. Using a simple cosine function, these maximum and minimum values were used to calculate the duration of daylight on each site on each day. Assuming, for simplicity, symmetry of sunrise and sunset around noon, predicted day length was used to ascribe each time step to occur either in darkness or daylight at each site.

Hourly tidal heights were obtained for a large number of tidal stations throughout Europe using the TideWizard software (Marine Computing International 2000-2002). Predicted heights were averaged across a number of stations for each super-site. In order to control the tidal availability of intertidal and saltmarsh resources the height of these two patches on each site was set equal to the site specific mean sea level and mean high water springs respectively. This ensured that on all sites, intertidal *Zostera* and algal beds were unavailable for half of the time and that saltmarsh patches were unavailable only over high water on above average spring tides. Farmland patches were assumed to be always available regardless of the tidal height.

Brent geese have been recorded feeding at night, but generally only on intertidal resources. Usage of terrestrial habitats at night is rare. The model, therefore, assumed that terrestrial patches are intrinsically less safe than intertidal patches at night and that provided that a bird is in good body condition it should not risk feeding in non-intertidal patches at night.

Table 10.1 Patch variables used in the multi-site goose model: Values given are the area (m^2) of each of the principal habitats utilised by brent geese at each of the 36 key sites. Values for arable and grassland are combined in the model as 'farmland', areas of high and low saltmarsh are combined as 'saltmarsh' and areas of *Zostera* and green algae are combined as 'intertidal'. Areas for each site are summed to yield values for each of the 12 'super-sites' used in the model. Values shown in bold are 'true' values derived from the review exercise. Values in normal font represent cases of missing or imprecise values that have been replaced with 'estimates' based on the 'true' values at other sites.

Super-site	Site	arable	grassland	saltmarsh (high)	saltmarsh (low)	Zostera	green algae
Danish Wadden Sea	Wadden Sea, Knude-Grådyb, Fanø side (Keldsand, Trinden, Pendersand, Søjord)	0	**990000**	**5673621**	**2431552**	**1220000**	**0**
	Wadden Sea, Lister Dyb (Rømø syd, Jordsand, Koldby)	0	**1060000**	**4681184**	**2006222**	**2760000**	**0**
North German Wadden Sea	Foehr-Amrum-Sylt-south	7770000	4000000	**850000**	**1230000**	**15000000**	**3630000**
	Rodenaes/Sylt North	7770000	4000000	**0**	**350000**	**15000000**	**3630000**
West German Wadden Sea	Elb-Eider mainland	7770000	4000000	**11840000**	**6390000**	**0**	**3630000**
	Norden-Bremerhaven mainland	7770000	**20320000**	**4580000**	**15730000**	**1700000**	**0**
	Norderney-Mellum	7770000	**6460000**	**6390000**	**6360000**	**1700000**	**0**
	Nordstrander Bucht Halligen	7770000	4000000	**6540000**	**1810000**	**15000000**	**3630000**
	Nordstrander Bucht mainland shore	7770000	4000000	**10620000**	**20470000**	**0**	**3630000**
Dutch Wadden Sea	Ameland	7770000	**9400000**	**3450000**	**370000**	**0**	**0**
	Frisian coast	7770000	**0**	**3030000**	**8500000**	**0**	**0**
	Groningen coast	7770000	4000000	**5450000**	**4180000**	**1130000**	**0**
	Terschelling	7770000	**8650000**	**5860000**	**3020000**	**190000**	**0**
	Texel	7770000	**5000000**	**2030000**	**770000**	**0**	**0**
Dutch Delta	Grevelingen e.o. incl.Philipsland, Oosterschelde-Noord en oostdeel Schouwen Duiveland	**25000000**	4000000	**0**	**0**	**130000**	**0**
	Oosterschelde oostdeel	**18000000**	**1150000**	**70000**	**0**	**640000**	**0**
	Oosterschelde westdeel (incl. Prunjepolder en ZW-Schouwen)	**10000000**	**7650000**	**220000**	**0**	**180000**	**0**
Norfolk Coast	North Norfolk Coast	**12570000**	**5820000**	**3960000**	**10780000**	**0**	**4410000**
	The Wash	**30030000**	**400000**	**1760000**	**23150000**	**13790000**	**30810000**
Essex Estuaries	Blackwater Estuary	**3380000**	**4780000**	**2540000**	**3490000**	**370000**	**3080000**
	River Colne	**750000**	**860000**	**2570000**	**3540000**	**20000**	**560000**
	Crouch & Roach Estuaries	**0**	**2850000**	**1140000**	**1570000**	**0**	**1410000**
	Hamford Water	**2320000**	**1170000**	**2300000**	**3170000**	**70000**	**670000**
Thames Estuaries	Medway Estuary	**920000**	**430000**	**3710000**	**5040000**	**230000**	**6830000**
	Thames Estuary	**10550000**	**4900000**	**1720000**	**2380000**	**5270000**	**2180000**
English South Coast	Chichister Harbour	**4320000**	**4150000**	**200000**	**0**	**380000**	**13200000**
	Langstone Harbour	**3180000**	**3060000**	**160000**	**0**	**200000**	**7730000**
	North West Solent	**260000**	**930000**	**350000**	**810000**	**50000**	**520000**
	Pagham Harbour	**2850000**	**2930000**	**60000**	**0**	**0**	**1040000**
Morbihan	Golfe du Morbihan	7770000	4000000	4000000	3000000	**14000000**	**0**
French West Coast	Baie de Bourgneuf	7770000	500000	4000000	3000000	9200000	3000000
	Ile de Ré	7770000	**1000000**	**800000**	**600000**	1000000	**10000000**
	R.N. Moëze/Oléron & abords	500000	500000	**200000**	**150000**	10000000	2500000
Arcachon	Bassin d'Arcachon	7770000	4000000	**600000**	**450000**	**64000000**	**0**

10.6.3 RESOURCES

The initial biomass density of each resource on each patch is shown in Table 10.2 along with the equations describing the seasonal change in biomass density, independent of the grazing of the geese. In some cases an upper limit to resource biomass densities was specified to prevent unrealistic values being generated by the empirically derived survival functions.

Table 10.2 Resource variables used in the multi-site goose model

Resource	Sites	Initial biomass density (grams dry mass m^{-2})	Seasonal variation in probability of daily survival	Upper limit to biomass density (grams dry mass m^{-2})
Pasture grasses	1-6	78.8	Pds=0.9855+0.000144*Day	150.5
Pasture grasses	7-12	78.8	Pds=1.005-0.000011*Day	
Saltmarsh Halophytes	all	69.2	Pds=0.9408+0.000485*Day	69.2
Saltmarsh Non Halophytes	all	20.45	Pds=0.9897+0.000099*Day	
Intertidal Zostera	1-9	100.9	Pds=0.9958-0.000396*Day+0.000002*Day*Day	
Intertidal Zostera	10-12	100.9	Pds=0.9973-0.000347*Day+0.000002*Day*Day	
Green algae	1-5	27.5	Pds=0.9349+0.000259*Day	
Green algae	6-9	27.5	Pds=0.9798+0.000086*Day	
Green algae	10-12	27.5	Pds=1.004-0.000011*Day	77.34

10.6.4 COMPONENTS

Initial values of the energy density and % nitrogen content of each resource, and the equations describing the seasonal variation in the latter, are shown in Table 10.3. The percentage of each resource comprising dry matter is also shown in Table 10.3.

Table 10.3 Resource variables used in the multi-site goose model

Resource	Initial energy density (kJ gram dry $mass^{-1}$)	Initial %nitrogen content and/or equation to describe seasonal change	% dry matter
Pasture grasses	17.19	%N=2.007+0.01763*date-0.000061*date*date	20.4
Saltmarsh Halophytes	20.9	1.14	12.9
Saltmarsh Non Halophytes	15.5	%N=2.236-0.007373*date+0.000021*date*date	22.7
Intertidal Zostera	15.84	%N=3.777-0.03421*date+0.000090*date*date	16.5
Green algae	11.46	%N=4.254-0.02466*date+0.000065*date*date	11.3

10.6.5 FORAGERS

The model was run with 1000 ‘super-individuals’ each representing 230 real birds. Forager constants and variables are shown in Table 10.4. Forager constants were: feeding efficiency, dominance, arrival site, arrival day, departure site and departure day.

The feeding efficiency of each individual within the population was drawn from a normal distribution, with a mean of one and a standard deviation of 0.066. This latter value was derived from an analysis of the variation in the intake rates of colour-ringed brent geese feeding on *Zostera* on the Exe estuary (R. Caldow unpublished data). The dominance score for each individual was drawn from a uniform distribution between 0 and 1. The arrival site of each bird in the population was defined by an analysis of the real world count data which yielded estimates of the proportion of the total population that occurred in each super-site in early winter. The arrival day of birds initially visiting super-sites in Denmark, Germany and the Netherlands was drawn from a uniform distribution between 1st October and 15th October.

The arrival day of birds going to sites in England and France was drawn from a uniform distribution between 1st October and 15th November. This served to simulate the observed earlier peak in numbers in Danish, German and Dutch sites and the later increase in numbers in France and England. The departure site of each bird in the population was defined by an analysis of the real world count data which yielded estimates of the proportion of the total population that occurred in each super-site in April and May. This resulted in all birds in the model, as in reality, congregating in Dutch, German and Danish sites in the spring. The model did not allow birds to depart from the system before the end of the model run on 21st May.

Forager variables used were: the area available for feeding, time available for feeding per step and susceptibility to interference i.e. a reduction in intake rate due to increasing competitor density. The area available for feeding was defined as the patch area minus any area affected by disturbance. This area was then used to calculate the degree of interference from conspecifics if the resulting density of birds exceeded a critical threshold.

The rate at which birds were able to feed in a patch depended partly on the strength of interference from other competitors, but primarily upon the abundance of food in a patch. The influence of resource abundance in a patch on a bird's intake rate was calculated using a series of functional responses, one for each resource (Fig. 10.2, Table 10.4) that were derived from the data review. With the exception of the functional response for *Zostera* it was necessary to impose either upper or lower limits to the allowable intake rates to avoid the prediction of either negative intake rates at low biomass densities, or intakes rates in excess of the maximum observed at the highest biomass densities. This was necessary given the limited range of the empirical data from which the functional responses were derived, and the nature of the non-linear relationships used to describe the functional responses.

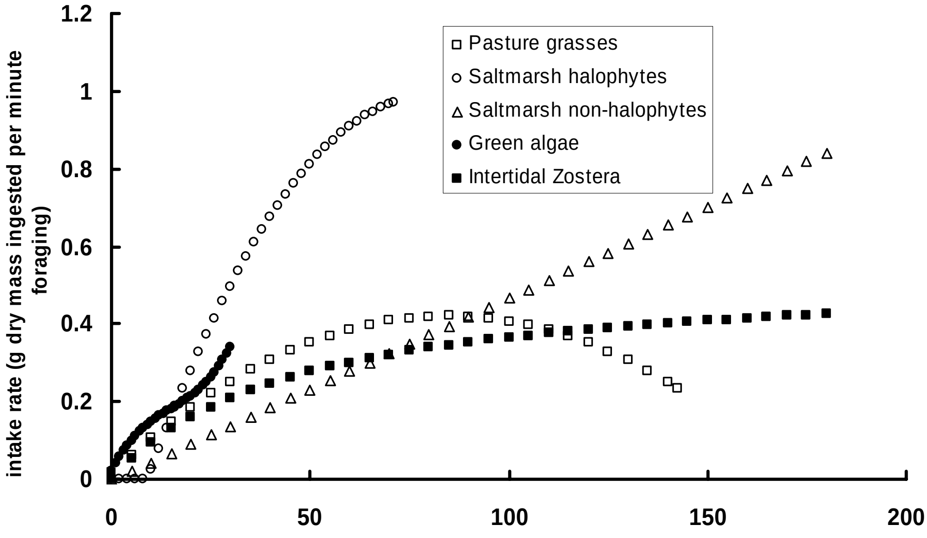


Figure 10.2 Functional responses for each of the 5 resources in the multi-site model of brent geese. Functions adapted from data sources: Pasture grasses – Tolsma 1998, Saltmarsh halophytes – J. Prop pers. comm., Saltmarsh non-halophytes – Bos 2002, Green algae – Rowcliffe *et al.* 1999, Zostera – R. Caldow unpubl. data.

The maximum amount of food that can be consumed by a bird over a short period of time such as an hourly time step (as used in the model) may be limited by a bird's gut processing rate and its crop capacity. This is especially true of herbivores that consume food of relatively low nutritional quality in comparison to carnivorous wading birds. This maximum limit was calculated on the basis of the gut capacity of brent geese and their rate of food processing. Because the limit to the amount of food eaten is dictated by the volume of fresh plant material ingested and because resources differ in their water content, the maximum amount of dry food matter that a goose could ingest per time step was allowed to differ between resources according to the proportion of dry material that different resources contain.

The quantity of energy and nitrogen assimilated from consumed food depended not only on the food's energy density and % nitrogen content (see above) but also on the efficiency with which geese digest organic matter in general and nitrogen in particular. The apparent digestibility of organic matter (ADOM) was taken as an indicator of the efficiency with which geese extract energy from their food. Values of ADOM for each resource were derived from the data review. In the case of 3 resources (i.e. farmland grasses and saltmarsh halophytes and non-halophytes) there were sufficient data to derive equations describing seasonal variation in the ADOM. For the other two resources a constant value had to be used throughout the year. Values for the apparent digestibility of nitrogen were only available for farmland grasses and saltmarsh plants. In both cases equations describing the seasonal variation in digestibility were derived. The equation relating to saltmarsh plants was also applied to algal and *Zostera* resources.

Assimilated energy was converted into increased mass by assuming that the efficiency of energy conversion and storage was 0.855 and that 33.4kJ of energy was stored in each g of storage tissues (Kersten & Piersma, 1987). It was assumed that geese have no nitrogen store *per se*, simply that their intake is used to meet their immediate requirements. As such, there was no value for conversion and storage of assimilated nitrogen. Birds were assumed to have a constant daily target body mass throughout the autumn-early spring period and an increasing target in late spring as the birds fatten in preparation for migration. The target values were derived from Ebbinge & Spaans (1995).

The rate at which geese metabolised energy while feeding and resting was taken to be the same and was derived from empirical measurements of the daily energy expenditure. This basic background rate of metabolism was allowed to be elevated in the model due to the extra energy costs associated with flight in response to disturbance events. The energetic cost incurred by geese due to increased flying time in response to a disturbance event was calculated using the following equation of Nudds & Bryant (2000):

$$C = 61.718tM^{0.7902} \tag{10.1}$$

Where C = energetic cost in J, t = duration of flight in seconds and M = mean body mass in kg. The duration of flight for an average flock member was derived from the average flight duration of brent geese following disturbance (69 secs) and the proportion of the flock that on average takes flight (57%). Body mass was taken to be the over-winter target mass (1.3kg).

The rate at which geese metabolised nitrogen was derived from one literature value and was assumed to be constant throughout the over-wintering period and to be the same while both feeding and resting.

The maximum range speed at which geese fly when moving between sites, and the rate at which they metabolise energy while doing so, were derived from Program 1 of Pennycuick (1989). Due to a lack of alternative information, nitrogen metabolism during flight was assumed to be the same as while feeding and resting

One source of forager mortality was included in all model simulations i.e. starvation. A forager died if it failed to maintain any fat reserves i.e. body mass ≤ starvation mass. The starvation mass was derived from the literature review.

In simulations in which the re-introduction of hunting in Demark was explored, another source of mortality was included i.e. being shot. The probability of being shot was applied only to the birds that occupied the Danish super-site. Probabilities were altered to simulate a range of annual bags between 0 and the entire Danish spring staging population.

Given that brent geese seldom feed on terrestrial habitats at night (or at least do so only very rarely), the model assumed that these habitats were inherently riskier at night than intertidal areas. Subsequently, geese in the model avoided terrestrial habitats at night unless they were close to starving (reserves ≤ 8% of total body mass), in which case they risked feeding within these habitats.

The model assumes that at a given point in time each bird has perfect knowledge of its potential fitness only on each of the patches on its current ‘super-site’. The model assumes that birds estimate their potential fitness to be 0 on any super-site other than the one it currently occupies. Thus, most birds most of the time simply stay on their current site. However, in order to enable birds to move between sites in the face of adverse circumstances the model assumes that at any point during the autumn and winter, prior to the onset of spring migration, a bird whose energy reserves fall below 8% of its total body mass will estimate that its potential fitness on any site to the south of its current site is higher site than its local fitness, and to be highest on the closest site to the south. Thus, in the winter, birds faced with starvation on their current site will move in a southerly direction in a series of short hops from one site to the next until they find a site on which their reserves increase again above the lower critical threshold of 8% of body mass where they will then settle. In early spring, the model assumes that birds whose body mass is less than 95% of their target mass estimate their potential fitness on any super-site other than the one it currently occupies to be 0. These birds will therefore not move. Birds whose body mass exceeds this threshold are assumed to be prepared for return migration to the spring staging grounds in the Netherlands, Germany and Denmark. Once this condition is met, they assess their fitness to be higher there than on their current site. This assessment then triggers their departure from their current site en route to their spring staging site.

Table 10.4 Forager variables used in multi-site goose model

variable	value/ function
Individual characteristics	
Foraging efficiency mean (st. dev)	1 (0.066)
Dominance scores (range)	0 - 1
Interference	
Aggregation factor	10
Threshold density (geese ha^{-1})	225
Strength of interference (as function of proportion of birds (P) with lower dominnace than self on current patch)	m=-0.12+0.12*P
Functional responses (g dry mass ingested minute active^{-1} as a function of biomass density of live vegetation (g dry mass m^{-2})	
Pasture grasses (if biomass < 142.5 gdm m^{-2})	0.01692+0.009502*Biomass-0.000056*Biomass^{2}
Pasture grasses (if biomass > 142.5 gdm m^{-2})	0.234
Saltmarsh halophytes (if biomass < 9.2 gdm m^{-2})	0
Saltmarsh halophytes (if 9.2 gdm m^{-2} < biomass < 71 gdm m^{-2})	-0.2736+0.0317*Biomass-0.0002*Biomass^{2}
Saltmarsh halophytes (if biomass > 71 gdm m^{-2})	0.9936
Saltmarsh non-halophytes (if biomass < 0.96 gdm m^{-2})	0
Saltmarsh non-halophytes (if 0.96 gdm m^{-2} < biomass < 180 gdm m^{-2})	-0.0045+0.0047*Biomass
Saltmarsh non-halophytes (if biomass > 180 gdm m^{-2})	0.84
Intertidal Zostera	(0.5363*Biomass)/(46.9692+Biomass)
Green algae (if biomass < 30.0 gdm m^{-2})	0.0205+0.0197*Biomass-0.0009*Biomass^{2}+0.00002*Biomass^{3}
Green algae (if biomass > 30.0 gdm m^{-2})	0.357
Maximum rate of consumption (g dry mass hour^{-1})	
Pasture grasses	(100+150)*0.204
Saltmarsh halophytes	(100+150)*0.13
Saltmarsh non-halophytes	(100+150)*0.23
Green algae	(100+150)*0.113
Intertidal Zostera	(100+150)*0.165

Table 10.4 continued

variable	value/ function
Apparent digestibility of organic matter	
Pasture grasses	0.357
Saltmarsh halophytes	$0.5331-0.002018*Day+0.000007*Day^2$
Saltmarsh non-halophytes	$0.5331-0.002018*Day+0.000007*Day^2$
Green algae	0.663
Intertidal Zostera	0.477
Efficiency of convserion of assimilated energy to stored energy	0.855
Apparent digestibility of nitrogen	
Pasture grasses	0.4227+0.000951*Day
Saltmarsh halophytes	0.5832+0.000754*Day
Saltmarsh non-halophytes	0.5832+0.000754*Day
Green algae	0.5832+0.000754*Day
Intertidal Zostera	0.5832+0.000754*Day
Energy density of body reserves (kJ g^{-1})	33.4
Daily Energy Expenditure (kJ day^{-1})	830
Daily nitrogen requirements (g)	2.72g kg body $mass^{-1}$
Rate of energy expenditure while flying at V_{mr} (j s^{-1})	100
Rate of nitrogen usage while flying at V_{mr} (g day^{-1})	2.72g kg body $mass^{-1}$
Speed of flight (km hr^{-1}) when flying between sites at V_{mr}	66.24
Starvation mass (g)	1045
Mean arrival mass (g)	1300
Target mass (g) (if day < 227)	1300
Target mass (g) (if day > 227)	1300+((400/40)*(Day-227))

10.7 Results

10.7.1 MODEL CALIBRATION

No calibration procedure was conducted with the multi-site goose model.

10.7.2 MODEL VALIDATION

10.7.2.1 Vegetation biomass densities

Although of no direct interest as model output, it was necessary to establish whether the vegetation dynamics, as described in the model, yielded realistic seasonal patterns in plant biomass densities. This was a necessary first step in model validation given that when daily vegetation survival rates exceed 1 i.e. there is net positive productivity, even a linear increase in these values with time can yield an exponential increase in biomass. The predictions of quadratic functions between daily survival rate and date (as used in several cases) are even more sensitive to the precise values for the coefficients used.

The starting values for resource biomass densities were set to be the same on all 12 sites but, where possible and appropriate, differing plant dynamic equations were applied to different sites (see Table 10.2). The resulting seasonal variation in resource biomass densities are shown in each of the three principal model regions in Fig. 10.3. Although in many instances the predicted biomass densities at the end of the model run i.e. in late May exceeded the initial densities, in no case did any resource density reach unrealistically high values. In all three regions, pasture grasses showed the greatest increase in biomass between autumn and spring. In the north-eastern sites this increase followed an initial period of loss until late winter but resulted from a more or less steady growth throughout the modelled period in England and France. *Zostera* biomass declined markedly in autumn in all regions, but to a lesser extent in France than elsewhere, before increasing again in mid-late spring. Green algal biomass declined to near zero by mid-winter in the north eastern sites. In contrast in English sites it declined more much more slowly while in France algal biomass remained more or less constant throughout the model run. Saltmarsh halophytes declined markedly in biomass in late autumn-early winter to reach very low values before increasing again markedly in mid-Spring. Saltmarsh non-halophytes exhibited a similar but much less pronounced seasonal pattern in biomass density. All of these patterns are more or less consistent with the observed seasonal variation in plant biomass densities from which the daily survival rate functions in the model were derived, and suggest that model's vegetation dynamics are not unrealistic.

10.7.2.2 Over-winter survival

Based on an analysis of re-sightings of colour-ringed brent geese Ebbinge (1992) calculated that between 1973 and 1989 the mean annual survival of adult brent geese was 84%. Ebbinge *et al.* (2002) re-calculated annual survival between 1973 and 1997 to be 85%. Based on an analysis of population count data, Ebbinge *et al.* (2002) estimated that between 1955 and 1997 the average survival during the non-reproductive season was 85%. However, none of these figures refer solely to survival during the over-wintering period of interest for the purpose of model validation. The first two figures are annual values and the last includes the period of autumn migration from the arctic breeding grounds when much mortality may occur outside western Europe. Moreover, the latter figure spans over 40 years and includes the period between 1955 and 1972 when brent geese were still widely hunted during their over-wintering stay in Europe. Thus, there is as yet no precise estimate of the over-winter survival rate of dark-bellied brent geese between October and May in the absence of hunting with which to compare model output. Clausen *et al.* (2001) calculated that the mean annual survival of east Atlantic pale bellied brent geese *Branta hrota* between 1991 and 1999 was 87%. A breakdown of this annual figure into values for each of four separate seasons yielded an estimate for survival between October and May of 95-96% i.e. 4-5% overwinter mortality. However, this population of geese winters only in northern Denmark and north-eastern England and must therefore contend with considerably colder winter conditions than dark-bellied brent geese, many of which winter in south-western France. Thus, the overwinter survival of dark-bellied brent geese is likely to lie somewhere between 100% and 96% under current circumstances.

The model predicted 100% overwinter survival under current circumstances (Fig. 10.4). This is unlikely to be far from the true value. However, a prediction of 100% survival is not a powerful model validation test. It does not indicate the ease with which birds are surviving. Conditions in the model may be far too easy for the birds. It is thus, necessary to examine other model outputs to establish whether the birds are behaving as expected (see below).

10.7.2.3 Population distribution

The initial distribution of birds between the 12 super-sites in the model was pre-determined by an analysis of the count data in order to ensure that the overall population distribution matched that observed at least in the early winter i.e. October/November. The final destination of the birds in spring in the model was also pre-determined from an analysis of the count data. However, from mid-November onwards the model, if incorrectly parameterised, could easily predict large scale between site movements and changes in distribution between countries that do not match those observed in reality. From early November onwards, the model could get the distribution of birds wholly incorrect. In fact, the model's predicted seasonal variation in the distribution of geese between countries is broadly in agreement with that observed (Figs. 10.5 & 10.6).

10.7.2.4 Seasonal variation in resource usage

Brent geese exhibit pronounced seasonal variations in their usage of different resources. In general, brent geese on their arrival in autumn feed solely on intertidal resources, principally *Zostera* and green algae. Where *Zostera* is abundant this will be used in preference to green algae. In the absence of abundant *Zostera* the birds' exploit green algae on their arrival. By mid-late November *Zostera* usage declines and birds exhibit an increasing use of green algae. From early December onwards *Zostera* is little used. An exception to this is in some French sites, most notably the Bassin d'Arcachon where the geese feed on *Zostera* throughout the winter. Throughout most of their wintering range brent geese shift by early winter from intertidal resources on mudflats to more terrestrial habitats including, in some places, saltmarsh but in most cases to farmland habitats including grassland and arable land. The bulk of feeding then occurs on such inland habitats for the whole of the winter, although a small proportion of birds may continue to use saltmarsh throughout. In many French sites this shift inland does not occur and birds remain on intertidal habitats throughout the winter. From February onwards geese may exhibit a partial return from inland resources to salt marshes and intertidal mudflats to feed on green algae. This 'switch' continues throughout March and from then onwards the bulk of feeding occurs on saltmarsh habitats (again excepting French sites). Traditionally all brent geese staging in Danish, German and Dutch sites in April and May fed virtually exclusively on saltmarsh. However, with an increasing world population, spring feeding on grassland has become more prevalent (Ebbinge 1992).

In general terms these seasonal variations in resource usage are replicated by the model (Fig. 10.7). Intertidal *Zostera* and algal resources are predicted to be the most heavily used resources initially, and their importance is predicted to decline through the over-wintering period such that at all sites, except those in France, the majority of birds feed on other resources for the rest of the over wintering period. In French sites intertidal resources are predicted to be by far the most important resource throughout the birds' stay. In Denmark, Germany, the Netherlands and England, terrestrial farmland resources are predicted to be the most heavily utilised between November and March. Saltmarsh becomes the principal habitat used by birds once on their spring staging grounds in Denmark, Germany and the Netherlands. Intertidal resources are, however, predicted to be the secondary resource at this time rather than grassland. Thus, although the model does not match precisely the timing and magnitude of 'habitat switches' it correctly predicts the broad pattern of goose habitat usage under current circumstances.

10.7.2.5 Instantaneous intake rates and assimilation rates

The model utilises 5 resource-specific functional responses to define the instantaneous rate at which birds ingest dry plant matter while actively feeding (Fig. 10.2, Table 10.4). The intakes that the birds actually achieve in the model depend upon both the form of these functions and on the biomass densities of the resources. It is clear from Fig. 10.8 (a,c,e) that due to the seasonal decline in biomass densities of most resources, geese can only attain high intake rates from one or two resources. Grasslands yield high intake rates throughout the over-wintering period in all countries. Birds only attain their asymptotic intake rates on *Zostera* very early in the winter and never do so on green algae with the exception of birds on French sites. Saltmarsh plants only yield high intake rates in spring. These patterns are mirrored in the seasonal variation in the rate at which feeding geese assimilate ingested material (Fig. 10.8 b,d,f) although minor differences in apparent digestibility of the various resources (Table 10.4) alter the trends slightly. Assimilation rates on *Zostera* approach those attainable on grassland only in October and early November. Assimilation rates on *Zostera* drop to those attainable from green algae by mid-December except in France where the growth of the algae maintains achievable assimilation rates at a high level and comparable to that on grasslands. Predicted assimilation rates on saltmarsh resources, especially halophytes, are predicted to be extremely high in spring. These seasonal and regional patterns in predicted assimilation rates are largely responsible in the model for driving the seasonal and regional patterns of habitat usage described above.

10.7.2.6 Daily food consumption, feeding effort, daily energy assimilation rate and body mass

A number of estimates exist of the daily food consumption of wintering brent geese. Estimates range from 116 – 176 grams dry mass day^{-1} (Percival *et al.* 1996; Mathers *et al.* 1998) (Fig 10.9a). Errors in model parameterisation regarding either i) resource component densities or ii) component assimilation efficiencies could result in the model correctly predicting e.g. daily energy assimilation rates while predicting wholly incorrect quantities of food being ingested. However, the daily consumption rate of dry food matter predicted by the model falls precisely mid-way between the observed upper and lower limits for over-wintering birds. Daily consumption of dry matter is predicted to fall in spring (Fig 10.9a) while daily energy assimilation rate is predicted to rise (Fig 10.9c). This reflects the increasing digestibility of saltmarsh plants at this time (Table 10.4). Comparable empirical estimates were not located during the literature review process to establish the validity of this trend.

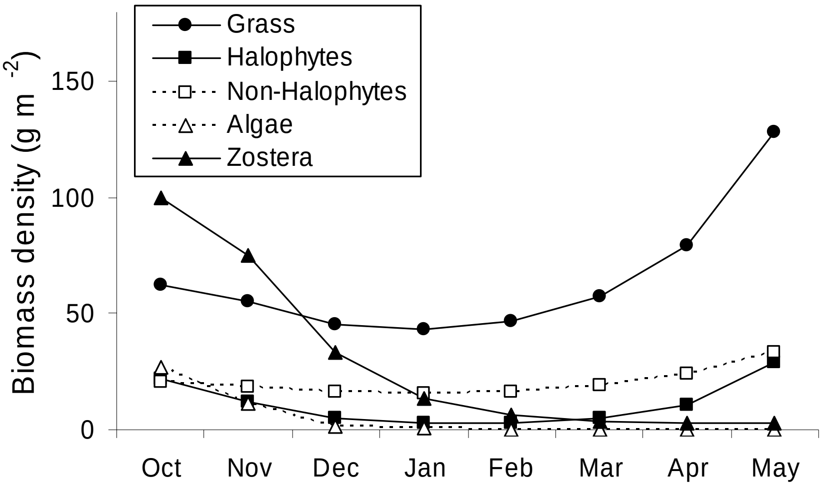
A key test of the model is whether it mimics the amount of time that geese have to devote to foraging each day in order to survive. This is a particularly significant test given that over-winter survival is predicted to be 100%. It is therefore essential to establish whether model birds have to 'work as hard' to survive as birds do in reality. If this were not the case, then predictions of the consequences of changes to the environment may be incorrect due to overly benign baseline conditions.

Empirical data reveal that brent geese in England spend 7.5 - 10.5 hours feeding each day (Fig 10.9b). Some studies indicate that foraging duration increases as food supplies diminish while other studies demonstrate no seasonal variation in total daytime feeding effort. The model predicted that brent geese do indeed spend between 7.5 hours and 10.5 hours feeding every day between October and March and that there is a general increase in feeding effort at least until late winter (Fig 10.9b). Feeding effort is predicted to decline in spring, presumably in response to the increasing biomass and digestibility of saltmarsh plants at that time. This clearly indicates that the birds in the model are behaving very much as real birds do.

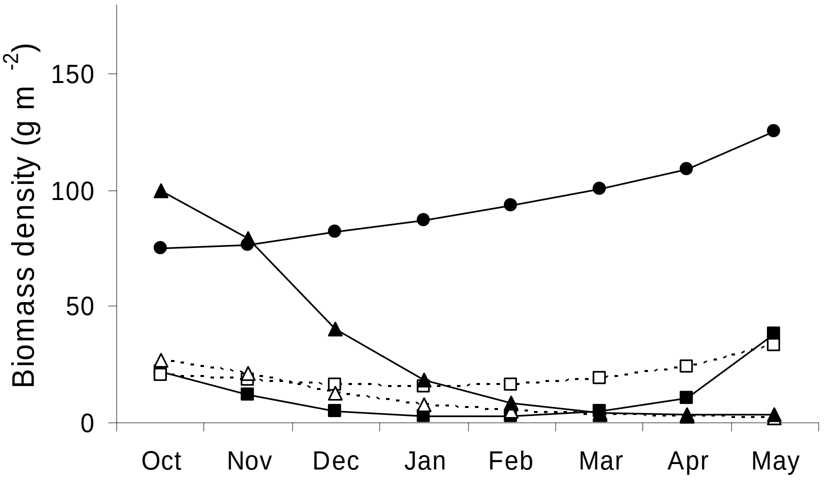
Brent geese need to assimilate between 829 and 840kJ day^{-1} in order to meet their daily energy requirements (Drent *et al.* 1978, Mathers *et al.* 2000). Accordingly a value of 830kJ day^{-1} was set as the daily metabolic rate of brent geese in the model (Fig. 10.9c). The rate at which brent geese assimilate energy has been estimated to be around 800kJ day^{-1} (Mathers *et al.* 1998, Percival & Evans 1996). The mean daily rate of assimilation predicted by the model matched this value very closely (Fig. 10.9c) except in the month of May when, due to spring fattening, the daily energy assimilation rate increased markedly above the baseline winter value. Thus, in order to maintain their body mass at 1300g throughout the winter, the birds' daily rate of energy assimilation was very close to that expected.

The body mass of adult brent geese is more or less constant between November and early April (with perhaps a slight dip in mid-late winter B. Ebbinge unupbl. data) but increases markedly during spring fattening between mid-April and late-May (Ebbinge & Spaans 1995). Daily body mass targets for model birds were set accordingly (Table 10.4). The average body mass at the mid-point of each month closely matched this target but occasionally fell below the target value (Fig 10.9d). This was most pronounced in January and February. This indicates that although all birds survived under baseline conditions, at least some of the population was struggling to maintain the average target body mass throughout mid-winter. The slight dip in average body mass of real brent geese in mid-winter suggests that this may indeed be the case in reality. This suggests that the lack of over-winter mortality in the model (Fig. 10.4) does not reflect an overly benign model world, and accordingly that predictions of the consequences of environmental deterioration (see below) are not unduly optimistic.

(a) Denmark, Germany and Netherlands



(b) England



(c) France

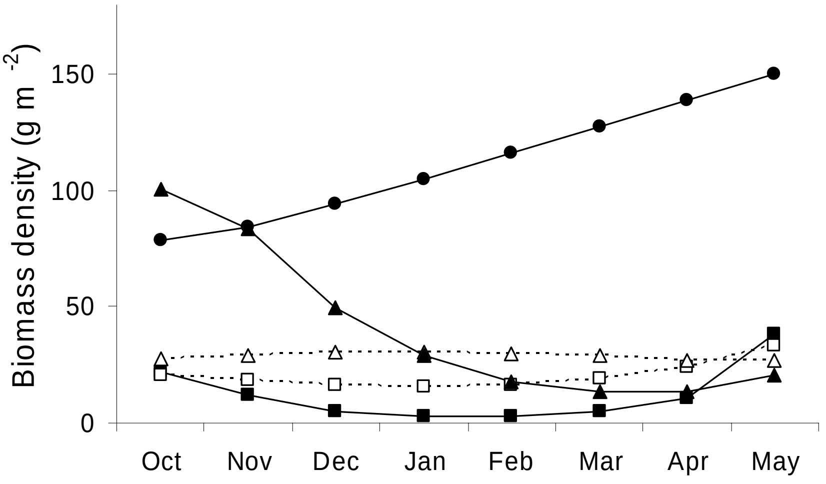


Figure 10.3 Predicted changes in the biomass density of different brent goose diets in three European regions. Predictions are 24 hour averages for the middle day of each month.

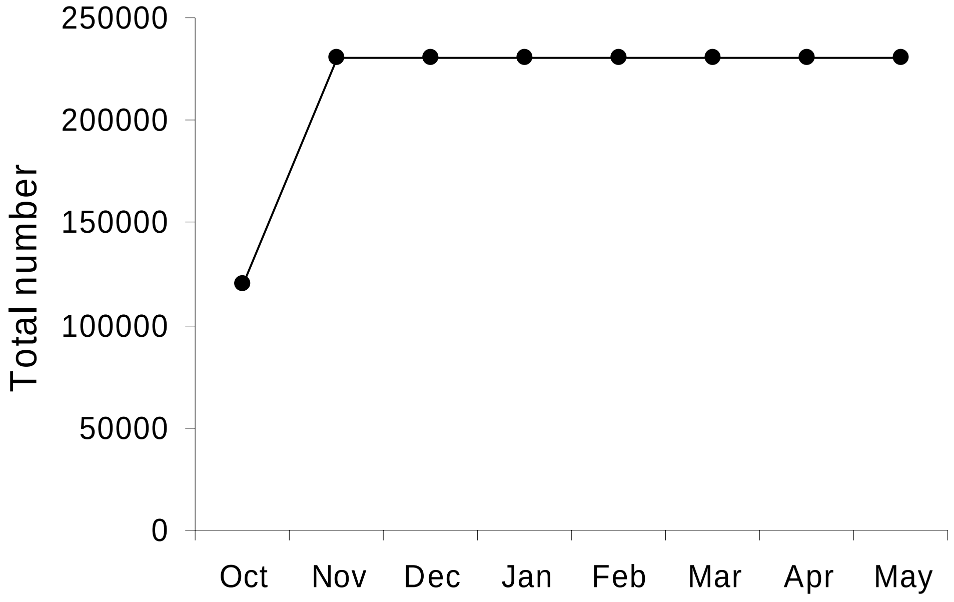
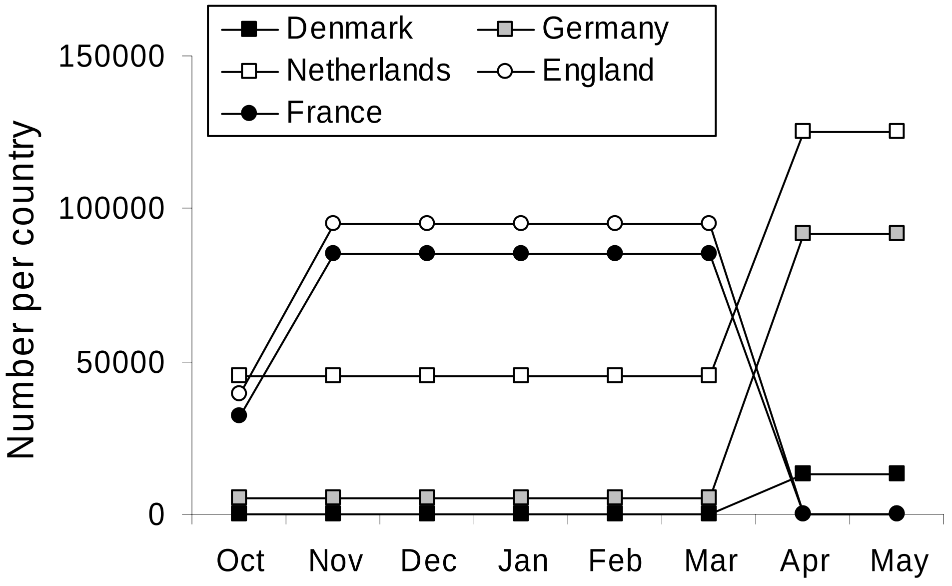
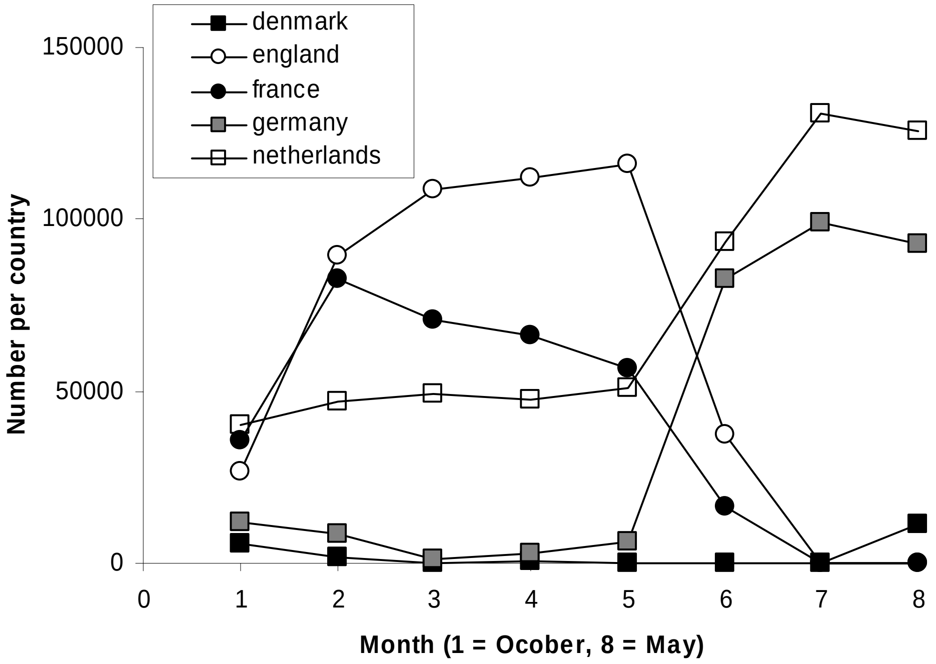


Figure 10.4 Predicted survival of brent geese between October and May.



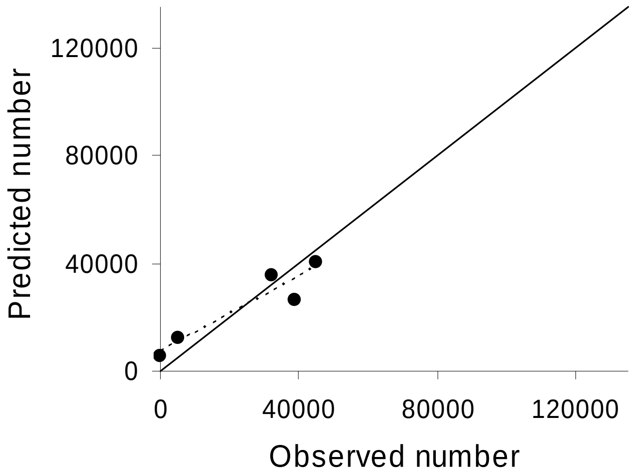
a) model predictions



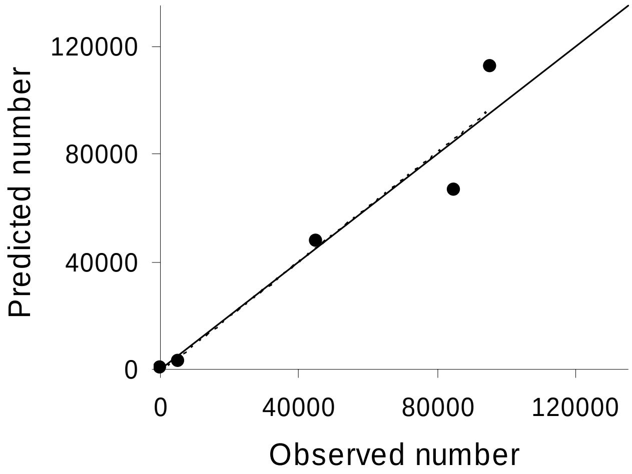
b) observed goose distribution

Figure 10.5 Seasonal variations in the predicted (a) and observed (b) distribution of brent geese between the five principal countries. Predicted values are based on the distribution on the 15th of each month. The observed distributions are based on counts between 1991 and 2000. Monthly observed count totals are adjusted to match the number of geese in the model i.e. 230,000 from November onwards.

(a) October distribution



(b) January distribution



(c) May distribution

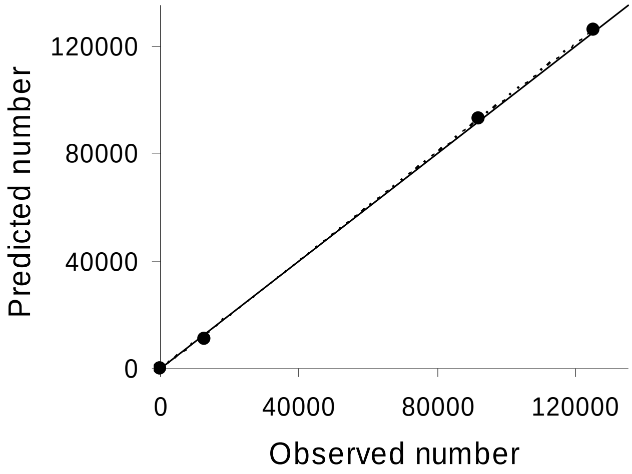
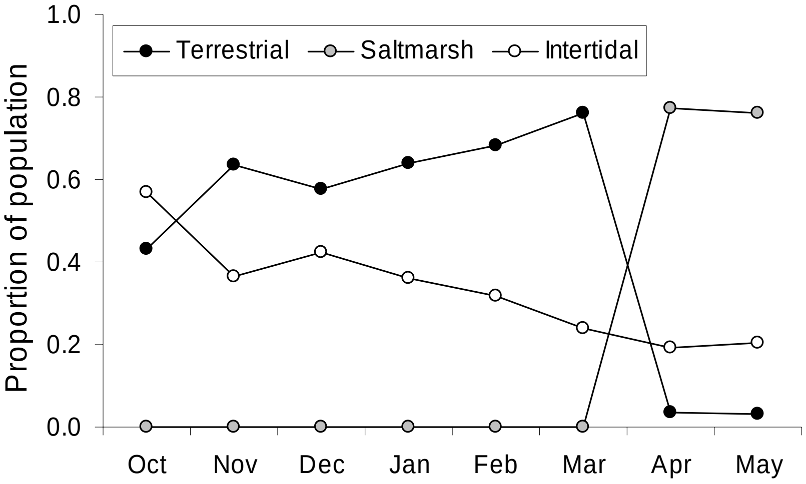
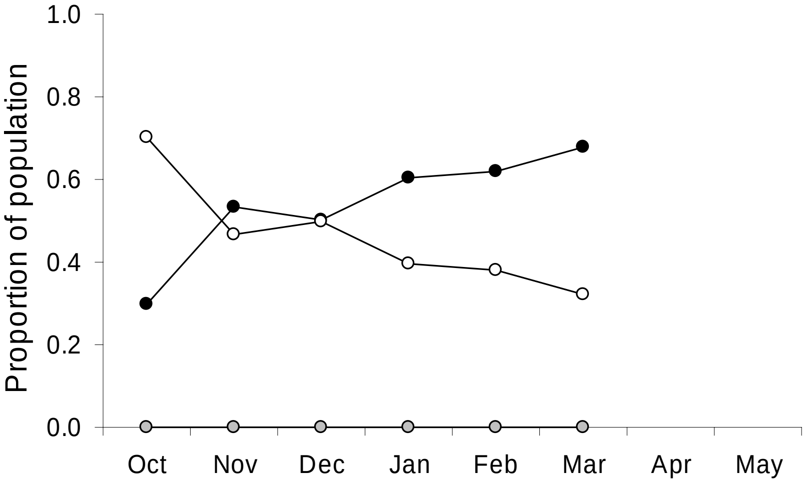


Figure 10.6 Predicted and observed distribution of brent geese between the five principal countries in October (a), January (b) and May (c). Predictions are 24 hour averages for the middle day of each month. The solid lines show a 1:1 relationship between prediction and observation, and the broken lines the regression between prediction and observation.

(a) Denmark, Germany and Netherlands



(b) England



(c) France

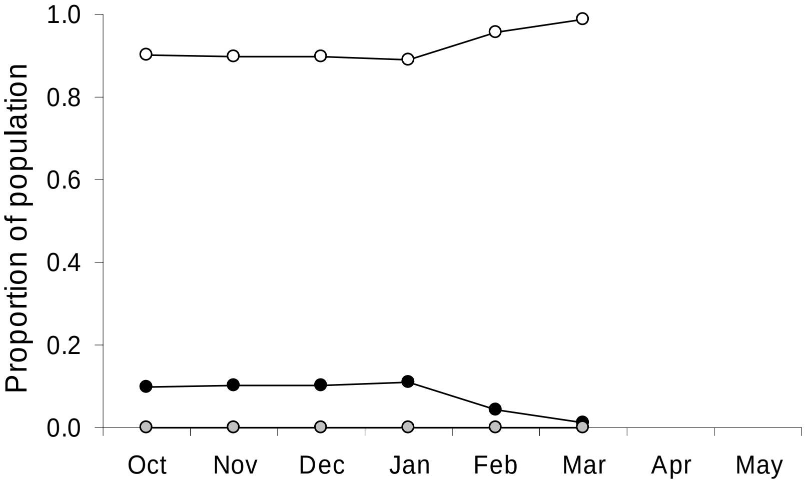
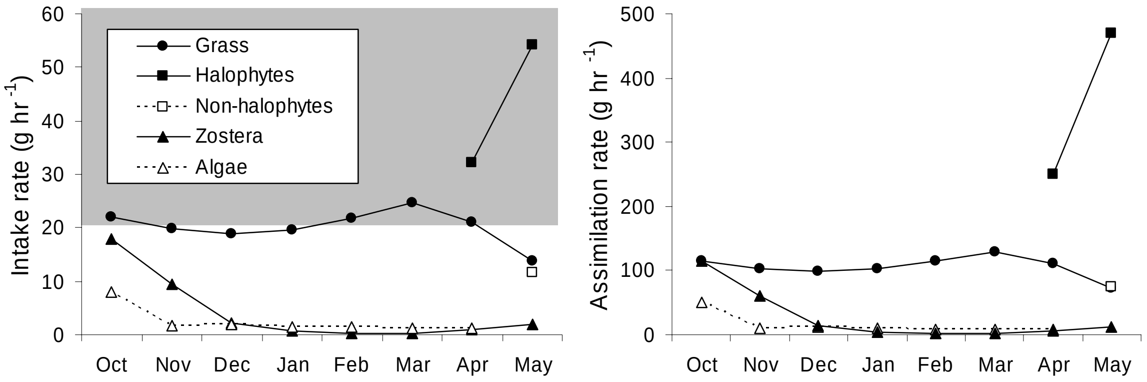
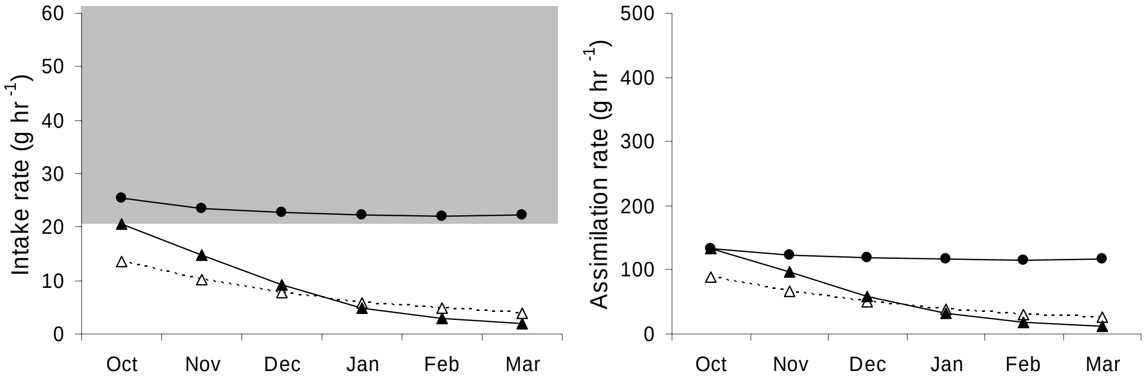


Figure 10.7 Predicted habitat selection of brent geese between October and May in three European regions. Predictions are 24 hour averages for the middle day of each month.



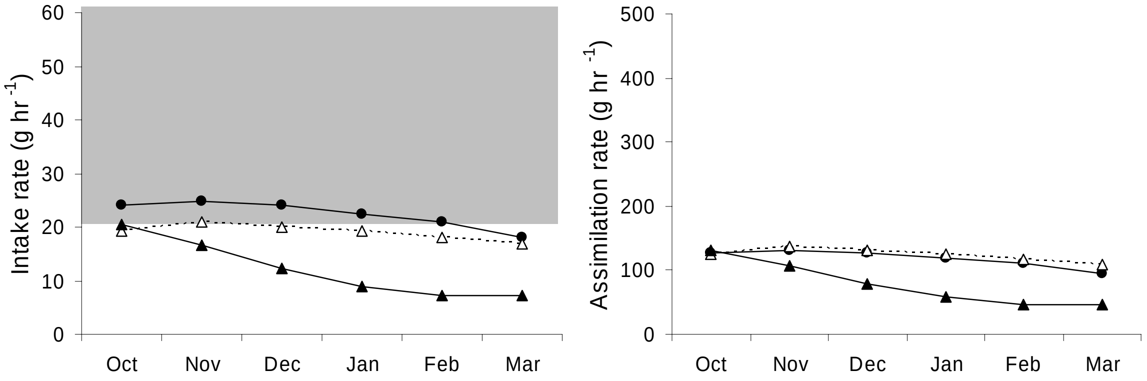
(a) Consumption: North East

(b) Assimilation: North East



(c) Consumption: England

(d) Assimilation: England



(e) Consumption: France

(f) Assimilation: France

Figure 10.8 Predicted food intake rate and energy assimilation rate of brent geese feeding on different diets between October and May. Intake rate is the rate at which food biomass is consumed, and assimilation rate is the rate at which energy is assimilated from this food into the birds' body. No predictions were obtained for halophytes between October and February or non-halophytes between October and April when no model birds fed on these diets. Predictions are 24 hour averages for the middle day of each month. The shaded areas show the range of asymptotic intake rates for brent geese.

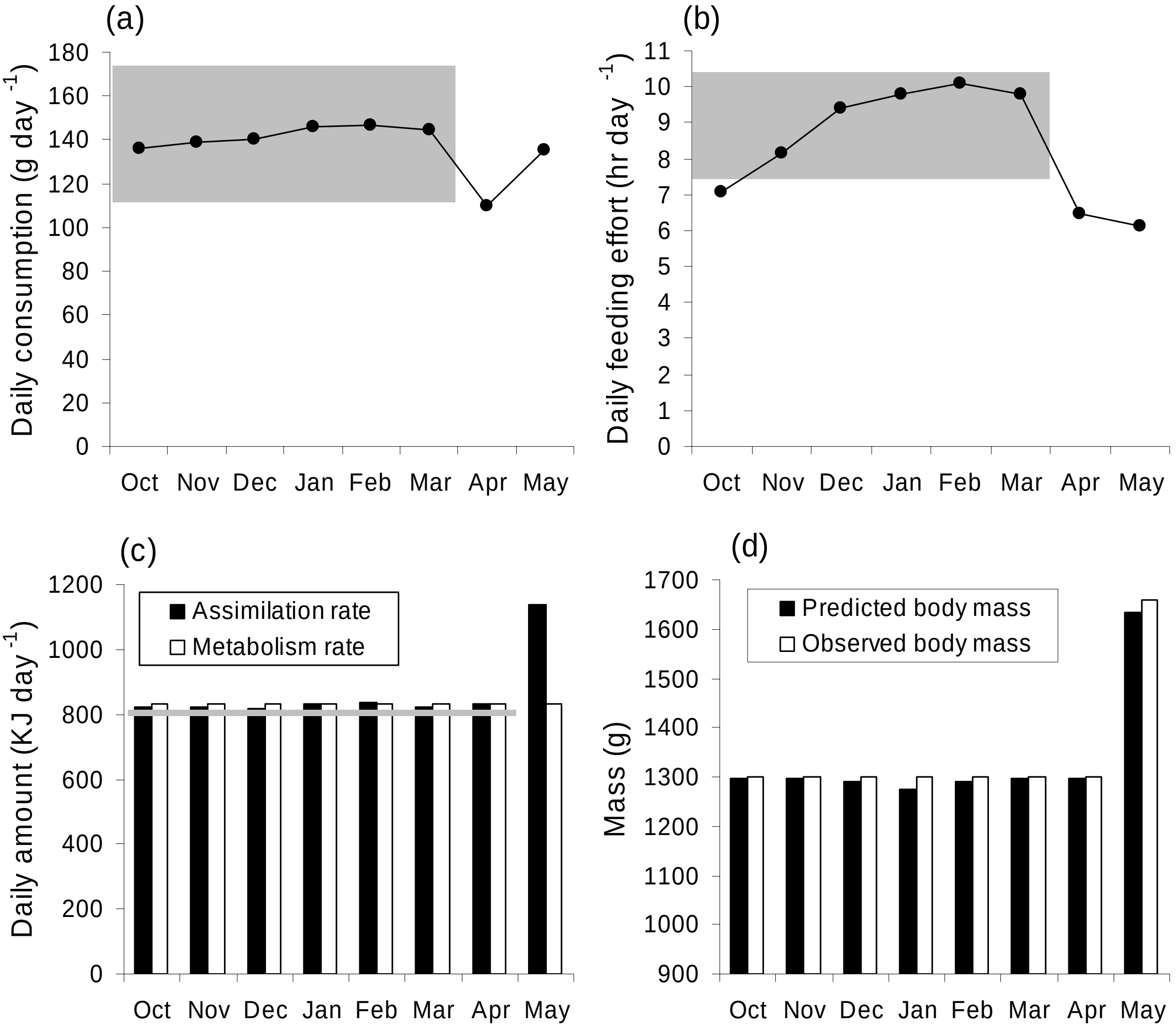


Figure 10.9 Predicted changes in the food consumption, feeding effort and energy budget of brent geese between October and May. (a) Consumption rate when feeding. (b) Proportion of time spent feeding during a day. (c) Daily energy assimilation and metabolism. (d) Actual and target body mass. The shaded areas show the observed range of (a) daily consumption, (b) proportion of the day spent feeding and (c) daily assimilation.

10.7.3 Issues

10.7.3.1 Change of agricultural practices

Reduction in the area of saltmarsh habitat, even to the point of its complete removal, had no noticeable effect on the distribution of birds between habitats in the winter in any country (Fig. 10.10 a,b,c). This reflects the fact that saltmarsh was predicted to be very little used between October and March, even under baseline conditions (Fig. 10.7). In contrast, loss of saltmarsh habitat resulted in a switch of the bulk of the spring staging birds in Denmark, Germany and the Netherlands to feeding on farmland i.e. grassland habitats (Fig. 10.10 d). Spring staging birds are predicted to switch to this resource rather than to their traditional intertidal resources which are likely to continue to be used by a minority of the population.

The loss of saltmarsh habitat also had no noticeable effect on the daily feeding effort or the mean body mass of brent geese during the winter (Fig. 10.11 a,b). Again, this reflects the predicted low usage of this habitat by wintering birds across Europe as a whole. In contrast, the gradual reduction in the extent of saltmarsh available to spring staging birds in Denmark, Germany and the Netherlands resulted in a gradual increase in their daily feeding effort (Fig 10.11 c). The birds had to forage for longer each day in order to compensate for the reduced area of available habitat. Under conditions of minor-moderate saltmarsh loss, this increased foraging effort was sufficient to allow the birds to maintain their spring fattening rate and hence end of spring body mass (Fig. 10.11 d). However, under conditions of extensive saltmarsh loss, even further increases in foraging effort were insufficient to enable the birds to maintain their rate of spring fattening and consequently the birds' end of spring body mass declined sharply (Fig 10.11 d).

Although saltmarsh removal caused the birds to increase their foraging effort in spring and ultimately resulted in a marked reduction in their end of spring body mass, saltmarsh removal did not cause any increase in over-winter mortality (Fig 10.12). However, in those years in which the reproductive success of brent geese is not constrained by adverse conditions during migration or on the breeding grounds, there is a very clear positive relationship between mean end-of-spring body mass and population level reproductive output (Ebbinge & Spaans 1995). This means that the extensive loss of saltmarsh habitat, either through physical removal by sea-level rise or by degradation due to cessation of grazing, while not increasing overwinter-mortality is likely to reduce the population through a detrimental effect on reproductive output.

Reduction in the area of grassland habitat had, up until the point of its complete removal, no noticeable effect on the distribution of birds between habitats in the winter in any country (Fig. 10.13 a-c). This is surprising given that under baseline conditions, grassland was predicted to be used by the majority of the over-wintering population, at least in all countries except France (Fig 10.7). The lack of effect may indicate either that the areas of grassland utilised in the model are seriously in error, or that the birds could feed profitably on much smaller areas than that which they currently exploit. The loss of grassland habitat also had no noticeable effect on the distribution of birds between habitats in spring (Fig 10.13 d). This is not surprising given the predicted low usage of this habitat at this time of year under baseline conditions (Fig 10.7a).

The total removal of grassland habitat resulted in a complete switch of wintering brent geese to intertidal habitats (Fig 10.13 a-c). It also precipitated mass movements of birds from Denmark, Germany, the Netherlands and England to France in mid-winter. Given this habitat switch and geographic displacement, it is surprising that both the average daily feeding effort and average over-winter body mass remained unchanged (Fig 10.14 a,b). However, in spite of between habitat and site shifts by geese, extensive loss of grasslands was predicted to lead to a marked increase in over-winter mortality (Fig 10.12). Thus, in the face of markedly reduced levels of competition, surviving geese fared well both in the winter and spring (Fig 10.14 a-d). Nonetheless, the high predicted levels of mortality under conditions of extensive grassland loss are unsustainable and would lead to population extinction.

10.7.3.2 Loss of intertidal resources

The gradual but partial removal of brent goose's traditional intertidal food resources (*Zostera* and green algae) had no effect on the average overwinter distribution of birds between habitats in Denmark, Germany, Netherlands and England (Fig. 10.15 a,b). This probably reflects the fact that in these countries only a minority of the population utilise this resource over the bulk of the winter under baseline conditions (Fig. 10.7 a,b) and that the decline in its usage in the early winter is driven at least in part by the relatively rapid non-grazing induced reduction in biomass density. In contrast in France, where the bulk of the population feed on intertidal resources throughout the winter under baseline conditions (Fig. 10.7c), the gradual removal of this habitat resulted in an increasing reliance of the birds on farmland habitat (Fig. 10.15. c).

The gradual but partial removal of brent goose's traditional intertidal food resources (*Zostera* and green algae) had no effect on the distribution of the birds between habitats in Denmark, Germany, and the Netherlands in spring (Fig. 10.15 d). It would appear that a markedly smaller area of intertidal resources might suffice for the minority of birds that utilise these resources in spring.

The complete removal of intertidal resources resulted in a marked increase in the birds' reliance on farmland habitat in the winter in all countries (Fig. 10.15 a,b,c) and on saltmarsh habitat in Denmark, Germany, and the Netherlands in spring (Fig. 10.15 d).

The gradual but partial removal of brent goose's traditional intertidal food resources (*Zostera* and green algae) resulted in a slight increase in the average number of daylight hours spent feeding during the winter and in the spring (Fig. 10.16 a,c). Thus, the birds had to spend a greater proportion of their time feeding as their intertidal resources diminished. This response was sufficient to enable the birds to maintain their average overwinter body mass (Fig. 10.16 b) but not to maintain the high rate of spring fattening achieved under baseline conditions. Thus, the average body mass on 21st May, following spring fattening, declined gradually from 1636g to 1618g (Fig. 10.16 d). This slight decline in the face of the loss of *Zostera* and green algae reflects the fact that only a small minority of the population were predicted to feed on these resources at this time of year.

The complete removal of intertidal resources resulted in a drop in the average number of daylight hours spent feeding during both the winter and spring (Fig. 10.16 a,c). This reflects the fact that, whereas birds faced with dwindling intertidal resources could compensate by increasing foraging effort on these resources to maintain their mass, this option was not open to them in the face of the complete removal of these resources. Accordingly, the birds' could no longer maintain their average over-winter body mass and the average end of spring body mass declined further (to 1605g i.e. a 2% drop) from baseline conditions.

Although the birds' habitat distribution, daily feeding effort, and ability to maintain their over-winter body mass and rate of spring fattening were altered to varying degrees by intertidal habitat removal, the loss of intertidal resources had no effect on the predicted over-winter mortality (Figure 10.12). Thus, by adjusting their habitat usage patterns and feeding effort the birds were able to survive in spite of the decline in the availability of their traditional intertidal resources. Nonetheless, this result is only possible given an increasing exploitation of farmland habitats, particularly in France. Were this to be precluded by a campaign of disturbance or hunting in the face of increasing goose pressure on farmland, then mortality would be expected to increase in the face of dwindling intertidal resources.

10.7.3.3 Disturbance

In those countries where intertidal habitats are used by a minority of the population during the winter, increasing levels of daytime disturbance on intertidal habitats had no effect on the average over-winter distribution of birds between habitats (Fig. 10.17 a,b). The same was true in the case of disturbance to intertidal habitats in the spring staging sites (Fig. 10.17 d). In contrast, in France where the vast majority of the wintering population rely on intertidal food resources throughout the winter (Fig 10.7c), increasing levels of disturbance on intertidal habitats resulted in an increasing use of farmland habitat.

Although there was no effect of intertidal disturbance on the birds' winter habitat usage throughout most of their wintering range, there was a slight increase in the amount of time that birds foraged each day (Fig. 10.18 a). Presumably, this was necessary to compensate for the increased energy expenditure incurred during disturbance events by birds that foraged on this habitat. This increased effort was sufficient to prevent any decline in average over-winter body condition (Fig. 10.18 b). Given the relatively minor use of intertidal resources in spring, increasing disturbance of this habitat did not cause any increase in the average bird's daily foraging effort in spring or a decrease in its final body mass (Fig 10. 18 c,d).

Increased levels of daytime disturbance on intertidal habitats did not cause brent goose over-winter mortality to increase (Fig. 10.19).

Increased disturbance of saltmarsh habitat did not result in a consistent effect on the distribution of birds between habitats in the winter in any country (Fig. 10.20 a-c). This reflects the fact that saltmarsh was predicted to be very little used between October and March, even under baseline conditions (Fig. 10.7). In contrast, increasing disturbance of saltmarsh habitat resulted in a gradual decline in the use of saltmarsh and an increase in the usage of farmland habitat by spring staging birds in Denmark, Germany and the Netherlands (Fig 10.20 d).

Disturbance of saltmarsh habitat also had no noticeable effect on the daily feeding effort or the mean body mass of brent geese during the winter (Fig 10.21 a,b). Again, this reflects the predicted low usage of this habitat by wintering birds across Europe as a whole. In contrast, the gradual increase in the intensity of disturbance on saltmarsh used by spring staging birds in Denmark, Germany and the Netherlands resulted in a pronounced increase in their daily feeding effort (Fig 10.21 c). The birds foraged for longer each day in order to compensate for the extra energy costs incurred due to the disturbing events. Under conditions of minor-moderate saltmarsh loss, this increased foraging effort allowed the birds to maintain their spring fattening rate and hence end of spring body mass (Fig. 10.21 d). However, under conditions of intensive disturbance to their preferred habitat, even further increases in foraging effort were insufficient to enable the birds to maintain their rate of spring fattening and consequently the birds' end of spring body mass declined sharply (Fig. 10.21 d).

Although the disturbance of saltmarsh caused the birds to increase their foraging effort in spring and ultimately resulted in a marked reduction in their end of spring body mass, it did not cause any increase in over-winter mortality (Fig 10.19). However, for the reasons outlined above, excessive disturbance of saltmarsh habitat, while not increasing overwinter-mortality, is very likely to reduce the population through a detrimental effect on reproductive output.

Increased levels of daytime disturbance on farmland were predicted to result in an increasing reliance by birds on intertidal habitats in Denmark, Germany, the Netherlands and England (Fig. 10.22 a,b). However, moderate to high levels of disturbance on farmland in these countries precipitated mass movements of birds from these countries to France in mid-winter. On arrival in France, where the resident birds make little use of farmland in any case, all birds continued to exploit intertidal resources (Fig. 10.22 c). Disturbance to farmland had no effect on the habitat usage patterns of spring staging geese (Fig. 10.22 d).

Given the reliance on grassland of the bulk of the birds in Denmark, Germany, the Netherlands and England during the winter, it is surprising that increasing levels of disturbance to this habitat and the resulting switch to intertidal habitat had no detrimental effect on either the average over-winter daily feeding effort or over-winter body mass (Fig 10.23 a,b). This arises from the fact that, in spite of the switch in winter habitat usage and indeed of movements across Europe, most farmland disturbance scenarios were predicted to result in large numbers of birds dying (Fig. 10.19). Thus, the results presented in Fig. 10.23 refer solely to the survivors. In the face of markedly reduced levels of competition, surviving geese fared well both in the winter and spring (Fig. 10.23 a-d). Nonetheless, the high predicted levels of mortality caused by disturbance to farmland habitats are unsustainable and would lead to population extinction.

10.7.3.4 Hunting

Hunting in the autumn will kill birds directly but will also disturb birds. This may lead to reduced feeding opportunities and increased energy expenditure and hence reduced body mass. Alternatively, disturbed birds may leave Denmark and winter further south than they otherwise would. Hunting in the spring would also kill birds directly and disturb others, so reducing feeding opportunities and increasing energy expenditure. In spring this may manifest itself as a reduction in the rate at which birds gain mass during the spring fattening period and a lower end of spring departure mass. Because in many years reproductive output is positively related to the mass brent geese attain prior to departure from the spring staging grounds (Ebbinge & Spaans 1995), hunting in spring, by reducing the birds' mass at this crucial time of year, has the potential to cause more harm than hunting in the autumn. On the basis of this idea, the fact that brent goose numbers in Denmark are higher in spring than at any other time of year, we have concentrated our simulations on exploring the consequences of the potentially most damaging hunting scenario i.e. a spring hunting season. This may of course be unlikely to be permitted in reality but the simulations presented here may represent a worst case scenario.

In order to explore the long-term population-level consequences of renewed hunting in Denmark it was necessary to combine the outputs of the behavioural model MORPH (i.e. i) the number of birds surviving the risks of being shot and of starving as a result of excessive disturbance, and ii) the mean end of spring body mass of the survivors) with demographic ‘models’ describing the relationship between reproductive output and i) population size and ii) spring body condition (Ebbinge & Spaans 1995, Ebbinge *et al.* 2002). Data presented by Ebbinge & Spaans (1995) reveal a positive relationship between brent goose mass at the end of spring and the proportion of the population comprising juveniles in the following winter. This relationship holds in years when success is moderate to high but not in years of complete breeding failure which have been attributed to adverse wind conditions during migration or very high predator pressure on the breeding grounds. Ebbinge *et al.* (2002) present two models describing density-dependence in the reproductive output of brent geese. Again these models apply only to years in which brent goose breeding success was not poor due to reasons other than density-dependence (these being excluded from the analyses).

Under each of the hunting scenarios explored, the mean end of spring body mass predicted by the model MORPH was used to predict the potential proportion of juveniles in the following winter. Similarly, under each of the hunting scenarios explored, the number of birds predicted by MORPH to survive the winter was used to generate a second estimate of the potential reproductive output i.e. that determined by the density-dependent exponential reproductive function of Ebbinge *et al.* (2002). The lower of these estimates of reproductive output was used to calculate the population size at the start of the following winter (assuming an adult survival rate of 0.85 during the spring-autumn period). Assuming that the distribution of birds between countries would remain unchanged, a new Danish spring population was then calculated and subjected to another spring hunting season in which the proportion of Danish birds shot was set to be the same as under the initial scenario explored by MORPH. The mean end of spring body mass was assumed to be the same as derived from the initial run of the behaviour-based model. These numbers were then used, as described above, to generate a new population at the start of the next winter and the process repeated to yield a population trajectory over a 100 year period under each hunting scenario. To incorporate the three-yearly breeding failures that characterise brent goose reproductive dynamics, a third estimate of the potential proportion of juveniles was calculated every third year. This was set to a random value <0.12 in every third year. If this was lower than the mass-dependent or density-dependent estimates, then this value was used to calculate the population size in the following winter.

On the basis of the count data gathered in the early 1990s it was assumed that c5% of the entire population stage in Denmark in the spring. Hunting was allowed on all three habitats within Denmark but was restricted to daylight hours between 1st April and 21st May. The intensity of hunting was varied such that the proportion of birds that occurred in Denmark that were shot in spring varied between 0 and 1. As the proportion of birds killed was increased, so too did the level of disturbance caused by the hunting activity. Again this disturbance affected all three habitats.

As the intensity of hunting in Denmark was increased, the mean end of spring body mass of birds staging in Denmark was unaffected until hunting pressure became intense. However, once a certain level of hunting pressure was exceeded the birds ability to accumulate mass was markedly reduced (Fig. 10.24a). Because the Danish spring staging population is only a small fraction of the total population, this reduction in the condition of the ‘Danish’ birds had virtually no effect on the mean spring body mass of the population as a whole (Fig 10.24a). Consequently, the effect of hunting on the potential reproductive output of the population as a whole, mediated via the increased levels of disturbance that it caused to birds in Denmark, was never sufficiently pronounced to reduce the success of the whole population below the constraint imposed by the density-dependence of their reproductive output.

Thus, the population trajectory under each hunting scenario was determined solely by the number of birds that were predicted to die in the model. Because no birds starved as a result of excessive disturbance due to hunting activity, the mortality rate predicted by the behaviour-based model under each hunting scenario was in fact simply determined by the Danish hunting bag that was used to parameterise the model in the first place. Thus, predicting the long-term consequences of Danish hunting reduced to a simple demographic exercise. Using the exponential reproductive density-dependent model of Ebbinge *et al.* (2002), in combination with an assumed poor breeding success every third year, the equilibrium population size of the population as a whole was predicted to decline as the intensity of hunting in Denmark increased (Fig 10.24).

Because a hunting season in the autumn would be less likely than a spring hunting season to affect the mean end-of spring body mass and would be unlikely to cause any birds to starve it is unlikely that the results of an autumn hunting season would be very different to those presented here. This, conclusion is however dependent upon no more birds being shot in autumn than the numbers explored here. Given that the autumn counts of brent geese in Denmark are lower than in the spring this is not an unrealistic assumption. However, were the large numbers of brent geese that traverse Denmark each autumn *en route* to sites further south and west to be subjected to hunting, then the potential kill in autumn could be much higher than that explored here and the consequences much more severe. As it stands, the model cannot yet address the probability of a bird being shot while in transit over a particular location. Further work will be required to address this issue.

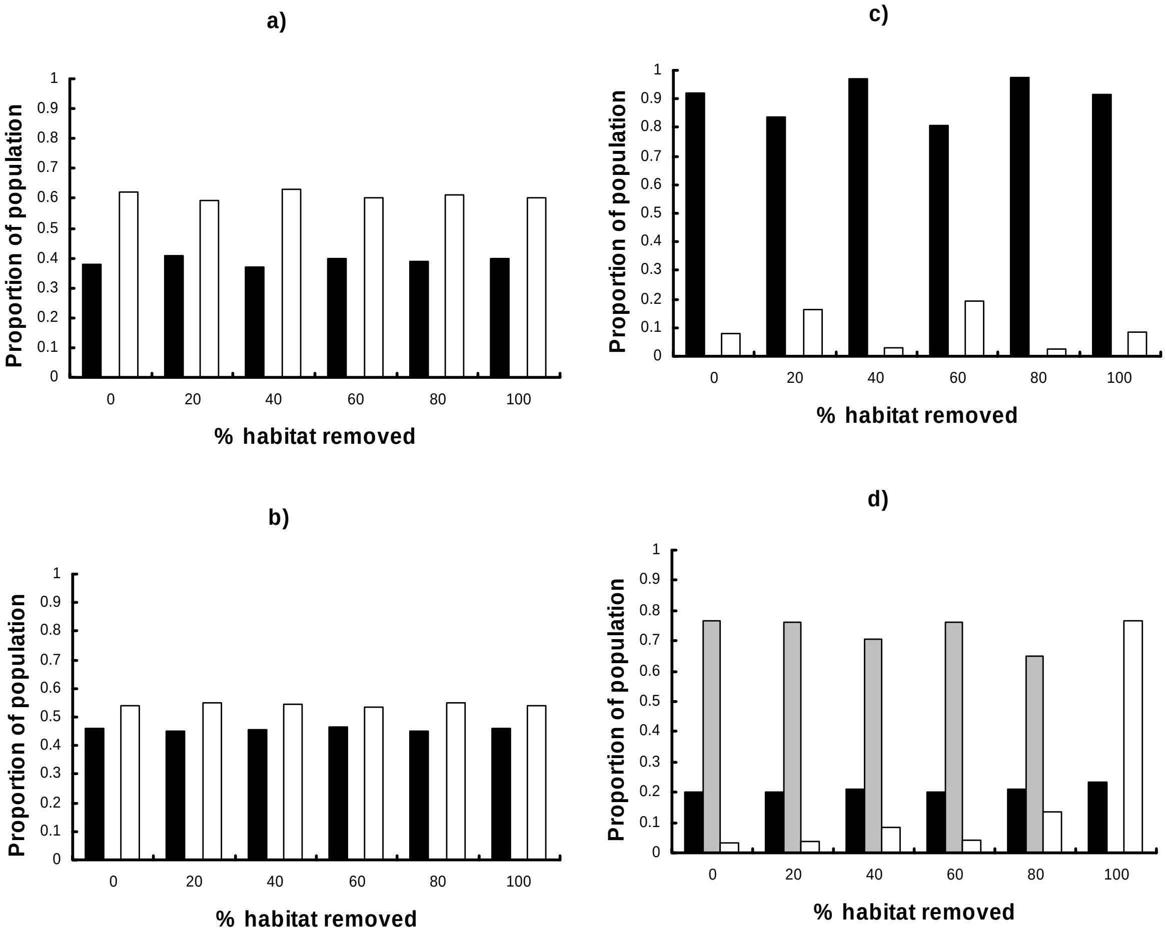


Figure 10.10 Effect of the extent of saltmarsh removal on the proportion of the population utilising: intertidal habitats (black fill), saltmarsh habitats (grey fill) and farmland habitats (open bars). a) October-March in Denmark, Germany and Netherlands, b) October – March in England, c) October – March in France and d) April-May in Denmark, Germany and Netherlands.

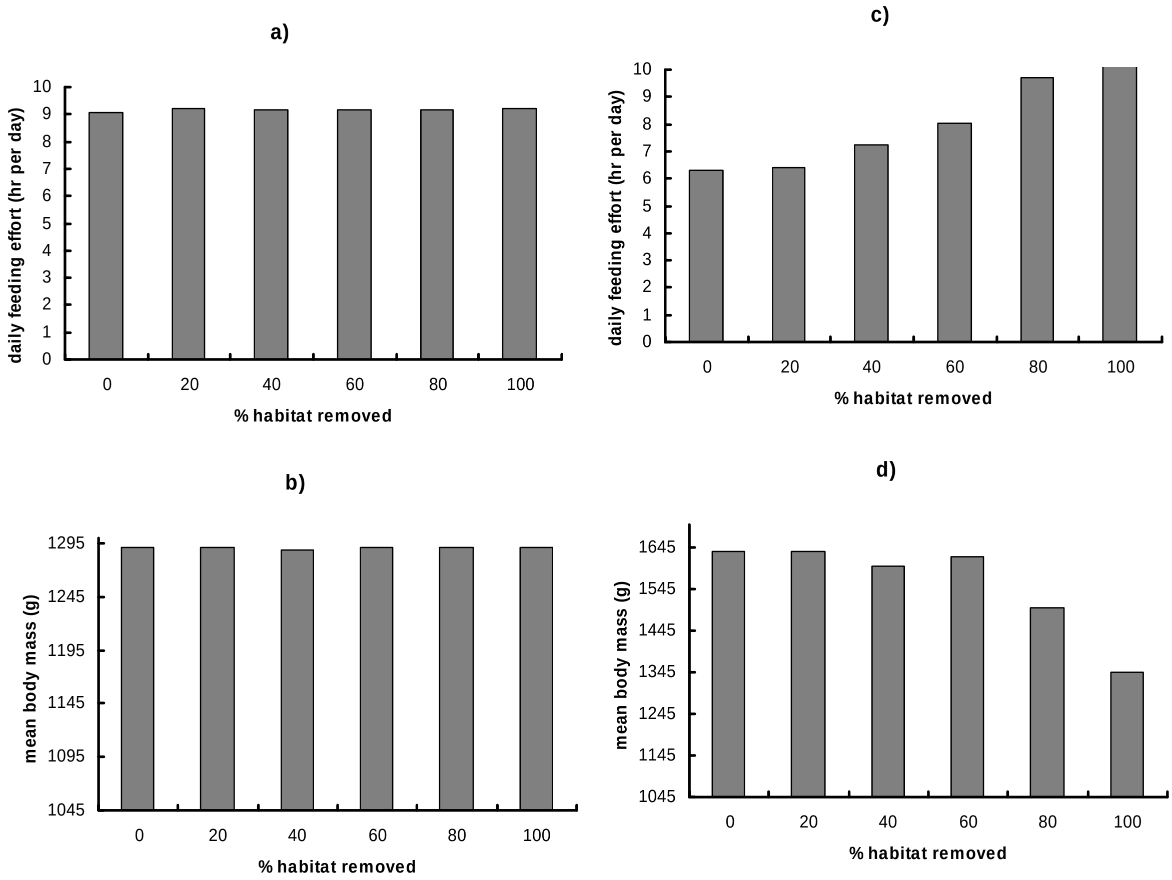


Figure 10.11 Effect of the extent of saltmarsh removal on: a) mean foraging time during daylight between October and March, b) mean body mass between October and March, c) mean foraging time during daylight in April and May and d) mean body mass on 21st May.

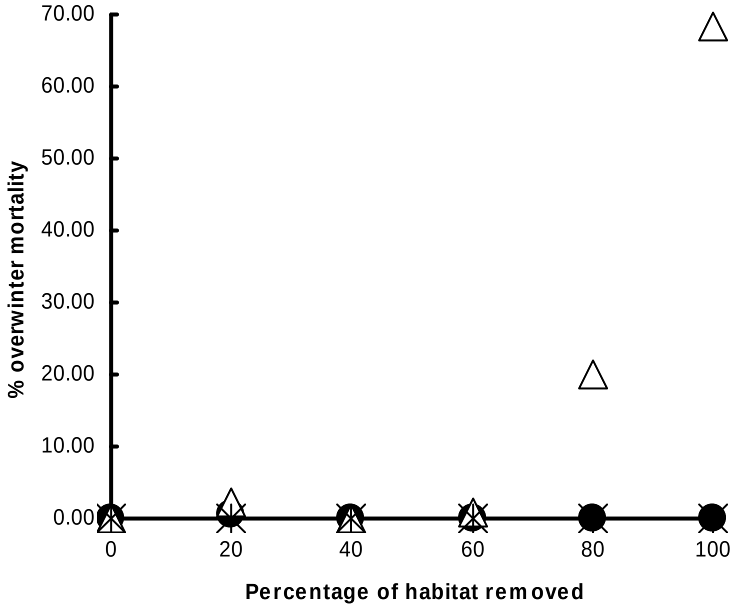


Figure 10.12 Effect of the extent of loss of: intertidal habitat (filled circles), farmland (open triangles) and saltmarsh (asterisk) on the predicted overwinter mortality of brent geese.

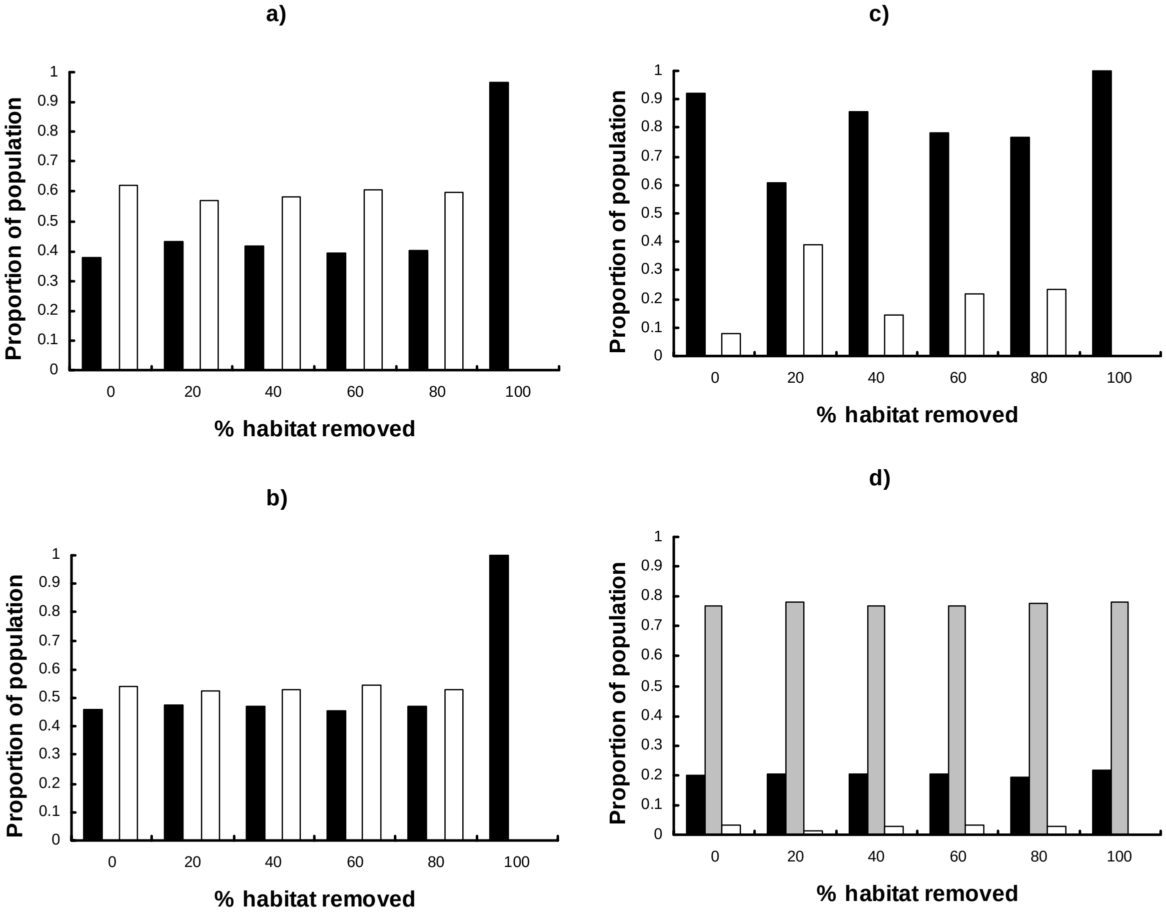


Figure 10.13 Effect of the extent of farmland habitat removal on the proportion of the population utilising: intertidal habitats (black fill), saltmarsh habitats (grey fill) and farmland habitats (open bars). a) October-March in Denmark, Germany and Netherlands, b) October – March in England, c) October – March in France and d) April-May in Denmark, Germany and Netherlands.

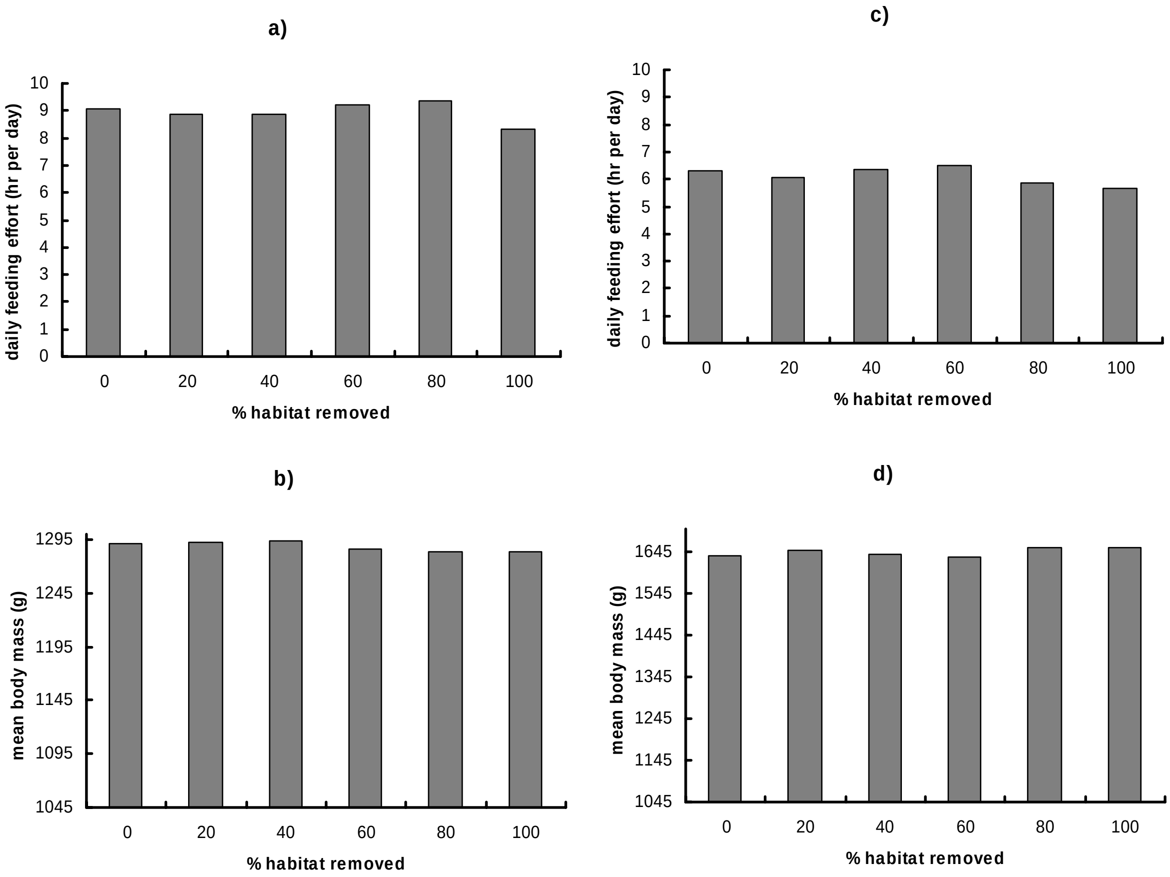


Figure 10.14 Effect of the extent of farmland habitat removal on: a) mean foraging time during daylight between October and March, b) mean body mass between October and March, c) mean foraging time during daylight in April and May and d) mean body mass on 21st May.

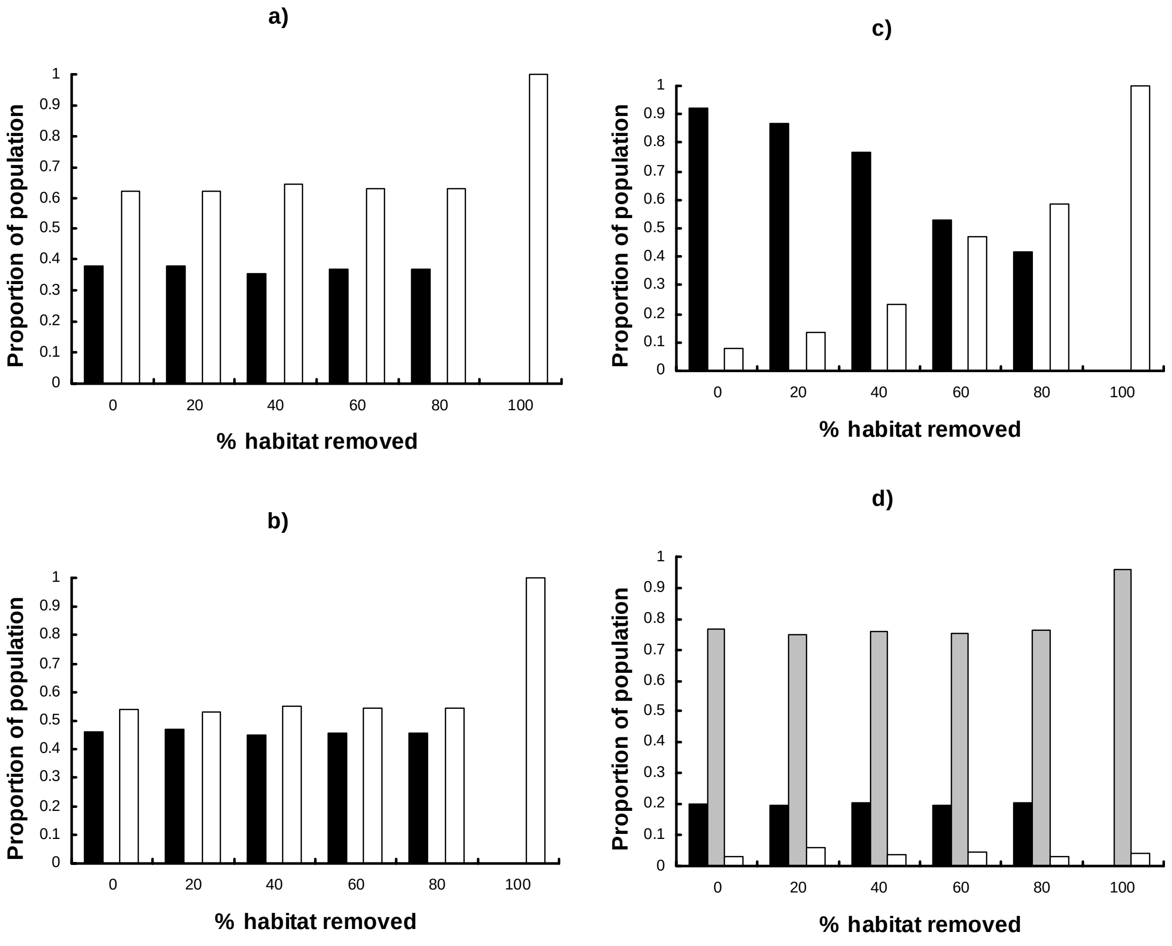


Figure 10.15 Effect of the extent of intertidal habitat removal on the proportion of the population utilising: intertidal habitats (black fill), saltmarsh habitats (grey fill) and farmland habitats (open bars). a) October-March in Denmark, Germany and Netherlands, b) October – March in England, c) October – March in France and d) April-May in Denmark, Germany and Netherlands.

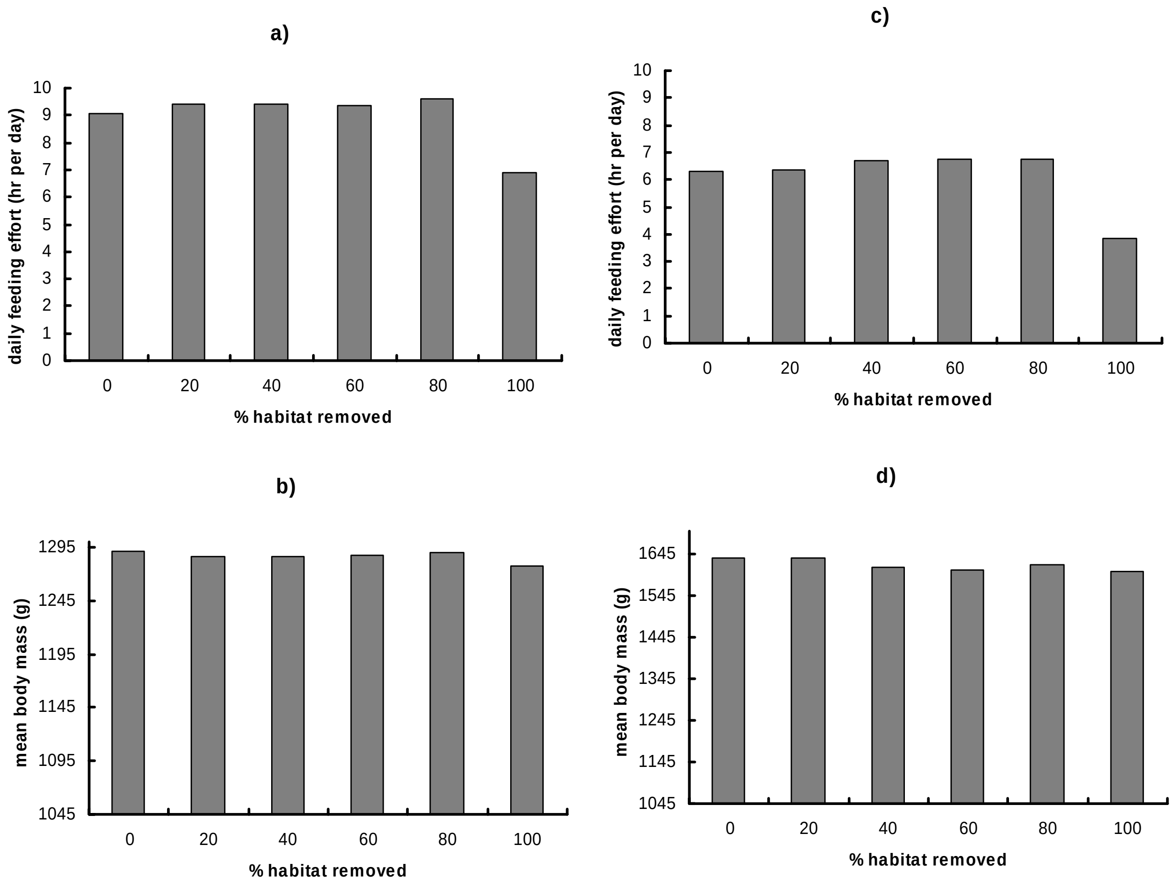


Figure 10.16 Effect of the extent of intertidal habitat removal on: a) mean foraging time during daylight between October and March, b) mean body mass between October and March, c) mean foraging time during daylight in April and May and d) mean body mass on 21st May.

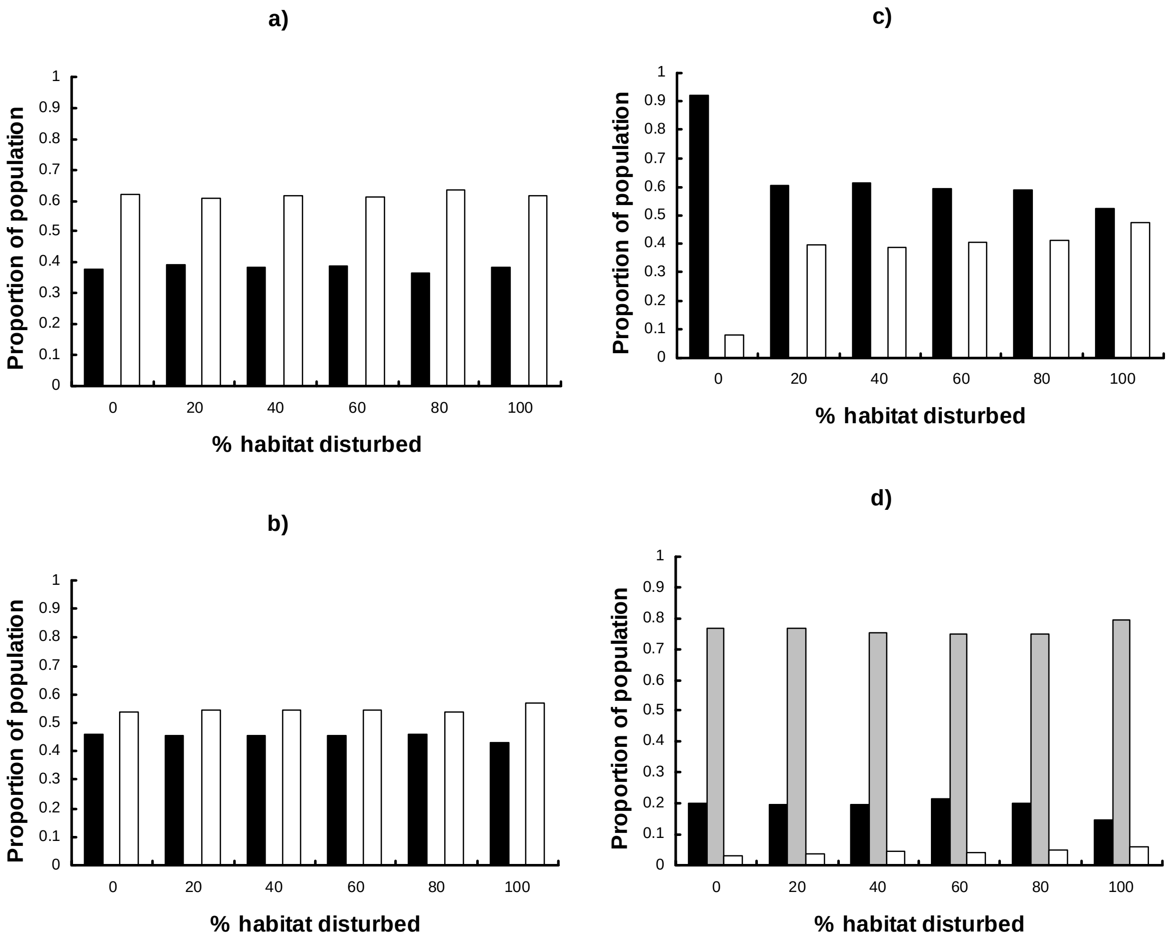


Figure 10.17 Effect of the extent of intertidal habitat daytime disturbance on the proportion of the population utilising: intertidal habitats (black fill), saltmarsh habitats (grey fill) and farmland habitats (open bars). a) October-March in Denmark, Germany and Netherlands, b) October – March in England, c) October – March in France and d) April-May in Denmark, Germany and Netherlands.

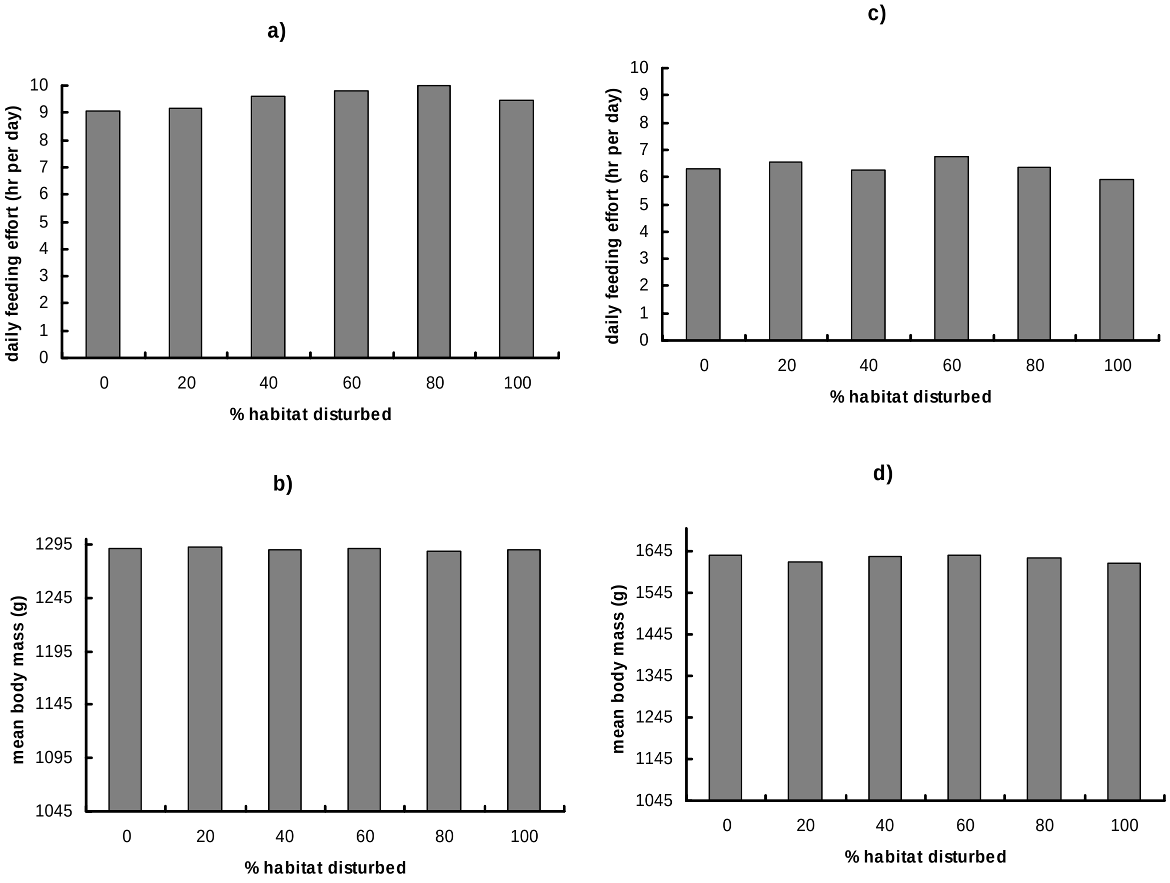


Figure 10.18 Effect of the extent of intertidal habitat daytime disturbance on: a) mean foraging time during daylight between October and March, b) mean body mass between October and March, c) mean foraging time during daylight in April and May and d) mean body mass on 21st May.

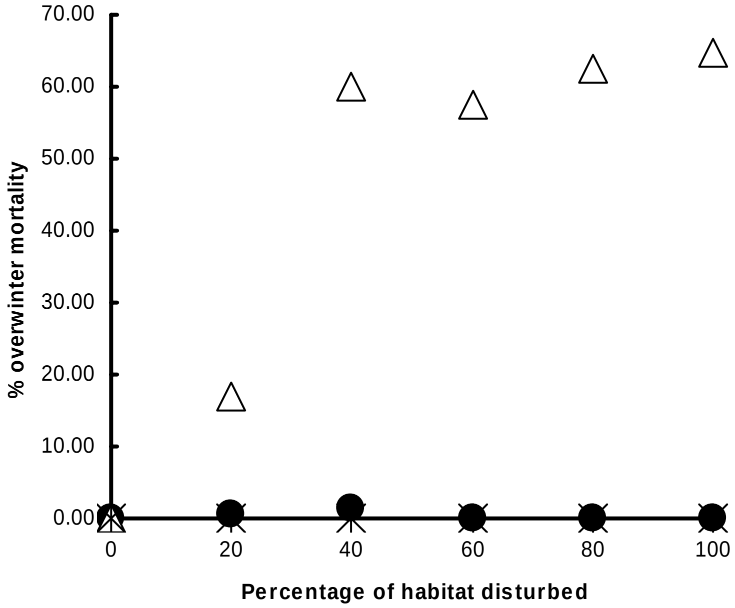


Figure 10.19 Effect of the extent of daytime disturbance of: intertidal habitat (filled circles), farmland (open triangles) and saltmarsh (asterisk) on the predicted overwinter mortality of brent geese.

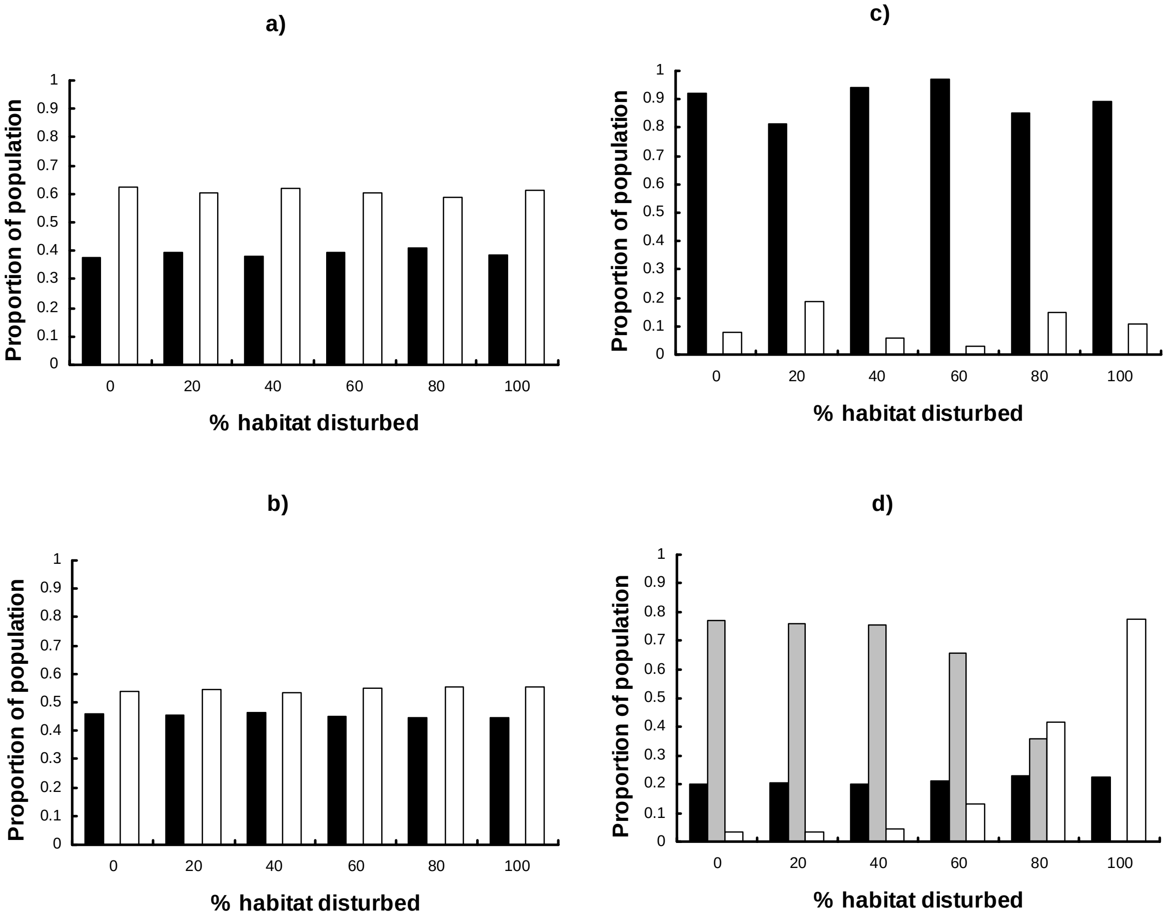


Figure 10.20 Effect of the extent of saltmarsh daytime disturbance on the proportion of the population utilising: intertidal habitats (black fill), saltmarsh habitats (grey fill) and farmland habitats (open bars). a) October-March in Denmark, Germany and Netherlands, b) October – March in England, c) October – March in France and d) April-May in Denmark, Germany and Netherlands.

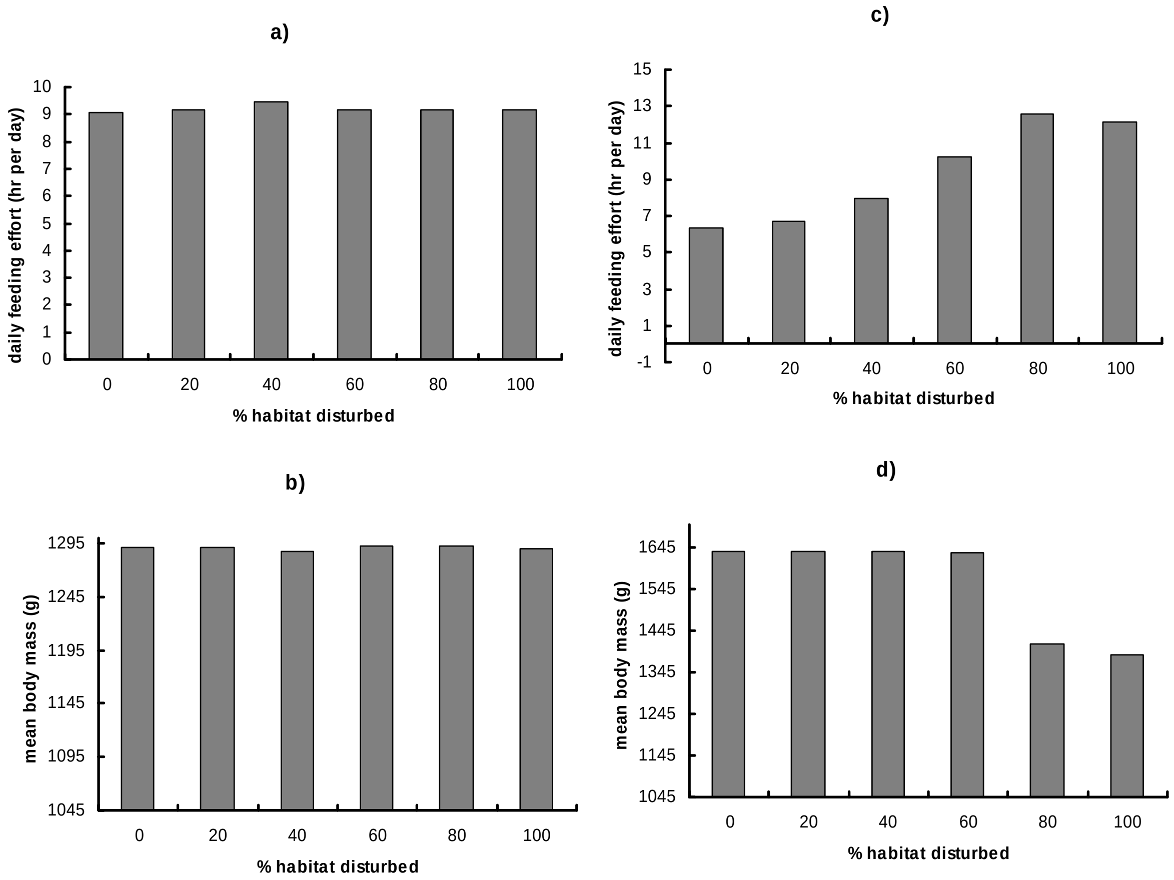


Figure 10.21 Effect of the extent of saltmarsh daytime disturbance on: a) mean foraging time during daylight between October and March, b) mean body mass between October and March, c) mean foraging time during daylight in April and May and d) mean body mass on 21st May.

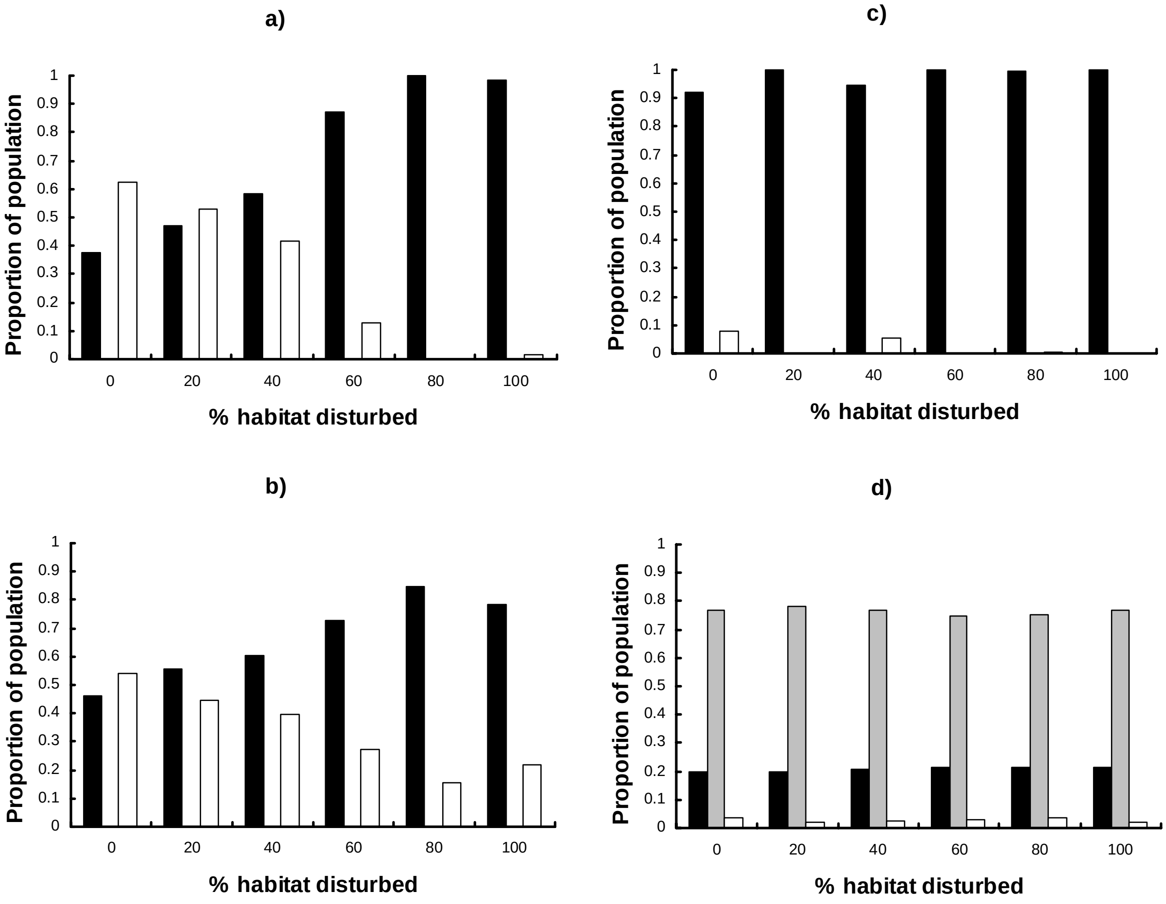


Figure 10.22 Effect of the extent of farmland habitat daytime disturbance on the proportion of the population utilising: intertidal habitats (black fill), saltmarsh habitats (grey fill) and farmland habitats (open bars). a) October-March in Denmark, Germany and Netherlands, b) October – March in England, c) October – March in France and d) April-May in Denmark, Germany and Netherlands.

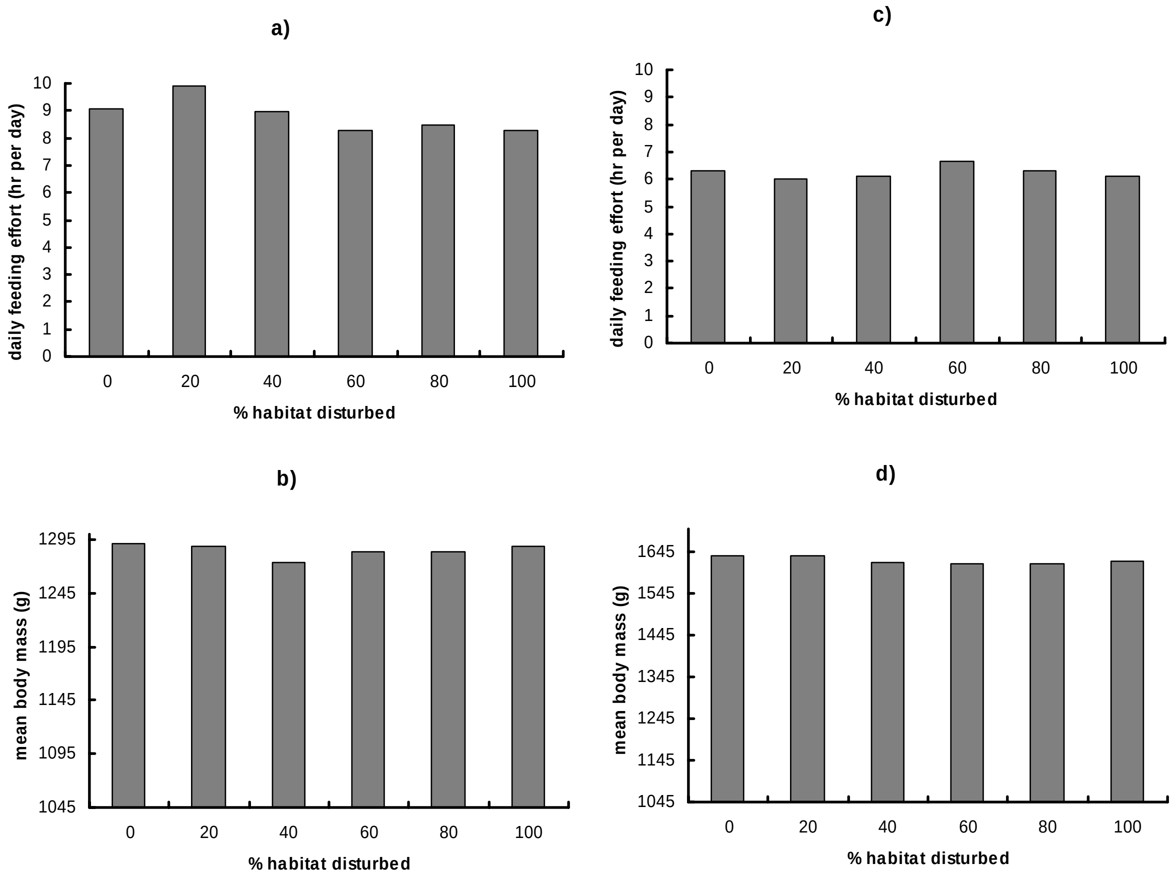


Figure 10.23 Effect of the extent of farmland habitat daytime disturbance on: a) mean foraging time during daylight between October and March, b) mean body mass between October and March, c) mean foraging time during daylight in April and May and d) mean body mass on 21st May.

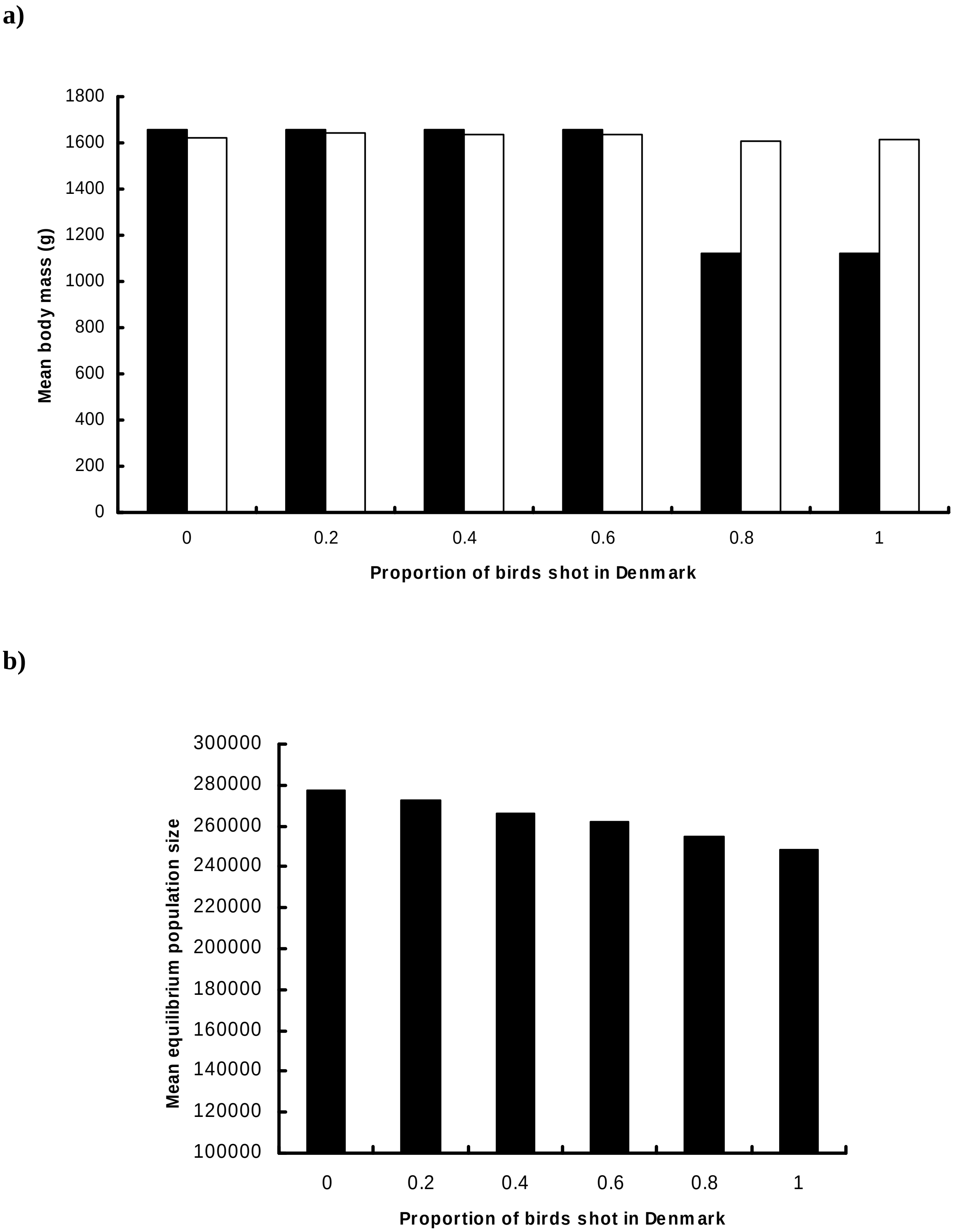


Figure 10.24 Effect of increasing the intensity of hunting in spring in Denmark on a) the mean end of spring body mass of birds staging in Denmark (filled bars) and of the entire spring staging population (open bars), and b) the long-term equilibrium population size.

10.8 Conclusions

The principal objective of this work package was to parameterize a multi-site model for one exemplary herbivorous wildfowl species, the brent goose. As described in Chapter 1, a new model MORPH was developed to replace both the single-site wader model and the multi-site wildfowl model that existed at the start of the project. This new multi-site model was parameterised using data collected by means of: i) a collaborative review of published and unpublished data pertaining to brent geese, their food supplies and the environments that they live in and ii) additional new fieldwork. Whereas each of the single-site wader models presented in preceding chapters required the accurate characterisation of one site, the multi-site goose model by its nature required accurate characterisation of very many sites. Thus, the parameterisation of the multi-site goose model, although dealing with only one species of bird, was a considerably more complex task than the parameterisation of any of the single site wader models.

Using the data collated under the literature review and the fieldwork programme in Denmark and France, we have developed a behaviour-based model of brent geese throughout their wintering range in western Europe. Although difficulties in obtaining all of the data necessary mean that the model is neither as well parameterised nor as powerful a predictive tool as was anticipated at the start of the project, the model is nonetheless an enormous advance on the more generic and inflexible multi-site model that existed at the start of the project (Pettifor *et al*. 2000).

The model, when parameterised with the best estimates of all the relevant parameters and functions did not require any calibration to bring its predictions of bird behaviour and survival under baseline conditions in line with independent empirical data. This in itself is a major achievement for such a complex model. The vegetation dynamics predicted by the model were not unrealistic. The birds' seasonal patterns of resource usage were predicted well as was the difference in these patterns between countries. The daily food consumption, energy assimilation rates and daily feeding effort were in line with empirical data. The model predicted that no birds would die from starvation under baseline conditions. Although up to 4-5% of light-bellied brent geese die over-winter (Clausen *et al*. 2001), this mortality will include death due to many agents that are not included in the model e.g. accidental death and disease. Thus, the model's prediction of no over-winter starvation is unlikely to be seriously in error. The precision with which the model predicted daily feeding effort and the slight dip in predicted body mass below target mass in mid-winter indicates that the birds in the model did not face an overly benign environment in comparison with reality.

Time constraints, and the length of time taken for each model run, meant that no repeat runs could be done for any of the simulations done for this Report. As a result, variation in stochastic elements of the model, such as feeding efficiency of individual birds and their initial distribution between sites, is reflected in the figures presented here. It also meant that no statistical analyses could be made of the results. Future work will involve repeat simulations and statistical analysis of our results.

In this Report, we used the model to address several issues concerning interactions between brent geese, their environment and man's activities within this environment. These concerned losses of, and disturbance events upon, each of the three principal habitats.

Although brent geese traditionally relied heavily on intertidal resources such as *Zostera* and green algae, reduction in the area of this habitat or increased levels of disturbance on it were predicted to have less effect on the birds than changes to either of the other two habitats. Although reduced access to intertidal resources through either habitat loss or increased disturbance precipitated an increase in usage of farmland habitat in winter (especially in France) the birds' over-winter mortality remained at 0% and the birds' ability to fatten in spring was largely unaffected. It appears that the ability of brent geese to exploit alternative resources means that they are no longer as heavily dependent upon access to their traditional intertidal resources as they once were. This conclusion is, however, contingent upon the condition that disturbance i.e. scaring activity on farmland does not increase in response to increased grazing pressure by geese no longer able to rely on their traditional intertidal resources. If this were to occur, higher goose mortality is possible (see below).

Loss or disturbance to saltmarsh habitat had no noticeable effect on the birds during the winter. However, as the area of saltmarsh habitat was reduced or the intensity of disturbance on it increased, spring staging brent geese suffered increasingly severe consequences. From even very low levels of saltmarsh loss/ disturbance the birds had to increase the daily foraging effort above baseline conditions in order to maintain their rate of spring fattening and end of spring body mass. Further deterioration in the saltmarsh habitat resulted in an increasing tendency to feed on farmland i.e. grasslands and further increases in daily foraging effort. However, even these responses were insufficient, and the birds' ability to fatten adequately in spring was predicted to be severely reduced. Although over-winter mortality was not increased by a loss of saltmarsh habitat, reduced access to this habitat, by reducing the birds' ability to accumulate reserves prior to spring migration, clearly has the potential to reduce the brent goose population size by reducing their capacity to reproduce successfully.

The loss of farmland habitat, unless severe, was predicted to have little effect on the birds. Severe loss of farmland did, however, precipitate a return to feeding on intertidal resources in winter and *in extremis*, mass movements of birds to France where intertidal resources were exploited. Nonetheless, extreme loss of farmland habitat was also predicted to increase over-winter mortality levels to unsustainable levels. Increasing levels of disturbance of farmland, which effectively combines habitat loss effects with increased energy expenditure for those birds that are disturbed, resulted in similar but somewhat more pronounced consequences for the birds. Thus, as disturbance levels on farmland increased, brent geese wintering in Denmark, Germany, the Netherlands and England gradually returned to feeding on intertidal resources. However, due to the scarcity of such resources in mid-winter, many of the birds from these countries were forced to fly south to France where they continued to exploit extensive intertidal resources. In spite of this, over-winter mortality of brent geese was predicted to reach very high levels under most farmland disturbance scenarios.

Re-introduction of hunting in Denmark at potentially the most damaging time of year for the geese i.e. during the spring fattening period, will not only result in birds being shot, but is predicted to lead to a marked reduction in the rate of fat accumulation by the surviving birds staging in Denmark. This reflected the reduced access to resources caused by the disturbance due to hunting and the increased rate of energy expenditure incurred while flying in response to such disturbance. The ability of these birds to reproduce would be severely compromised. These results give some indication of the indirect consequences that the re-introduction of hunting in other parts of the spring staging grounds might have for brent geese. However, because, at present, the Danish spring-staging population is only a small fraction of the total, it would seem that the reduced breeding potential of these birds is unlikely to have much effect on the reproductive output of the population as a whole. Nonetheless, simply by killing brent geese in Denmark in spring (and indeed at any other time between October and May), a simple demographic analysis suggests that, even given the density-dependence of reproductive output, an increase in density-independent winter mortality due to the reintroduction of hunting in Denmark will reduce the equilibrium population size of brent geese.

Overall, we succeeded in the principal aim of this work package, i.e. to develop and test a multi-site, behaviour-based model of brent geese within western Europe. However, in all of the environmental change scenarios explored, quite major modifications to the environment were required in order to elicit noticeable effects on the birds' habitat usage patterns, foraging effort, body condition and survival. This may be the case were the birds' environment to change in reality, but may also reflect the limited precision with which it was possible to parameterise a model at the scale of the whole of western Europe. In particular, uncertainty over factors such as: the extent of each habitat at each site, the biomass density of vegetation, its digestibility, energy and nutrient content (and seasonal and geographic variation in these), the shape of functional responses, and indeed the need to amalgamate sites into super-sites, may well have very pronounced consequences for the precision of the model's predictions. Without much greater certainty over all of these issues (and others) the predictions generated here can only be taken as broadly indicative of the likely consequences of various changes to various habitats. Given the difficulties in precise parameterisation of a model of a single site, it is unlikely that a multi-site model at the scale of western Europe can ever be developed to yield precise quantitative predictions. However, future work can build on the lessons learnt here and will undoubtedly lead to an improvement in the predictive power of multi-site models such as that developed here.

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11 CONCLUSIONS

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11.1 Introduction

This chapter summaries the key results of the project in the following sections.

- *Key scientific advances* - general advances made during the project which have contributed to the project's overall success.
- *Key site-specific predictions* - the major model predictions for each of the sites and systems included in the project.
- *Policy guidelines* - simple policy guidelines which can be used when the development of site or system-specific model is not possible or practical.
- *Future research requirements* - future research areas which would increase the utility of the modelling approach developed during the project.

Each section explains how these results are linked to the project's overall objectives, which were as follows.

- To adapt, simplify and parameterize two existing individual-based population models, the single-site wader model and multi-site goose model, so that they could be applied rapidly whenever policy decisions are required and at any geographic scale. The single-site wader model had been extensively tested for one common wader species. The multi-site goose model had been parameterized and tested, in a preliminary fashion, for one common wildfowl species.
- To provide policy guidelines for occasions when the models cannot be applied to the particular case because of shortage of time, resources or expertise.

Achieving these objectives required five detailed scientific objectives.

6) To parameterize the single-site (no emigration) model for the common European wader species through a combination of literature search and new fieldwork on key function parameters.
7) To test the utility and to maximize the speed with which the simplified single-site model could be applied to solve policy dilemmas in a particular system by parameterising the model for three exemplary systems in Spain, France and England which, between them, are subject to diverse activity (salt production, fish-farming, shellfishing, bait-digging, hunting, cycling, disturbance, shore-level rise, habitat loss). The aim was to demonstrate that population predictions for a wide range of policy options are obtainable within an environmental impact investigation of typical duration (e.g. two to three years).
8) To parameterize the multi-site, year-round model for one exemplary herbivorous wildfowl species, the brent goose, which is currently the focus of much debate as to

how best to limit its conflict with various human activities, including agriculture, while protecting its most important sites.

9) To explore how predictions are affected by the assumption in single-site models that hard-pressed, or 'stressed', birds do not emigrate to another site (e.g. estuary) in search of better feeding conditions. This will allow a judgement to be made as to the circumstances in which the models provided for policy-makers should be multi-site or single-site.

10) To explore how population predictions are affected by the rate-maximizing assumption that is made in the present models, when state-dependent decisions may be more biologically realistic.

11.2 Key scientific advances

This section describes the major scientific advances made during the project. It concentrates on general scientific advances, rather than more site- or system-specific results, which are discussed in the next section.

11.2.1 GENERAL SHOREBIRD FUNCTIONAL RESPONSE

The functional response is the relationship between the rate at which a forager consumes food and the amount of food available in the habitat. Typically, intake rate is low when little food is available and rises to a maximum value as the amount of food increases (Figure 11.1). Knowing the shape of the functional response is critical for the individual-based models developed during this project because it determines the minimum food densities at which birds are able to survive and hence largely determines the response of animal populations to environmental change. Functional responses can be time consuming to measure in the field because this needs observation of animals feeding at a wide range of food densities. Because animals tend to avoid areas of lower food density, it is often difficult to measure the shape of the functional response at low food densities.

A key scientific advance made during the project was the discovery in work package WP1 (objective OB1) that the shape of the functional response in waders can be determined by a few simple parameters, in particular, the mass of the bird and prey species concerned (Figure 11.1). This advance meant that the feeding behaviour of waders in work packages WP2, WP3 WP4 and WP6 could be predicted from a general equation and did not need to be measured for each species on each site, an alternative that would have been much more time consuming and not possible within the time scale of the project. The results of this work package have been written up as the following submitted paper.

J. D. Goss-Custard, A. D. West, M. G. Yates, R. W. G. Caldow, R. A. Stillman, J. Castilla, M. Castro, V. Dierschke, S. E. A. le V. dit Durell, G. Eichhorn, B. J. Ens, K.-M Exo, P. U. U. Fernando, P. N. Ferns, P. A. R. Hockey, J. A. Gill, I. Johnstone, B. Kalejta-Summers, J. A. Masero, F. Moreira, R. Nagarajan, I. P. F. Owens, C. Pacheco, A. Perez-Hurtado, D. Rogers, G. Scheiffarth, H. Sitters, W. J. Sutherland, P. Triplert, D. H. Worrall, Y. Zharikov and L. Zwarts. Predicting the functional response in wading birds Charadrii eating macro-invertebrates: the role of Holling's disc equation. Submitted to Ecological Monographs.

Apart from being invaluable within the scope of the current project, the finding that the behaviour of a range of bird species can be determined by a few simple rules, has a wider importance. This is because the finding may be applicable to a wider range of species than just wading birds. Simple rules may determine the feeding behaviour of other species, such as brent geese and other wildfowl. The functional responses used for brent geese in this project were measured independently for the different food types, grass, saltmarsh vegetation, algae and *Zostera*, consumed by the geese. If a new food type were to be included in the brent goose model, a new functional response would need to be measured or derived from the literature. If the shape of the functional response could be predicted from a few simple parameters (e.g. the size of the bird species, structure of the vegetation), it would not be necessary to perform this time consuming work every time a new food type is added to the model. The results from waders suggest that general rules may also determine the behaviour of wildfowl.

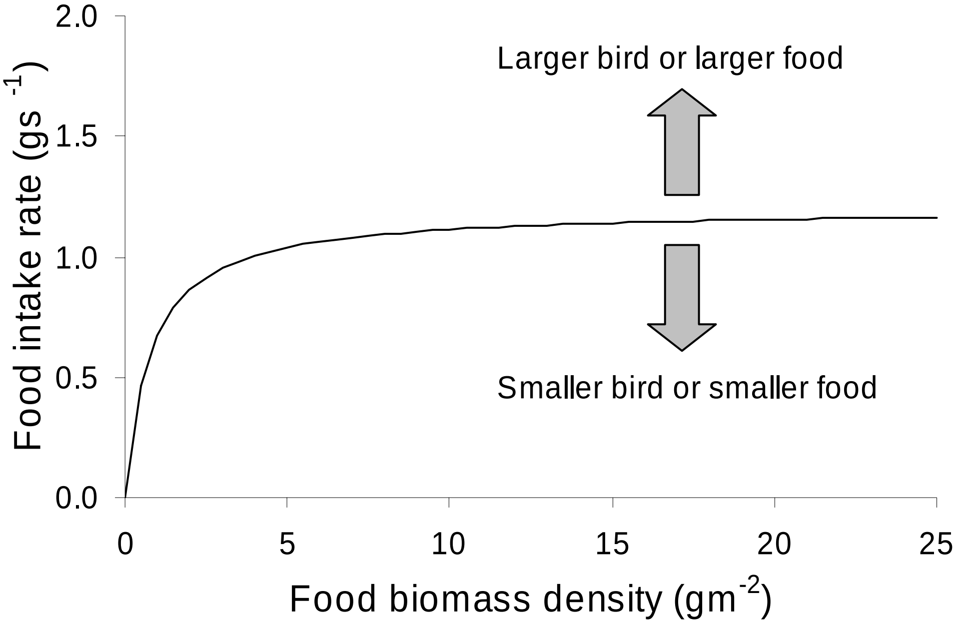

Figure 11.1 Key factors affecting the shape of the functional response in waders. The maximum intake rate at high food densities is higher in larger bird species and when birds are consuming larger food.

11.2.2 GENERAL INDIVIDUAL-BASED MODELLING FRAMEWORK

One of the two main scientific and technological objectives of the project was to derive predictions from two existing models, the single-site wader model and the multi-site goose model. This objective was extended during the course of the project, and instead of adapting these models, a new model was developed which was capable of making predictions for both geese and waders. Figure 11.2 shows how the two models available at the start of the project were superseded by a new more general and flexible model. The new model was called MORPH to indicate that it can take on many forms and be applied to a much wider range of systems and issues than could either of the initial models. The new model is based on the same principles as the existing models and is also individual-based. It builds on the strengths of the existing models, and adds improvements where the previous models were limited.

The development of the new model has been one of the major scientific advances made during the project. The new model has the following advantages over the initial models.

- *Increased flexibility* - the new model is much more flexible than the original models and so can be applied to a wider range of environmental issues. By developing the new model it has been possible to address a wider range of environmental issues than would have been possible with the existing models.

- *Increased insight into the similarities between systems* - by using a single model for both geese and waders highlighted the similarities between these systems, rather than differences.

- *More general* - the existing models were developed primarily for waders or geese, and hence application to other systems was difficult. The new model has been developed in a more general way and so it not simply restricted to these systems. This increases the potential application of the model in the future.

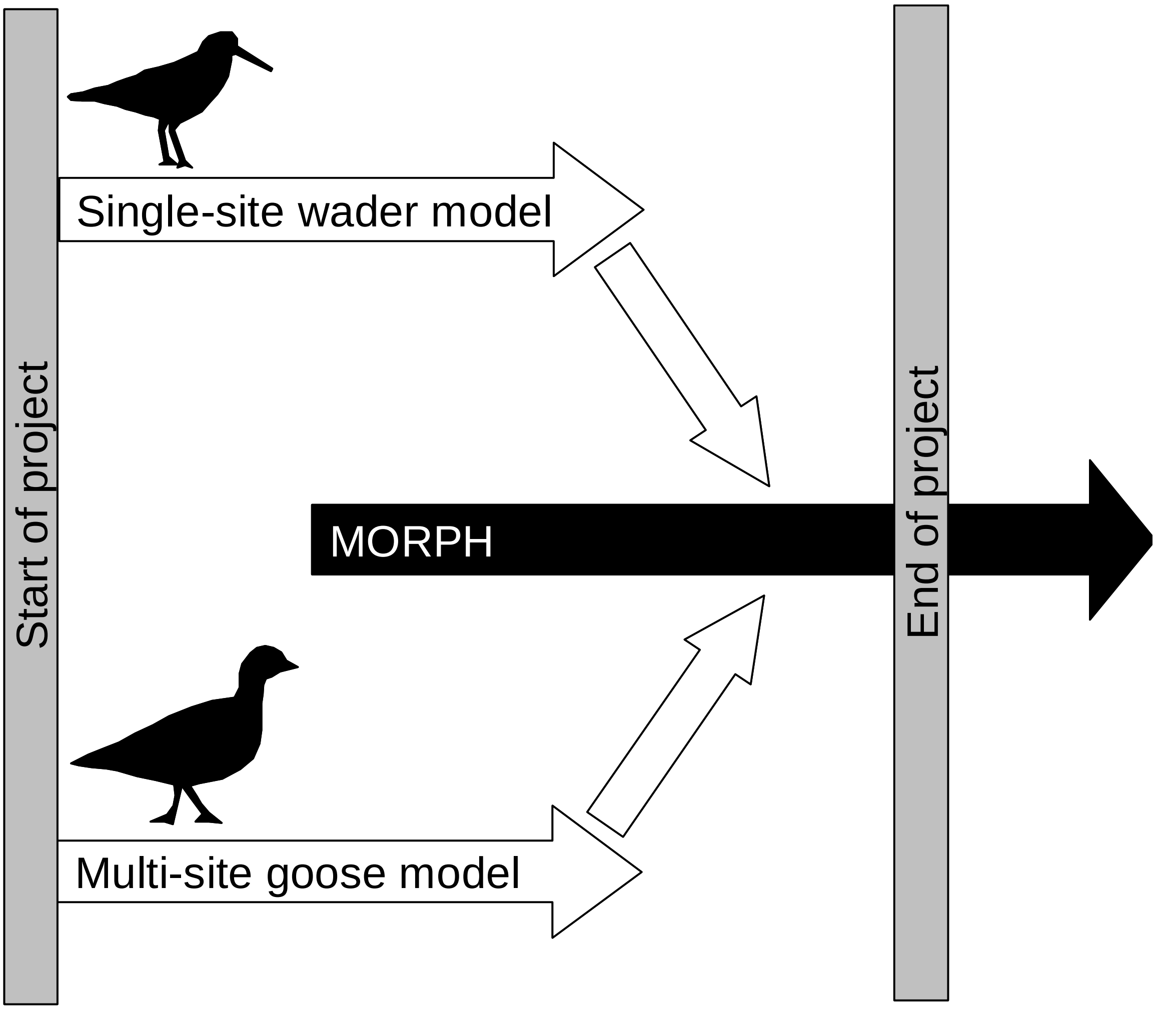

Figure 11.2 How the two models existing at the start of the project have been combined to produce a much more flexible model (MORPH) applicable to waders, geese and a wide range of other species.

11.2.3 RAPID APPLICATION OF MODELS TO REAL-WORLD ISSUES

If individual-based models are to be valuable tools for advising policy, they must be developed within a relatively short time span (e.g. a few years) and produce realistic predictions. The project team had previously developed a detailed model of one wading bird, the oystercatcher, on two sites, the Exe estuary and the Burry Inlet, and a more general model of brent geese. However, it was uncertain at the start of the project whether individual-based models could be developed for a wider range of species, whether realistic predictions could be produced for these species, or whether a wider range of environmental issues could be addressed. Objectives OB2 and OB3 were to test the utility of the single- and multi-site models by parameterizing them from three exemplary wader systems in Spain, France and England and geese through western Europe.

Three site-specific multi-species wader models and a multi-site brent goose model were successfully parameterised using data collected or collated during the four years of the project. The models successfully predicted much of the observed behaviour (e.g. amount of time spent feeding, rate of consuming food) and ecology (e.g. distribution between habitats) of the birds in the real systems. They were also used to answer a wide range of key site or system specific policy issues (e.g. hunting, disturbance, habitat loss of saltpans, fish farms, intertidal vegetation and sandflats). The successful parameterisation, testing and application of the wader and goose models is one of the key scientific advances made during the project, because it shows the potential of the approach to address European coastal issues.

11.3 Key site-specific predictions

This section summarises the key predictions of the models developed during the project. These address objectives OB2, OB3, OB4 and OB5.

11.3.1 SINGLE-SITE WADER MODEL: RATE-MAXIMISING AND RISK-MINIMISING DECISIONS

- This work compared the predictions of models assuming that oystercatchers use either rate-maximising or risk-minimising decision rules to determine their prey selection. These models mimicked the observed behaviour of oystercatchers in the Burry Inlet (risk-minimising) and Dee estuary (rate-maximising). The risk-minimising model predicted that birds should select a safe diet when safe food is abundant, but switch to a risky diet when the density of safe food declines. This prediction is in accordance with the observation that oystercatchers avoid more risky prey on the Burry Inlet, where feeding conditions are better, but consume risky prey on the Dee estuary, where feeding conditions are poorer. The different decision rules changed the order in which the safe and risky diets were consumed. The two models produced different survival predictions if the prey differed in their seasonal changes in quality or their rates of loss to additional mortality sources. This means that it is important that individual-based models incorporate decision rules that mimic those used by birds in the real system, particularly if different prey types differ in their changes in quality or abundance.

11.3.2 BAHIA DE CADIZ WADER MODEL

- Simulations suggested that the abandonment of traditional salinas and the intensification of aquaculture would have very little effect on the bird species included in the model, but it should not be concluded from this that the loss of salinas from the Bahía de Cádiz natural park would cause no harm. There are several reasons for this.

First, the majority of the species included in the model feed predominantly on intertidal muds, so salina abandonment should not be an issue for these birds. Other species that were not included in the model, avocet, *Recurvirostra avosetta*, or spoonbill, *Platalea leucorodia*, for example, might be more dependent on the salinas. Second, we were not able to include pre-migration fattening in the model, although it could be added at a later date if the necessary information becomes available. There are indications that the salinas might play an important role in pre-migration fattening for some species, so their loss could cause some birds to fail on their spring migration, or indeed to be unable to migrate at all. Finally, some of the richest areas in the Bahía de Cádiz are the river muds. Although these are very rich in invertebrates, they are also narrower than the intertidal mudflats and it is possible that many waders avoid feeding in these areas because of perceived predation risk. Many birds in the model did feed in these areas when supratidal prey were removed, but if real birds perceive them as too risky, the effect of supratidal habitat loss would be greater.

11.3.3 BAIE DE SOMME WADER MODEL

- Reducing the area hunted in the Baie de Somme resulted in improved chances of survival in all three shorebird species modelled, even though only two of the species, oystercatcher and curlew, were actually shot. Reducing the length of the hunting season by up to six weeks resulted in increased survival in oystercatchers, but not in curlew and dunlin.

- If *Spartina* encroachment continues at present rates, dunlin survival is likely to be affected in five to ten years' time.

- Oystercatcher survival clearly decreased when daily disturbance events within the Reserve (over and above disturbance from cockle fishers) exceeded a threshold of 2.5 h^{-1}.

- Oystercatcher survival decreased when mean cockle densities (>15mm) at the start of the winter were less than 250 m^{-2}.

- Numbers of cockle fishermen could be doubled before there was any decrease in oystercatcher survival. Long-term disturbance by fishermen (where birds merely avoid feeding in a certain area) was much less deleterious to oystercatcher survival than short-term disturbance events (involving the cost of flight).

- Simulating the effect of accretion by removing upshore cockle populations alone had no effect on shorebird survival. However, simulating the loss of all upshore prey populations significantly reduced survival in all three shorebird species.

- Increasing the population size of dunlin and oystercatchers resulted in a steady decrease in overwinter survival. Increasing curlew numbers by up to 50% had no effect on curlew survival, indicating that higher numbers of curlew could overwinter on the Baie de Somme.

11.3.4 EXE ESTUARY WADER MODEL

- Disturbance of shorebirds feeding on mudflats beside a proposed cycle path along the side of the Exe estuary is unlikely to affect the survival of any of the six shorebird species modelled.
- Disturbance of shorebirds feeding in fields at high water could affect the survival of curlew and black-tailed godwit.
- Disturbances of up to $5h^{-1}$ at the high water roost at Dawlish Warren had no affect on shorebird survival.

11.3.5 MULTI-SITE WADER MODEL

A multi-site model will tend to produce different predictions to a single site model (i.e. predict a higher survival rate) if:

- Alternative sites are close enough together so that alternative sites can be reached by birds forced to emigrate from a site.
- The alternative sites can support the emigrating birds because they (i) have a lower initial density of birds, (ii) are larger than the birds' initial site and / or (iii) have a higher food density than the birds' initial site.

The survival of birds initially starting on the alternative sites can be decreased when:

- These sites can not support the resident and immigrating birds because they (i) have a high initial density of birds and / or (ii) are smaller than the site from which birds are emigrating.

11.3.6 MULTI-SITE BRENT GOOSE MODEL

- Loss of, or increased levels of disturbance on, intertidal habitats i.e. *Zostera* and green algal beds is predicted to have little effect on brent goose over-winter survival or rate of spring fattening, subject to the condition that increased grazing pressure on alternative habitats, notably farmland, is not prevented by increased scaring activities by farmers.
- Loss of, or increased levels of disturbance on, saltmarsh habitats is predicted to have little effect on brent geese during the winter months but to result in increased foraging effort, a switch to farmland habitats and decreased rates of fattening in spring.
- Loss of, or increased levels of disturbance on farmland habitats (if severe enough) is predicted to result in a return of brent geese to feeding on intertidal resources in winter, large scale movements of birds to the south and high levels of over-winter mortality. Birds surviving to the spring are predicted to be little affected by loss of or disturbance to farmland.
- Changes to brent goose's traditional intertidal resources are predicted to be less damaging to them than either changes to saltmarsh habitats or farmland habitats. Changes to the former habitat are most likely to affect the brent goose population by

altering the rate at which birds fatten in spring and hence their probability of breeding successfully. Changes to the latter habitat are most likely to affect the brent goose population by altering their over-winter survival rate.

- Renewed hunting of brent geese in Denmark, if conducted in spring, has the potential to reduce the rate at which spring staging birds in Denmark accumulate fat reserves prior to migration. This, however, is predicted to have a negligible effect on the overall reproductive performance on the population as a whole. Nonetheless, the direct kill of geese staging in Denmark is likely, on the basis of a simple population demographic analysis, to reduce the brent goose equilibrium population size.

11.4 Policy guidelines

The previous section described the key predictions of the models developed during this project. These models can be used to advice policy within each of the specific systems included in the project. Although the models were developed relatively quickly, model development will not always be an option. A key objective of the project was therefore to provide policy guidelines for occasions when the models cannot be applied to the particular case because of shortage of time, resources or expertise. This section describes the major policy guidelines (highlighted in *italics*) which can be derived from the project's results.

11.4.1 MONITOR BIRD FOOD RESERVES AS WELL AS BIRD NUMBERS

Estuary managers are often required to monitor the quality of a site for important bird species or to assess how potential changes to a site may influence site quality. The conservation importance of an estuary is often measured in terms of bird numbers using the estuary, but monitoring numbers is not necessarily a reliable way of assessing changes in site quality. In particular, this is because the numbers of birds using a site depend not only on the conditions at the site, but also the conditions at other sites both within the non-breeding and breeding seasons. A reduction in numbers at a site might be due to a decrease in the site's quality, but it might also be due to an increase in the quality of other sites. A decrease in reproductive rate or an increase in overall mortality rate will reduce the overall population size, which could reduce the number of birds using the site, even though its quality had not changed. Another draw-back of assessments using bird numbers is that they are not predictive and so it is often too late to take remedial action by the time the change has been detected.

The models developed during this project have mainly predicted the effect of food abundance and quality on bird survival rate. They have predicted site quality as the survival rate of birds on a site rather than simply the numbers of birds on the site. The survival rate of birds depends on the amount of food available within a site. When food is abundant, survival rates are high, but survival decreases when food abundance declines below a threshold value. From this is it possible to derive critical amounts of food required to maintain high body mass and survival (e.g. Stillman *et al*. 2003; Goss-Custard *et al*. 2004). Changes in the food supply can be used in combination with bird numbers to determine whether any decline in bird numbers is likely to reflect a problem on the site itself. Decreasing bird numbers in combination with a decrease in the amount of food would indicate that the problem was within the site, whereas decreasing bird numbers without a decrease in the food supply would indicate either that the problem was not limited food within the site, or that the decrease in bird numbers was due to factors outside of the site.

A policy derived from these predictions would be to establish a monitoring programme to record the abundance of food on sites at the start of winter as well as continuing the usual procedure of monitoring bird numbers. Recording the food supply on a site can be recorded with a few weeks (as shown in the current project), but can require considerable resources on large sites. For this reason, monitoring may only occur on a 5-7 year basis and perhaps on a limited number of key sites.

11.4.2 MONITOR THE USE OF MARGINAL HABITATS AND FEEDING TIMES

The models developed during this project all predicted that birds fed in the most profitable and safest places and times when feeding conditions were good and survival rates high, behaviour which mimicked that of real birds. For example, when survival was high, both brent geese and waders were predicted to:

- Avoid terrestrial habitats (e.g. grassland) at night when predation risk from land-based predators (e.g. foxes) was assumed to be higher.
- Avoid disturbed or hunted areas, where they would risk being shot.
- Just feed on their preferred food (e.g. large bivalves or worms, or intertidal vegetation), and roosting when their preferred food was unavailable because it was covered by the tide (e.g. roosting instead of feeding in terrestrial habitats).
- Remain on the same site throughout winter rather than emigrating to alterative sites.

In contrast, birds were predicted to feed more in marginal habitats or at more risky times when feeding conditions were poorer, again behaviour which mimicked that of real birds. For example, both geese and waders were predicted to:

- Feed in terrestrial habitats at night, despite the higher predation risk.
- Feed in disturbed or hunted areas, despite the risk of being shot.
- Feed in marginal habitats when their preferred food is covered by the tide.
- Emigrate to alternative sites.

In summary, increased use of marginal habitats or feeding times is a sign that birds are having increasing difficulty surviving. *A potential policy would be to establish a monitoring programme to detect such changes in the behaviour of bird populations as an early warning that survival rates are likely to be falling.* This approach would pick up possible detrimental changes on a site before increases in mortality rate could be detected through traditional approaches based on bird ringing programmes, increasing the chance that management can be implemented to improve conditions before bird survival declines greatly.

11.4.3 MAINTAIN A NETWORK OF SITES

The multi-site wader and goose models both predicted that birds emigrated from a site when the feeding conditions declined on the site. The consequences for the population depended on whether emigrating birds were able to find and survive on an alternative site. Whether or not birds survived on an alternative site depended on the characteristics of the site compared to those of the site from which the birds had emigrated. However, birds could definitely not survive if they did not have the energy reserves to successfully fly between the two sites (i.e. alternative sites must be relatively close together). *A simple policy derived from this prediction is that wherever possible a network of high-quality sites should be maintained.* This maximises the chance that emigrating birds are able to find and survive on an alternative site, if conditions deteriorate on their initial site.

11.4.4 INCLUDE TERRESTRIAL HABITATS IN CONSERVATION AREAS

Of the three principal habitats exploited by brent geese, farmland habitat proved to be the only one which, if subject to serious deterioration, was predicted to lead to an increase in over-winter mortality. Wading birds, as well as geese were predicted to use terrestrial habitats when feeding conditions declined on their intertidal habitats, a pattern also observed in real birds. Waders consumed more earthworms from terrestrial fields when intertidal food was depleted in late winter. These terrestrial habitats are often critical to the survival of waders and geese, even though they are often considered as marginal habitats. These habitats are often excluded from the designation of Special Protection Areas, but this means that vital habitat is not being protected and as a result may be lost to building developments, suffer high disturbance levels or simply be subject to changes in the way in which it is managed. *A simple policy derived from these predictions is that wherever possible conservation areas should include the terrestrial habitats around estuaries as well as the intertidal habitats of the estuary itself.* This would ensure that the full range of habitats required by birds is protected.

11.5 Future research requirements

This section describes future research which would increase the range of systems and issues to which individual-based models can be applied.

11.5.1 GENERALISED WILDFOWL FUNCTIONAL RESPONSE

One of the key scientific advances of the project was the development of a general mathematical equation to predict the shape of the functional response in waders (i.e. the relationship between the amount of food available and the rate at which food is consumed). This breakthrough was vital for the quick development of the multi-species wader models, because it meant that the general equation could be used to predict feeding rate, instead of the much more time consuming alternative of directly measuring the shape of the functional response for each bird species within the model. Wader feeding rate depended on the size of the bird species, and the abundance and size of the food being consumed.

The brent goose functional responses used in the model were measured separately for each of the different food types consumed. A future research requirement is to derive a general equation to predict the shape of the functional response in brent geese and other wildfowl. The lesson from waders is that this can be done once enough functional responses have been measured over a wide range of different food types.

11.5.2 APPLICATION TO A WIDER RANGE OF SPECIES

Although the model was parameterised for waders and wildfowl, it has been developed in a general way and so can be applied to a much wider range of species. The basic assumption on which the model is based – that birds behave in ways that maximise their fitness (e.g. survival and reproduction) – applies equally to any species. A key future research requirement is to parameterise and test the model for a wider range of species. The following data would need to be collected or collated in order for the model to be developed for other species.

- The range of food types consumed.
- The abundance and quality of the food supply and changes through the season.
- Seasonal and daily changes in the availability of food (e.g. through the tidal cycle)
- The effect of food and competitor density on food intake rate.
- Sources of variation in the food intake rate of different individuals.
- The daily food requirements of animals.
- Target fat store of animals.
- Decision rules which determine the behaviour of individuals (e.g. are these intake rate-maximising or risk-minimising).

Priority species for future study are those of conservation concern, which consume food that can be surveyed relatively easily, occupy relatively open habitats (increasing the ease with which food intake rate can be observed) and have already been intensively studied. Bird species which meet these criteria and so could be modelled in future projects are other wildfowl species (e.g. swans, ducks and geese), storks (*Ciconia* sp.), cranes (*Grus grus*), flamingo (*Phoenicopterus ruber*) and spoonbill (Platalea leucorodia).

11.5.3 APPLICATION TO THE BREEDING SEASON

The model developed during the project is restricted to the non-breeding season, but many sites are of importance for their breeding birds and many coastal issues impact on both breeding and non-breeding birds. The fitness-maximising assumption on which the model is based applies equally to the breeding season. Similarly, birds need to consume food and avoid risks to survive and breed successfully during the breeding season. Extension of the model to the breeding season is therefore a key future research requirement. The following data would need to be collected to develop a breeding season model.

- The habitat required for breeding / nesting.
- The range of food types consumed by both parents and young.
- The abundance and quality of the food supply and changes through the breeding season.
- Seasonal and daily changes in the availability of food (e.g. through the tidal cycle)
- The effect of food and competitor density on food intake rate.
- Sources of variation in the food intake rate of different individuals.
- The daily food requirements of parents and young (particularly changes as the young increase in size).

- Target fat store of parents and young.
- Decision rules which determine the behaviour of individuals (e.g. are these intake rate-maximising or risk-minimising), and how the behaviour of adults is influenced by the condition of their young and mate.

As in the previous section, priority species are those of conservation concern, which consume food that can be surveyed relatively easily, occupy relatively open habitats (increasing the ease with which food intake rate can be observed) and have already been intensively studied. An additional advantage would be to model colonial breeding / nesting species (rather than dispersed breeders / nesters), as this would make collecting breeding data more straightforward. Bird species which meet these criteria and so could be modelled in future projects are storks, flamingo and spoonbill.

11.6 Summary

The Coast Bird Diversity project has developed a general individual-based model for predicting the effect of a wide range of environmental factors on the body condition and survival of coastal wader and wildfowl populations. The model has been parameterised and tested for three wader systems, and brent geese throughout their European range, and has been used to address a wide range of environmental issues. The overall predictions from these systems have been used to make more general policy recommendations. The model has been developed in a flexible way so that its use is not simply restricted to these systems, and in the future can be applied to many other systems for which suitable data are available or can be collected.

11.7 References

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APPENDIX   TECHNOLOGICAL IMPLEMENATION PLAN

Richard A. Stillman

This appendix describes the Coast Bird Diversity project's Technological Implementation Plan (TIP).

In designing the work programme and in selecting the users of its results, we were aware that the resources available to different user organisations vary greatly. At one extreme, an organisation may be able to commission a team of scientists to conduct a comprehensive Environmental Impact research programme over a two-three year period. The project has developed a suite of models to enable such predictions to be made for waders in the Bahia de Cadiz, Spain, the Baie de Somme, France and the Exe Estuary, England, and for dark-bellied brent geese throughout their western European range. The general individual-based model is also available to make such detailed predictions for any other site or system for which appropriate data can be collected or collated. At the other extreme, an organisation may have no opportunity to commission research; it just wants the best advice available at present on which to base its decisions. In this case, the user organisation would only be able to use some clear and simple guidelines as to what effect a particular policy will have on the local coastal birds. This report has described the general policy guidelines that can be derived from the site and system-specific models.

The models have reached the point at which we have defined (a) their applicability to particular sorts of policy matters; (b) their scientific strengths and weaknesses, and (c) the simplest way in which they can be employed, given the resources available. Five wader-specific models and one goose-specific model have been developed during the project and are now available to the scientists and users involved in the project.

The results and methodologies of the project will be made available to the wider community through the following avenues:

- Data and model description in this final report.
- Data and model description in subsequent scientific papers.
- Dissemination to the scientific and user communities through the representatives of the different countries, research organisations and user groups involved in this project.
- Information articles and 'notices' in the appropriate professional newspapers and magazines.
- A web site describing what is now available and how the expertise and information can be acquired. This is located on the Centre for Ecology and Hydrology web site at www.dorset.ceh.ac.uk/shorebirds. The site contains a description of the individual-based models developed during the project and their application to a wide range of coastal bird environmental issues. The web site also contains a "Contact us" page which can be used to obtain more information and access to the models developed during the project.

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