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**Modelling the multispecies functional response of  
generalist marine predators**

Submitted for the degree of PhD on 12<sup>th</sup> December 2005



Th F258

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## Abstract

Generalist predators are important components of many food-webs, and may come into conflict with human interests - for example, by competing for a common resource such as a fishery.

What generalists consume, and in what quantities, depends on the availability of all potential prey. Only by including sufficient complexity into multi-species functional response models (MSFRs) can we understand the impacts of predators on prey, and the consequences for predator populations.

I present two consumption models parameterised for marine mammals: the minke whale, and the grey seal. Some challenges were:

1. The requirement for a large amount of data to parameterise an MSFR. Bayesian methods enabled independent information to be used to suggest prior distributions for parameters, and had the advantage that the posterior distribution of parameters could be sampled to indicate the uncertainty in resulting inferences.
2. Potential error and bias in the available estimates of consumption from stomach sampling (for the whales) and scat analysis (for the seals).
3. The availability of prey had to be estimated by modelling predator movements, and the spatial distribution of prey. Measures of predator-prey overlap, and the uncertainty in these, were obtained.

Using the grey seal model, fish consumption and predation mortality were calculated. Predictions agreed well with estimates based on independent data from a diet survey in 2002. Simple graphical methods suggested that seal predation mortality is less significant for the recovery of the mature cod stock than recruitment variability or fishing mortality.

Simulations based on the minke whale model suggested that whales can deplete aggregations of capelin on a localised scale, and illustrated the importance of the form of the functional response (sigmoidal or hyperbolic).

Plans to investigate the interactions between grey seals, minke whales and their prey by using the consumption models to inform ecosystem models are outlined.

## Chapter 1. Modelling Prey Consumption by Generalist Predators

### Summary

Generalist predators are important components of many food-webs. They may come into conflict with human interests if they compete for a common resource, such as a fishery. Generalists may also pose a threat to prey species that humans wish to conserve but, in some cases, the predators themselves may be of conservation concern. Therefore there is considerable interest in predicting the impacts of generalist predators on their prey, and the consequences of this for predator dynamics.

What prey species generalists consume, and in what quantities, is likely to depend on the availability of all suitable prey. In order to predict the impacts of a predator on a particular prey species reliably, it is important to include sufficient complexity in predation models.

A multi-species model of consumption may, in itself, suggest certain crucial aspects of the relationship between predator and prey. For example, the form of the predator's functional response has implications for the stability of the predator prey interaction. Multi-species consumption models are also a crucial component of larger ecosystem models (Pikitch *et al.* 2004). Consumption models parameterised from independent data sets may be incorporated into such models directly, or they may be used to provide starting values or priors

for subsequent fitting of such models. In this way, multi-species models of consumption may also illuminate indirect effects within ecosystems, such as apparent competition. However, it is important that such models are, if possible, parameterised using data collected from free-living animals.

In this chapter, I use the results of some studies of generalist predation to demonstrate in more detail how models of consumption might be applied in practice, and why they are of particular interest. The biological principles and mathematical form of some well-known FR models are introduced, firstly for specialist predators and then for generalists, and the concepts of preference and switching are discussed.

I then address the problems of collecting and analysing data on consumption and on prey availability to predators, and introduce two marine mammal generalists - the minke whale (*Baleonoptera acutorostrata*) and the grey seal (*Halichoerus grypus*). Finally, some general problems that must be addressed in modelling predation by marine mammals such as these are highlighted, and the aims of this thesis are summarised.

### 1.1. The role of generalist predators in biological communities

The dynamics of a predator-prey interaction will depend on the underlying dynamics of the prey in the absence of predation, the impact of predation on the prey (determined by the predator's functional, aggregative and numerical responses), and the impact of prey density and prey consumption on the predator's dynamics. The functional response (FR) relates the rate of consumption by the predator to the abundance of prey (Holling 1959, Case 1999). If predators move in response to spatial variation in prey abundance, showing a preference for areas according to the availability of prey there, this is an aggregative response (AR). The numerical response is here taken to mean changes in predator numbers that are due to changes in the population size of the predator resulting from reproduction rather than movement, (Turchin 2003).

The impacts of generalist and specialist predators on their prey differ in two key ways: populations of generalists may be relatively stable despite changes in prey populations, due to their ability to adapt their diets and switch prey; when generalists switch from one prey to another, they may mediate indirect interactions between different prey species. In addition, the life histories of generalist predators are 'slow' compared with those of their prey, so that predator dynamics may not need to be modelled explicitly. Instead, their numbers may be assumed to be fixed, or predicted using a straightforward form of aggregative response (Gascoigne and Lipcius 2004, Graham 2005). It

should be noted, however, that in reality a generalist predator may still be dependent on one prey type more than any other, for its survival. One example is the arctic fox (*Alopex lagopus*) in Sweden, which appears to depend on lemmings *Lemmus lemmus* (Elmhagen *et al.* 2000).

In communities, generalists may play an important role in influencing overall diversity, allowing competing prey species to co-exist (Cramer and May 1971, Parrish and Salla 1970). Predation on one prey species may be reduced if the numbers of another prey species increase. In theory, the magnitude of this effect can be understood if the details of predator's FR are known, (Abrams and Matsuda 1996, Eubanks and Denno 2000). However, generalists may also be responsible for extinctions, and consequent reductions in species diversity. A generalist predator may persist even if one of its prey is eliminated, because it is buffered by the continuing presence of alternative prey, an example of 'decoupling' of predator and prey populations. For example, generalist lizard predators have been shown to reduce species richness in island populations of spiders (Spiller and Schoener 1998).

If predators aggregate in response to concentrations of one prey species, this may have a deleterious effect on other prey species, a phenomenon known as apparent competition (Holt and Kotler 1987). Apparent competition may also occur as a result of longer-term numerical responses of the predator mediated by increased consumption of food (Holt and Lawton 1994). However, whether an increase in predator numbers is due to aggregation or reproduction, the

presence of alternative prey will also have a positive indirect effect on the focal prey species, because predators will be partially satiated by alternative prey. Positive indirect effects between prey species can emerge, if the reduction in prey consumption by individual predators outweighs the increase in overall predation generated by the predator's aggregative and numerical responses (Abrams and Matsuda 1996). Detailed models of the FR, along with models of numerical and aggregative responses, are required if indirect effects of this kind are to be modelled realistically (Gascoigne and Lipcius 2004).

Prey populations sometimes show cyclic behaviour, and various models exist to explain why this occurs (Turchin and Hanski 2001, Matthiopoulos *et al.* 2005). Generalists can suppress the recovery of such populations from the low point of their cycles if their abundance is not tightly coupled to prey abundance (Hanski *et al.* 1991, Lambin *et al.* 2000). In some regions, cyclic fluctuations of lemmings may be completely suppressed by predation (Krebs *et al.* 1995). Generalist predators may also synchronise the cycles of several prey species by switching from one prey type to the other, thus keeping them out of phase: this is known as the alternative prey hypothesis (Wilson and Bromley 2001).

In one recent study, the three themes of coexistence, apparent competition and population cycles were brought together in a study of the hen harrier preying on three key prey species in the UK (Matthiopoulos *et al.* 2006). A

multi-species functional response (MSFR) model was used along with models of predator aggregative response and prey population dynamics to explore the potential impact of a generalist predator on the persistence, population cycles and mean abundance of a commercially important prey, the red grouse (Graham, 2005). The individual models were parameterised independently using field data (Asseburg 2005, Matthiopoulos *et al.* 2005). The balance between positive indirect interactions between prey species (mediated by multi species predation) and negative ones (mediated by predator aggregative responses) could not be easily predicted without this detailed analysis, which relied on sub-models that were parameterised using field data, one of which was the MSFR.

In ecosystem models, the consequences that emerge for stability (May 1972, McCann 2000), and for direct and indirect interactions within the system appear to depend crucially on the nature of the trophic links between species. Significant properties of the system may not be discovered unless trophic relationships are correctly modelled in sufficient detail. The accurate modelling of consumption by generalists is therefore extremely important, particularly in marine systems where food-webs tend to be large and complex (Yodzis 2000 1998).

## 1.2. Modelling prey consumption by predators

Consumption  $C$  by a specialist predator can be represented as a function  $f(n)$  of prey availability,  $n$ .

For a generalist predator, this can be rewritten as

$$\mathbf{c} = f(\mathbf{n}) \tag{1}$$

where  $\mathbf{c}$  and  $\mathbf{n}$  are now **vectors** of consumption rate and availability for all prey species.

$\mathbf{c}$  is generally measured in terms of individual items (Real 1979) or biomass (Prime and Hammond 1987) consumed during some defined time interval.  $\mathbf{n}$  may be measured in the laboratory or in caged field experiments by counting the number of prey in a shared arena of known size (Bergstrom and Englund 2004). In field experiments, where predators and prey are free-ranging, it is generally assessed by quantifying prey density in the area where predators are foraging (Redpath and Thirgood 1999). The availability of prey to a predator may be easily quantified in terms of prey abundance, but in some cases a more detailed comparison of the spatial distribution of predators and prey may be required in order to calculate the true availability of prey. The nature of consumption rate and prey availability data is discussed in more detail below.

For some generalist predators it may not be possible to quantify absolute consumption rates, but relative quantities of prey in the diet can be measured. In these cases, measures of predator preference are used to describe the relationship between prey availability and diet composition. One useful measure of preference, which is calculated as the ratio of the proportion of a given prey in the diet to the proportion available in the environment, is Chesson's alpha index (Chesson 1978). Throughout this thesis, the term 'preference' will be used according to this definition: a type of prey is preferred if the value of Chesson's index for that prey is greater than 1. Concepts of preference (sometimes called "suitability" in the fisheries literature) and changes in preference ('switching') are often used in studies of generalist predation. Here, 'switching' is taken to mean any change in a predator's preference for a given prey.

Absolute consumption can be estimated from diet composition if the energetic content of prey and the energetic requirements of the predator are known, and if it is assumed the predator's energetic requirements are always met (Fedak *et al.* 1985). Alternatively, preferences may be incorporated into a generalised FR model that describes the rate of change of total prey consumption with total prey density. This is the approach used in some fisheries models (Begley 2005). However, models of preference cannot be used to predict predation rates when overall prey availability is low. They therefore have limited use for modelling predator prey-dynamics when prey abundance is likely to vary widely. However, preference models may indicate

some of the properties of the predator-prey interaction. In particular, they can suggest whether predator preferences change according to prey availability - this may have important consequences for the stability of predator prey interactions.

The following steps are involved in fitting a multi-species consumption model:

- i. A mathematical model, or a set of models, relating consumption to prey availability is chosen.
- ii. Measurements of prey availability and predator consumption rate are collected.
- iii. A suitable method is chosen for fitting the consumption model to the data. This should produce not only point estimates for the model parameters, but some measure of the uncertainty associated with them. Uncertainty in model predictions should also be quantified.
- iv. Alternative models may also be compared and selected.

I will now explore the first of these steps by briefly reviewing some of the models of consumption that have been proposed in the literature. This provided the basis for choosing appropriate models for the grey seal and minke whale studies described in Chapters 4 and 5. Single-species FR models are first introduced in terms of their graphical form and their consequences for prey dynamics in simple predator-prey systems. Some of the models that have been used to represent the single species FR are then examined. Many of

these have a mechanistic basis, and the biological reasoning behind the different models may suggest which are most suitable for representing consumption within a particular system. I then discuss how these single-species FR models can be extended to include multiple prey, and models of switching and preference are also introduced.

### 1.2.1 Consumption models

In the classical continuous time Lotka-Volterra predator prey model for a specialist predator and its prey:

$$\frac{dN}{dt} = rN + Pf(N) \quad (2)$$

$$\frac{dP}{dt} = kPf(N) - dP \quad (3)$$

Here,  $P$  is the population density of predators, and  $N$  is the population density of prey.  $t$  is time,  $r$  is the intrinsic growth rate of the prey,  $k$  is the efficiency of conversion of consumed prey into predator offspring, and  $d$  is the death rate of the predators. For the present,  $N$  is assumed to be equivalent to  $n$ , the prey availability to the predator discussed above.  $f(N)$  represents the FR (a function used to calculate the rate at which prey is consumed by the predator). The FR could also be expressed as a function of other variables including predator density  $P$  (Yodzis 1994, Abrams 1994).

An equivalent discrete time model (Case 1999) is

$$N_{t+1} = N_t + \lambda N_t - P_t f(N_t) \quad (4)$$

$$P_{t+1} = P_t + kP_t f(N) - dP_t \quad (5)$$

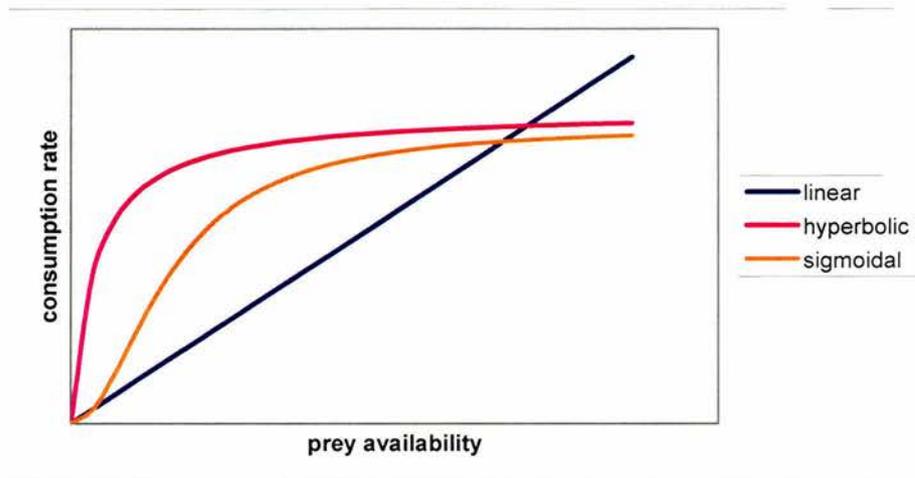
Where the symbols are defined as above, except that  $\lambda$  is now the per capita increase in prey during each complete time step and  $f(N)$  the functional response now represents consumption during one time step, based on prey availability at the beginning of that time step.

Figure 1.1 shows three of the forms that the single-species FR may take, (Holling 1959). A fourth type of functional response (Gentleman *et al.* 2003, Jeschke and Tollrian 2005), in which consumption is depressed at very high predator densities due to toxicity (an effect generally found in bacteria) or predator confusion (an effect most likely to be important when consumption is measured over short time scales), is probably not appropriate for the marine mammal studies in this thesis, and is not considered.

A predator with a linear FR takes food in proportion to what is available. The predator is ‘insatiable’: it can always consume the same proportion of the available prey, however much there is. This kind of FR is occasionally

## Figure 1.1: Forms of functional response

The relationship between the rate at which an individual predator consumes prey and the availability of that prey to the predator when the predator's functional response is linear, hyperbolic and sigmoidal.

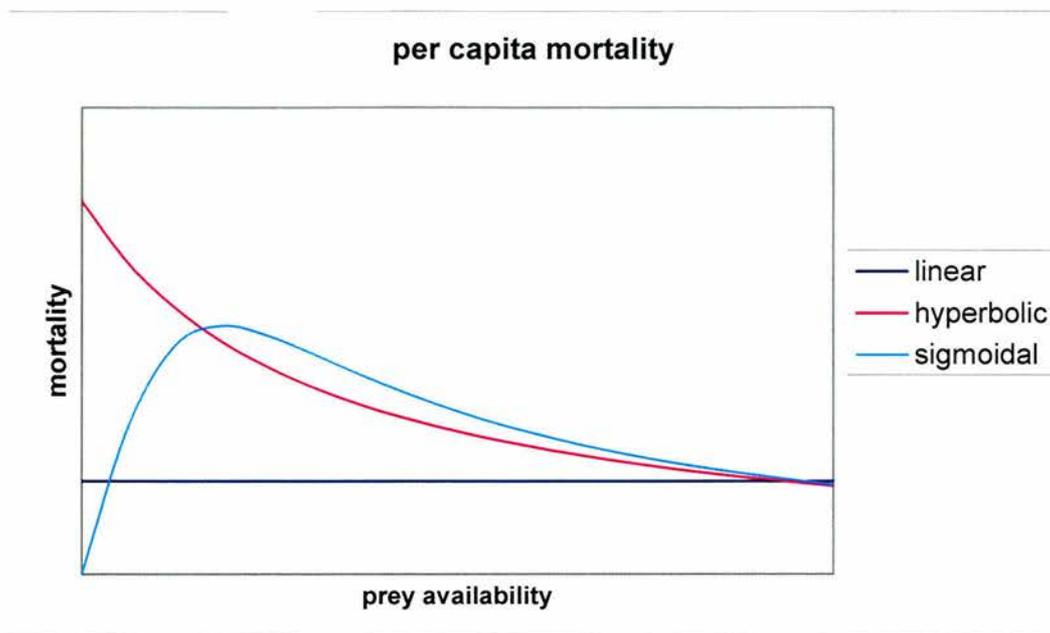


reported, for example in lemmings foraging on plants (Batzli 1981). Filter feeders may also display linear responses over a wide range of prey densities. However, it is very difficult to conceive of a real predator that can consume food at an indefinitely increasing rate, and linear responses that have been observed in real systems probably represent the rising arm of a hyperbolic FR curve. In reality the linear response must level off at some high level of prey availability because predators have a finite ability to process prey. In the simplest modification (Holling 1959), a linear response flattens out abruptly at the maximum rate that is biologically feasible. In a hyperbolic FR, this satiation threshold is approached more gradually, and in a sigmoidal response there is an inflexion at low prey densities such that consumption rate is reduced at these densities.

The precise form of a FR can have important implications for prey dynamics which can be characterised in terms of the **predation risk** or per-capita prey mortality  $c/N$ , which can be calculated from the gradient of the FR, provided that the relationship between prey availability and prey population size is known, e.g. if it can be assumed that availability  $n = N$ .

Plots of predation risk,  $dc/dN$ , against prey numbers, for fixed predator numbers, are shown in Figure 1.2. These relationships will hold true for a system in which predator numbers are 'decoupled' from the dynamics of the prey, and this simplification may be appropriate in some real cases. For example, if the predator's life history progresses over a much longer time

Figure 1.2 Relationship between the per capita prey mortality rate (also known as predation risk) generated by a single predator and the availability of that prey for linear, hyperbolic and sigmoidal functional responses.



scale than that of its prey, or if the predator is a generalist with a 'background' diet of alternative prey such that it is not dependent on the prey of interest for its own growth and fecundity.

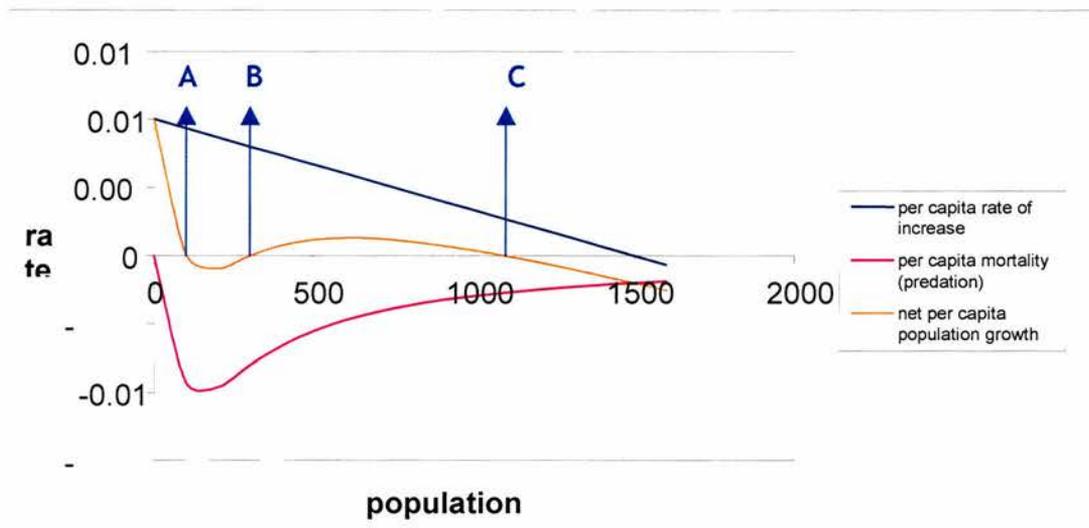
For prey subject to predation by a predator with a linear FR, if predator density remains constant, predation risk does not change with prey abundance.

Hyperbolic FRs result in a predation risk that increases steadily as the prey population decreases, i.e. it is inversely density-dependent, or depensatory (Case 2000). Stable equilibria may exist for prey subject to hyperbolic predation but this is determined by the form of intrinsic density-dependence shown by the prey in the absence of predation. If predator density is sufficiently high, or prey density sufficiently low, that predation mortality exceeds the intrinsic rate of increase of the prey, then the prey species is liable to be driven to extinction (Schoener *et al.* 2001). Prey may be reduced to levels at which predation becomes important by a variety of factors including climatic variation, habitat loss, or over-harvesting by humans. Sinclair *et al.* (1997) documented a number of examples of this effect in interactions between Australian marsupials and introduced predators, such as foxes, *Vulpes vulpes*.

If the FR is sigmoidal, predation risk is positively density-dependent at very low prey densities. This can give rise to a stable equilibrium at low prey

**Figure 1.3: Consequences of predation by a predator with a sigmoidal functional response, and the importance of the intrinsic growth rate of prey**

The consequences of predation by a predator with a sigmoidal functional response for a prey population whose intrinsic growth rate, in the absence of predation, is determined by a logistic function. The net per capita population growth is calculated as the sum of the per capita rate of increase, and the predation mortality (always negative). Prey equilibria occur at population densities where the net population growth rate is zero.



density, sometimes referred to as a 'predator pit', (Holling 1965). Above some threshold prey density, predator-induced mortality becomes inversely density-dependent. A prey species that is 'trapped' at the low density equilibrium can 'escape' if its population exceeds this threshold, and increase to a new, high density equilibrium determined by some other factor, such as the carrying capacity of the environment.

Figure 1.3 illustrates these relationships for a prey population that shows logistic population growth in the absence of predation. The overall rate of change of the prey population at any population density can be calculated from (growth - mortality). In this case, there are two stable equilibria (marked A and C), and an unstable equilibrium at point B. This simple example shows how the nature and position of any prey equilibria depend on the parameter values of the growth and consumption equations. For example, if the intrinsic growth rate of the prey population was higher, A and B could disappear leaving only one stable prey equilibrium, close to the level that would be observed in the absence of predation. While the form of a consumption model gives some indication of the number and kinds of prey equilibria that might occur, the true importance and impact of predation can only be predicted if the parameters of the predator's aggregative response and the prey's density-dependence are known.

Because of the known potential for a sigmoidal response to produce stable dynamics (Murdoch 1975, Moksnes 2005), studies in the field have often

searched for sigmoidal FRs. The classical system in which this was first established is the spruce budworm moth *Choristoneura fumiferana* (Clark and Holling 1979). Pech *et al.* (1992) showed that red foxes preying on rabbits *Oryctolagus cuniculus* in Australia regulate rabbit populations at low levels, but because the foxes show a type 3 functional response, the system is bistable. The rabbit population can occasionally escape from predator control as a result of unusually successful breeding or a reduction in predator numbers, and increase very rapidly in an 'outbreak'.

However, data from laboratory and field studies often provide a good fit to a hyperbolic FR (Fernandez Arhe and Corly 2003, Lundberg 1988). Since many of the predator prey systems that are examined in these studies are known to persist, yet simple dynamical models suggest that that co-existence might be improbable, the apparent prevalence of type 2 functional responses seems anomalous and requires some explanation.

Liermann and Hilborn (2001) reviewed studies of marine predator FRs and noted that, although hyperbolic FRs are commonly reported, the anticipated compensatory population dynamics do not appear to be widespread in marine systems. They suggest the following explanations:

- 1 stochastic effects may mask underlying trends in dynamics at low population levels, e.g. episodes of exceptional recruitment might raise the prey population size such that the prey 'escapes' from a predator

- pit;
- 2 field populations rarely experience population densities that are low enough for depensation to occur, i.e. the effects of inverse density-dependence are not detectable when prey populations are large because the impacts of predation mortality on these populations are insignificant;
  - 3 prey at low prey densities are able to make use of refuges, and the effects of this behaviour are not apparent at normal prey densities;
  - 4 the combined effects of different types of predators acting on a prey population in a complex food web may be more complex than a hyperbolic FR due to one predator alone (May 1972, McCann 2000). This argument is consistent with the observation by Fernandez Arhe and Corly (2003) that predators with hyperbolic FRs are not necessarily better bio-control agents than those with sigmoidal FRs;
  - 5 hyperbolic FRs are an artefact of the procedures that are used to measure consumption and prey availability.

Some authors such as Jost *et al.* (2005) assume that all specialist predators have hyperbolic FRs, whereas others make use of more flexible forms (Messier 1994). What is clear is that data from predators foraging at low prey densities are required to distinguish between hyperbolic and sigmoidal FRs (Hassell 1977). The statistical methods used to fit the FR may have a significant influence on the outcome of the fitting process (Asseburg 2005). Therefore,

some cases of co-existence may actually be a consequence of sigmoidal FRs which have been mistakenly identified as hyperbolic.

The spatial configuration of laboratory studies (Aljetlawi and Sparrevik 2000), the scale of field studies (Jost *et al.* 2005), and the presence or absence of refuges (Anderson 2001) can all affect the estimates of the parameters of FR models. Dale *et al.* (1994) suggested that caribou and wolves are able to coexist, despite the fact that wolves appear to have a hyperbolic FR, because caribou congregate at high density in resource-rich areas. This will result in reduced per-capita mortality and suggests that the form of the FR of wolves to caribou might depend on the spatial and temporal scale over which it is parameterised.

The dependence of FRs on context (Buckel and Stoner 2000), and on temporal and spatial scales (Bergstrom and Englund 2004), suggests that the feeding behaviour of predators may be more complex than that described by a simple hyperbolic FR: the assumptions of the original Holling disc equation may be too simplistic in many field situations, and it may therefore be necessary to use more detailed descriptions of predator behaviour (Abrams 1990).

### 1.2.2 Mathematical expressions for the single-species functional response

A short summary of the mathematical expressions that have been used to describe single-species FRs is presented here, a more comprehensive review is available in Gentleman *et al.* (2002).

Ivlev (1961) developed a model of hyperbolic FRs based on the concept that predators feed according to their level of hunger. As a result, consumption levels off at high prey densities, in a manner analogous to a capacitor filling up with charge.

$$c = b(1 - e^{-aN}) \quad (6)$$

where  $c$  represents consumption rate,  $N$  represents prey availability, and  $a$  and  $b$  are constants.

Holling developed an equation which produces a similar hyperbolic shape, and which has been more widely used, perhaps because it is more tractable algebraically.

$$c = \frac{aN}{1 + atN} \quad (7)$$

In Holling's original formulation,  $c$  is the instantaneous consumption rate and  $N$  is density of prey, where the prey is assumed to be uniformly distributed in space. The parameter  $a$  represents the 'encounter rate' between predators and prey. In one unit of time,  $aN$  is the number of prey items encountered by a randomly-searching predator. The parameter  $t$  represents the time needed to handle each prey item. At high prey densities most of the predator's time

is spent handling prey, so the maximum possible feeding rate is  $1/t$ . At low prey densities,  $C$  is an approximately linear function of  $N$ .

It should be noted that it is possible for the disc equation to predict that  $C > N$ , depending on the parameter values. This apparently counter-intuitive result arises for two reasons:

- i)  $c$  is an instantaneous consumption rate: if depletion is taken into account, prey consumed will not outnumber prey available.  $C$  will be sustained at a steady value only if prey is constantly replenished e.g. by an experimenter feeding prey items into an arena as they are consumed.
- ii)  $N$  may be a count of all prey available to a predator, but it may also be some other indicator of prey availability such as number of prey per  $\text{cm}^2$ . If the predator forages over a larger area, it may consume more prey than this.

The assumptions used to derive the disc equation include:

- (a) encounters between predator and prey occur at random
- (b) the prey are identical, and are uniformly distributed in space
- (c) individual predators cannot search for prey while they are occupied with consuming a prey item that has been captured. The time taken to handle an item of prey does not vary.

(d) predators search for prey at a constant rate, (the 'encounter rate') whenever they are not occupied with consuming a prey item. The encounter rate can be interpreted in terms of the area that a predator searches in a given amount of time, and its ability to detect prey within that area; this does not vary.

Holling's equation is often applied in situations where its assumptions are not strictly met. In particular, the true nature of encounters between predators and prey may often be rather different from that originally suggested by Holling. Aljetlawi *et al.* (2004) calculated encounter rate, using estimates of predator speed and foraging awareness obtained in the laboratory, which they compared with values measured in the field. The two sets of values differed by several orders of magnitude, possibly because prey abundance was not a reliable measure of actual availability. One solution to this problem is to interpret the attack rate as a calibration factor that takes account of cryptic prey that may have a low probability of detection, of the clumping of prey into groups, of mis-matches between the vertical distributions of the predator and its prey, and of uncertainties in the measurement of prey abundance - it may then be possible to model functional responses successfully using equation 7 provided that the spatial scale over which it is applied is consistent with the scale of data collection.

Hassell *et al.* (1975) provide further criticisms of the basic assumptions of Holling's equation, and Abrams (1990) highlights a number of biological issues

that are not taken into account in its conventional form. However, because of its relative simplicity, Holling's equation has been widely used in modelling consumption. It has also provided a basis for more complex FRs that explicitly account for prey aggregation and predator interference (see below). Holling's equation can also be easily generalised to take multiple prey species into account.

One possible modification to Holling's equation is to make attack rate a function of prey abundance (Gendron and Rovert 1987). For example, if  $a$  is made a hyperbolic function of prey density (Hassell 1977)

$$a = \frac{bN}{1+gN} \quad (8)$$

The Holling equation becomes

$$c = \frac{bN^2}{1+gN+b\tau N^2} \quad (9)$$

The justification for these models is that a predator may decide to reduce the effort it puts into searching for prey when they are scarce, in order to optimise its net energy gain (Gurney and Nesbit 1998). There is also some evidence, mostly from host-parasitoid systems, that attack rate does change with prey density and this is probably a result of parasitoids being attracted by the concentration of chemical stimuli (kairomones) associated with high prey densities (Schofield 2005). Large predators such as marine mammals may be attracted by the presence of high densities of prey (Benoit-Bird and Au 2003) and may only be able to attack efficiently where prey is more

concentrated (Acevedo-Gutierrez *et al.* 2002). Predators may also prefer prey that are abundant, or they may quickly become more adept at catching them (Gendron 1987). Predators may also increase their foraging time when prey availability is high (Thompson and Fedak 2000, Sparling *et al.* in prep, Cornick and Horning 2003).

Real (1977) proposed a more general form of Holling's equation based on chemical- kinetic considerations.

$$c = \frac{aN^m}{1 + aN^m} \quad (10)$$

This equation can be obtained by assuming that encounter rate in the Holling equation is related to  $N$  by a simple power law  $aN^{m-1}$ , (Yodzis 1994). The value of the exponent  $m$  affects the shape of the relationship between predation risk and prey density, and hence the nature and magnitude of prey equilibria (see Figure 1.3).

Sigmoid FRs may emerge if the prey has a refuge, a physical or temporal hiding place where it can escape from predation (Forrester and Steel 2004). Refuges can give rise to sigmoidal curves provided that either (i) the refuge is of limited size (i.e. the proportion of prey in the refuge must go down as the prey density increases, as a result density-dependent mortality occurs as prey are forced outside the refuge so that they can be taken by the predator - evidence for such effects has been found for example by Forrester and Steele

in their studies of coral reef fish or (ii) prey spend more time in the refuge as predation pressure increases.

The existence of such a refuge will tend to stabilise the system, provided that effect (ii) is not so strong as to reduce the total attack rate of the predators as predator density increases, (Sih 1987). Moses and Sih(1998) showed that mosquito larvae spent more time in a refuge from the predator *Notonecta* when the predation risk was increased. Similar risk-dependent use of refuges has been demonstrated for certain fish that use a refuge (weed) in response to predation (Anderson 2001). An interesting application of this reasoning is that habitat manipulation might assist with conservation efforts. Sinclair *et al.* (1997) suggested that the adverse effects of inverse density-dependent predation by introduced generalist predators on endangered indigenous prey in Australia could be reduced by providing suitable refuges.

Prey inside a refuge may have reduced opportunities to feed, breed and forage. Krivan (1998) examined the trade-off between these costs and benefits by allowing prey to modify the amount of time they spent inside and outside a refuge in a two-patch Lotka-Volterra system. This resulted in stable oscillations. However, McNair (1986) questioned the stabilising effects of refuges based on more detailed modelling of refuge effects, and Collings (1995) describes how refuges can result in uncontrolled outbreaks of prey if a sufficiently large population can build up within the refuge.

Sutherland (1996) has pointed out that empirical estimates of handling time are usually shorter than those calculated from the asymptote of the FR. He suggests that interference may be partly responsible for this. Interference is the term used to describe interactions between predators that reduce individual predator efficiency. This can occur due to aggressive behaviour between predators or effects of predation on prey behaviour and refuge use. For example, Stillman *et al.* (2000) found that bivalves adopt a ‘safe’ condition when they are aware of the presence of redshanks (*Tringa totanus*) nearby: predators do better when other predators are absent, because predators interfere with one another by ‘scaring’ prey into a refuge state.

Yodzis (1994) reviewed some of the ways interference has been incorporated into the FR. For example, Hassell and Varley (1969) modelled interference by writing the attack rate as

$$a = \frac{QN^{n-1}}{P^m} \quad (11)$$

where  $N$  and  $P$  are prey availability and predator density as defined above, and  $Q$ ,  $n$  and  $m$  are constants, resulting in the following equation (derived from the Holling equation)

$$c = \frac{QN^n}{QtN^n + P^m} \quad (12)$$

Where  $t$  is the prey handling time.

Other workers (Beddington 1975, DeAngelis 1975, Crowley and Martin 1989) have proposed modifications of the Holling equation that have a more mechanistic basis. They assumed that predators lose time they could be spending in searching for prey as a result of interference, and introduced predator abundance into the denominator of the FR, alongside  $t$ . Beddington and DeAngelis obtained the following equation:

$$c = \frac{aN}{1 + bN + cP} \quad (13)$$

Where  $c$ ,  $N$ , and  $P$  are defined above, and  $a$ ,  $b$  and  $c$  are constants.

Interference may give rise to stable dynamics (Hassell 1978, Moksnes 2005). However, although interference has been demonstrated under laboratory conditions (Skalski and Gilliam 2001) and may account for some field observations (Sutherland 1996, Jost *et al.* 2005, Schenk *et al.* 2004), it may not be so important in real situations where the density of predators is often relatively low (Free *et al.* 1977, Van Gils and Piersma 2004). Some caution also needs to be used when applying interference models to predators, such as wolves, killer whales and dusky dolphins that feed co-operatively, because anomalous effects may occur when predator densities are low and co-operative hunting is impossible (Jost *et al.* 2005, Benoit-Bird *et al.* 2004, Baird and Whitehead 2000).

The assumption that predators and prey are uniformly distributed underlies many FR models. However, natural environments tend to be patchy and prey

may aggregate in high quality patches in order to breed or forage. Predators will then seek out these areas of high prey density. Prey aggregation can also stabilise some predator-prey models. Hassell and May (1973) were able to generate stable dynamics in a system based on the inherently unstable Nicholson-Bailey equations for parasitoid-host dynamics by incorporating patches with different host densities, and parasitoids that searched according to a fixed strategy. Cuddington and Yodzis (2000 2002) show that limited mixing, which tends to result in non-uniform predator and prey distributions, can limit prey encounter rates and reproductive rates, and thereby stabilise population dynamics.

Another way of modelling the effects of predator aggregation is to assume that prey outside these aggregations are in a refuge, in which case the FR may be sigmoidal (Sutherland 1996). van Baalen and Sabelis (1993) showed that natural selection may favour the evolution of aggregating behaviour in both prey and predator, provided there are patches of marginal quality for the prey that can act as refuges.

May (1978) took a simpler statistical approach to modelling 'unevenness' in predator attacks. He assumed that attacks by parasitoids in host patches could be described by a negative binomial distribution. This resulted in a stable equilibrium if attacks were sufficiently aggregated. Attacks targeted at especially vulnerable or desirable hosts are quite commonly found in nature,

including vertebrate systems, for example Hudson *et al.* (1992) showed that red grouse with a heavy parasite burden are more vulnerable to predation.

Beddington *et al.* (1978) suggested that aggregation could explain the differences between the behaviour of host-parasitoid systems in the field and in the laboratory. They pointed out that there were differences in the level of suppression a biological control agent could achieve in these two situations. They suggested two possible explanations: that heterogeneous landscapes can provide a refuge for hosts against attack; and that aggregation of parasitoids could reduce their attack rate through 'pseudo-interference' (Free *et al.* 1977) where parasitoids overall search efficiency is reduced when they are at high density because they deplete patches of prey .

The concept of optimal foraging (Abrams 1982, Sih 1984), in which individuals behave so as to optimise some measure of fitness, has also been used to model consumption. In individual based models the theory can predict, for example, inverse density-dependence due to predator aggregation (Kacelnik *et al.* 1992, Comins 1979). Mori and Boyd (2004) found that optimal foraging provided a useful framework for modelling the diving behaviour of Antarctic fur seals *Arctocephalus gazella* foraging on krill *Euphausia supurba*, and they concluded that their observations were consistent with a sigmoidal FR over a range of temporal scales.

There are some important difficulties with the concepts behind optimal foraging models (Pierce and Ollason 1987, Stearns and Schmid-Hempel 1987). Probably the most important is that fitness, the quantity that is maximised, must be clearly defined and may be difficult to measure. Darwinian fitness (measured for example by the number of offspring that are ultimately recruited into the adult population) is likely to be influenced by many other factors in addition to absolute food intake. Nevertheless, the concepts of optimal foraging have proved useful in studies of predators and their prey, and may offer particularly useful insights into modelling preference and switching by generalist predators (Krebs 1978).

### 1.2.3 MSFRs, preference, and switching.

A multi-species version of Holling's equation is

$$C_i = \frac{a_i N_i}{1 + \sum_j a_j t_j N_j} \quad (14)$$

Where  $C_i$  is the consumption rate of prey type  $i$ . This equation takes account of the foraging time that is lost due to handling items of all prey types. It assumes a randomly searching predator and uniform distributions of all prey. A version of equation (14), re-parameterised in terms of maximum consumption rate and half-saturation prey abundance, is often used in fisheries models (Hilborn and Walters 1992, Mackinson *et al.* 2003). Because the predator makes no active choices between prey types, the multi-species

version of Holling's equation should be predictable from measurement of the predator's FR to each of its prey species (Gentleman *et al.* 2002).

If the availability of other prey is constant the resulting conditional FR might still be expected to have a recognisable form and could probably be successfully parameterised using one of the single species FR models, though the meaning of the parameters obtained would be different from those which would be determined by fitting in the true 'single species' prey case. More commonly in field studies, however, the observed FR of a predator to one of its prey is measured in the presence of variable amounts of alternative prey - the 'marginal' FR (Redpath and Thirgood 1999). This may appear similar to a single species FR if alternative prey are scarce, or are not taken in significant amounts. If other prey do make an appreciable contribution to the predator's diet, the marginal FR may appear almost devoid of meaning with little correlation between consumption and availability, due to large unquantified effects of the other prey in the system. There is therefore a danger of concluding that no significant relationship between consumption and prey availability exists, because this relationship is masked by 'noise' that results from the variable consumption of other prey. Distinguishing the consumption signal from this background noise is likely to be a particular problem where data are sparse. If a single species FR can be fitted to data of this kind, there is no reason to expect that the parameters recovered will correspond with the 'true' parameters of the conditional FR for zero alternative prey. Rather, 'compromise' parameters would probably be recovered, which reflect the

‘averaged’ background effect of alternative prey on the consumption of the target species.

Therefore, an important step when modelling consumption by a generalist, is to decide what prey species should be included in the model. All ‘important’ prey species should be included. This may seem a trivial question for some generalists whose diet is well known, and which consume only a restricted number of prey types. However, where generalists may consume a broad range of prey then obtaining sufficient data to parameterise a large multi-species model for many different possible prey items may be very difficult. If some prey make up only a small part of the predator’s diet, there is a question as to whether such prey should be included in a consumption model.

Some insight into the problem of which of the available prey should then be added to the consumption model is offered by Yodzis, who suggests that relatively ‘weak’ trophic links (those which represent as little as ten percent of a predator’s diet) may need to be included in order to model ecosystem dynamics successfully (Yodzis 1998, Yodzis 2000). The idea of a ‘minimum realistic model’ which can capture the important behaviour of an ecosystem by incorporating the most important trophic links is explored by Punt and Butterworth (1995). Considering the strength of trophic links in terms of the proportion of prey in a predator’s diet may then be an appropriate approach in choosing prey for a multi species consumption model, if the ultimate aim is

to apply this model to predicting long-term consequences for predator and prey populations

Another way of investigating the diets of generalists has been by means of preference: how does the composition of the predator's diet compare with the relative abundance of available prey?

Equation 14 has the convenient property that the denominator is the same for all prey species. It is therefore easy to show that the ratio of the consumption of two species  $i$  and  $j$  is given by

$$\frac{c_i}{c_j} = \frac{a_i N_i}{a_j N_j} \quad (15)$$

So, the relative proportions of the two prey species in the diet should be directly proportional to the ratio of their abundances, i.e. the predator shows a constant (i.e. frequency-independent) preference for prey  $i$  relative to prey  $j$ . There are many different measures of preference in use, Cock (1978) and Manley (2002) provide helpful reviews and summaries of the relative merits of the different indices. Frequency-independent preferences are often assumed, for example in many fisheries models (Hilborn and Walters 1992, Floeter and Temming 2005), and have been demonstrated in experimental situations (Hassell 1978). However, deviations from constant preference are also known to occur (Murdoch and Oaten 1975, Colton 1987) and are often referred to in the literature as 'switching'. Although some authors (Abrams and Matsuda

1996, Abrams *et al.* 1996) have objected to this usage, the term switching will here be retained to indicate any change in preference that is dependent on prey availability, no matter what the underlying cause.

Possible causes of switching include:

- Predators become ‘trained’ in hunting one type of prey when it is abundant, for example whelks may learn to adapt their behaviour to hunting a particular type of prey (Murdoch 1969)
- Predators need to develop a ‘search image’ for a prey species and they can only do this when that species is relatively common (Bond and Kamil 1999)
- Predators are attracted to aggregations of prey by signals that can only be detected if they exceed some threshold
- Predators may optimise their energy intake, switching away from low-density prey where other prey is available at higher density (Northridge 1990)

As in the single-species case, the multi-species FR model can be adapted to incorporate a variable attack rate that depends on prey density. For example:

$$c_i = \frac{a_i N_i^{m_i}}{1 + \sum_{j=1, \dots, n} a_j t_j N_j^{m_j}} \quad (16)$$

This model can accommodate changes in preference for particular prey types because:

$$\frac{c_i}{c_j} = \frac{a_i N_i^{m_i}}{a_j N_j^{m_j}} \quad (17)$$

Attack rates may vary with prey availability because predators choose to hunt in areas that are most rewarding. When prey become scarce in one area, the predator may move elsewhere and as a consequence 'switch' to another prey species (Akre and Johnson 1979). A possible example of this is the 1986-1988 invasions of the Norwegian coast by harp seals *Pagophilus groenlandicus*, which is believed to have been a response to the collapse of capelin *Mallotus villosus* stocks in the Barents Sea (Bogstad *et al.* 2000). Locally, the predator may still have been acting in accordance with a straightforward hyperbolic FR, but globally the effect was to reduce the pressure on scarcer prey. Hines *et al.* (1997) found that foraging by eagle rays *Myliobatis tenuicaudatus* on bivalves dropped off rapidly when prey density fell below a critical level. The rays concentrated their efforts on high density prey patches, which suffered 4% mortality, compared to the 1.6% mortality experienced by the total bivalve population.

Viewed on a large spatial scale, it may be possible to represent changes in habitat use resulting from changes in prey availability in terms of attack rates that change with prey density according to a simple power law. However, such a model cannot describe switching that is not simply the result of the FR to individual prey but represents some kind of behavioural preference or choice on the part of the predator. For example, predators might turn to a prey which it knows to be abundant in the environment (Abrams 1990). Buckel and Stoner (2000) found that the switching behaviour of bluefish *Pomatomus*

*saltatrix* under laboratory conditions was inconsistent with the estimated parameters of their single species FRs. In these situations, the predator's preference for a particular prey species may depend on the abundance of that species relative to the abundance of all other prey species, rather than its absolute abundance as would be predicted by equations 14 and 16. If a preferred prey becomes scarce, the predator will switch to a more common prey. Several models of FR that are based on the principle that predators make foraging decisions based on the relative abundance of all available prey ('active choice' or 'active switching', Joly and Patterson 2003) are reviewed in Gentleman *et al.* (2002).

Optimal foraging approaches seem particularly well suited to modelling decisions of this kind. Northridge (1990) made use of optimal foraging concepts to analyse grey seal diet data, and was able to rank prey items in order of their preference. Warnink and Zwartz (1985) also used optimal foraging principles to derive a FR for oystercatchers *Haematopus ostralegus* feeding on bivalves. The oystercatchers utilised two prey types: one with high net calorific value per item, and one that was easier to locate. The oystercatchers switched exclusively to the more easily-located prey when the density of the more calorific prey fell below some threshold value. Joly and Patterson (2003) derived a two-species FR model on the assumption that attack rates are adjusted according to optimal foraging principles.

The disadvantage of including 'active choice' in multispecies models is that extra parameters are required to describe it. Given that field data from predation studies are generally scarce, there is an important compromise to be made between the underlying complexity of a consumption model, the number of prey species to include in that model, and the ability of statistical methods to fit the chosen function to the available data. The importance of identifying the correct biological mechanisms when applying models to predict the behaviour of predator prey systems has been emphasised by several authors (Fussman and Biasius 2005, Matthiopoulos *et al.* 2005). However, relatively simple consumption models may still be able to capture the most important aspects of the relationships between predators and prey provided they are fitted and interpreted at appropriate spatial and time scales (Essington 2004).

One important general prediction that emerges from optimal foraging theory is the 'zero-one rule'. This results in a stepwise FR, in which a predator is predicted to switch from ignoring a scarce prey to consuming all of the available individuals of this prey when prey density exceeds a certain threshold. In practice, however, such discrete stepwise predator behaviour is not observed (Zemek and Krivan 1998), nor does it seem entirely plausible. Theory also suggests that switching would not produce stable predator-prey interactions (Baalen *et al.* 2001). However, experiments (Krebs *et al.* 1977) have demonstrated sigmoidal rather than stepwise predator responses to changes in the relative density of a focal prey type, which could correspond

with a sigmoid FR. This could be because individual predators have different thresholds: they may not be omniscient, but experience their environment and estimate prey abundance in a stochastic way (Northridge 1990); they may be only locally omniscient (Berec and Krivan 2000); or they may need to monitor the density of scarce prey from time to time (Gurney and Nisbet 1998).

#### 1.2.4 The data required to estimate the parameters of a multispecies functional response

In order to estimate the parameters of an MSFR, data for the availability of each prey species to the predator and the consumption rate are needed. If diet composition is known, but absolute consumption rates are not, then preference and switching may still be modelled.

Ideally, measurements should span the probable range of prey availability for each prey type. In this section I will discuss the problems that arise in obtaining these data. Some general issues about spatial and temporal scales will then be discussed, along with possible approaches to tackling these.

#### *Consumption rates*

In the field, consumption rates can be measured by observing predation directly or by using video (Schenk and Bacher 2002), possibly with the aid of

image processing (Hooker 2002). Alternatively, experimenters sometimes measure the amount of prey that has been killed, attacked or removed by foraging predators over a known time interval (see for example experiments by Sundell *et al.* 2000 with the least weasel (*Mustela nivalis nivalis*) preying on voles (*Microtus agrestis*); investigations of the mortality of reef fish by Forrester and Steele (2005); and the study by Bezemer and Mills (2001) of parasitism by the wasp *Mastrus ridibundus* on codling moth, *Cydia pomonella*). Stomach contents of predators can also be used to measure consumption rate only if the time taken for a stomach to empty is known, and the rate of emptying is the same for all prey - conditions which are rarely met, in practice (see Asseburg 2005, and references therein).

It is sometimes possible to determine the composition of the diet of a generalist, even when absolute consumption rates cannot be measured directly. For example, if the rate of stomach-emptying is not known, the proportions of various prey in stomach contents can be used as an estimate of proportions in the diet provided that the rate of stomach-emptying is the same for all prey (see above). Santos *et al.* (2004) used this approach in their study of diets based on stomachs from harbour porpoises (*Phocoena phocoena*). Fatty acid analysis, which requires biopsy samples that can be acquired from living animals, (Iverson *et al.* 2004) can also be used to infer the composition of predator diets. If faecal samples (scats) or regurgitated pellets are available, prey may be identified from hard parts of prey that survive the effects of digestion, for example Eide *et al.* 2005 examined the

diet of arctic foxes on Svalbaard based on scat samples, and Martinez, J.A. & Zuberogitia (2001) used the pellets of eagle owls (*Bubo bubo*) to investigate changes in their diets resulting from an epidemic affecting the population of one of their main prey species. Pierce and Boyle (1991) discuss some issues of uncertainty and bias that may arise in the analysis of scat and pellet data.

Absolute consumption rates can be inferred from diet composition, if the net intake rate of prey is known. Generally, this analysis is carried out using energy as currency. Metabolic measurements and behavioural studies are used to estimate the energetic requirements of a predator, (Folkow *et al.* 2000, Sparling and Smout 2003, Winship 2000), and the rate of intake of each prey can then be estimated from the diet if the energetic content of prey items is known. However, such calculations make some strong assumptions, including that prey only differ in their energetic content - in all other respects they are considered to be nutritionally equivalent. Another assumption is that the energy intake of predators can be estimated independently of prey availability: the predator will always obtain the energy it requires, whether prey is scarce or abundant.

Some methods for analysing the diet of predators detect only the presence or absence of a particular prey in a sample. For example, using molecular techniques, it may be possible to identify prey that has been degraded by digestion so that it is unrecognisable morphologically. The use of a PCR-RFLP assay to detect salmon in seal scats is discussed in Parsons *et al.* (2005), and

there is a more general review of molecular methods used to identify prey in Sheppard and Harwood 2005. Deagle *et al.* (2005) report that proportions of fish DNA in scat samples from Steller sea lions were roughly proportional to the mass of prey items consumed, raising the possibility that DNA quantification methods could provide semi-quantitative diet composition data. However, at present, molecular approaches are generally able only to indicate presence or absence rather than quantities or relative quantities of prey consumed. Only by calculating frequency of occurrence in the population of individual samples could the composition of predator diets be estimated from such data, and this approach may be problematical (Trites and Joy 2005) - it is not discussed further here.

Whether diet is measured in terms of absolute consumption rates or composition, diet measurements should be collected at the same time and in same area as prey availability measurements (Lindstrom 2001), to allow for variations in the abundance and distribution of prey that might influence the diet of the predator.

### *Prey availability*

In laboratory experiments with tractable predator-prey systems, such as parasitoids and their hosts, prey populations can be manipulated in order to obtain a wide range of prey densities. The precise number of hosts or prey is known, and depletion of prey can be easily measured so that the integrated

forms of FR equations can be applied (Skalski and Gilliam 2001). However, it may be difficult to reproduce the 'normal' habitat of prey and predators and so the resulting models may not be applicable to field situations (Schenk and Bacher 2002). This is particularly likely to be true for large marine vertebrates. Refuge use by prey (Anderson 2001), and the spatial distribution of hosts or prey in experimental set-ups (Bergstrom and Englund 2004) are likely to be particularly problematic. As a result the availability of prey to predators in laboratory situations may be very different from that experienced by predators in the field (Ontiveras *et al.* 2005).

In field experiments, other difficulties arise. The abundance of prey species may be very difficult to measure directly. The difficulty of determining how many fish there are in the sea is the subject of a considerable literature (Harley and Myers 2001). One example, particularly relevant to this study, is the challenge of assessing the abundance and distribution of sandeels *Ammodytes marinus*, an important prey of marine mammals and seabirds in the North Atlantic, which spend most of their lives buried in sediment (Wright *et al.* 2000, Greenstreet *et al.* 2005 in prep). Even when abundance is measured accurately, determining the true availability of prey to a predator may present further challenges.

The fine-scale spatial distribution of prey may influence the success of foraging. Local non-uniformity may create patches that are profitable for a predator to harvest, while uniformly distributed prey may be considerably

more difficult for a predator to feed on successfully (Boyd 1996, Lindstrom pers. com.). The effect of prey aggregation on the CPUE of trawls has been modelled and found to be highly significant in the case of krill. It is therefore entirely possible that aggregation, which varies seasonally, might be crucially important for foraging by baleen whales such as minke, (Kasatkina *et al.* 2005). In marine systems the vertical distribution of prey may also be very important to predators that forage near to the surface such as minke whales, or to those which forage on the sea floor, such as grey seals. Many marine animals undertake daily vertical migrations and the availability of such prey can be particularly difficult to assess (Harley and Myers 2001).

In both marine and terrestrial habitats, prey may be virtually inaccessible to predators if the habitat is rich in refuges - an effect that was demonstrated using caged reef fish (Forrester and Steel 2004). Refuges may hide prey from scientists as well as from predators. A consumption model can often be fitted to data on the availability of prey which is outside the refuge, but the size of the entire prey population may be impossible to calculate. As a result, the true nature of the interactions between predator and prey may not be captured by the model. The difficulties of surveying rocky-bottomed areas of the ocean for fish abundance are considerable, although such areas may represent a very important refuge and nursery area for young fish (Jennings *et al.* 2001). Refuges may also take less obvious forms. For example, they may be areas that are not easily accessible to central-place foragers (see below). Quinn and Cresswell (2004) showed that the foraging success for avian raptors

preying on shorebirds depended on prey vulnerability (the distance of prey from locations where predators could launch an ambush attack) rather than simple prey abundance. In this case, the ability of the raptors to make successful strikes was strongly influenced by the proximity of prey birds to cover, from which a raptor could launch an ambush. In this example, it could be argued that areas far from cover represent a refuge and prey availability cannot easily be calculated from a measure of prey abundance. Additional information on the spatial overlap between predators and prey is required.

When spatial overlap must be calculated in order to estimate prey availability to predators, the distribution of predators and prey must be known (Heikenheimo 2001, Bradshaw *et al.* 2002). Recent improvements in spatial modelling techniques (Matthiopoulos 2003, Wood and Augustin 2002) have made it easier to estimate this overlap for marine predators and their prey (Matthiopoulos *et al.* 2004). The size of the area that can be searched by a free-ranging predator in a given time is limited by the speed at which it can move (Asseburg 2005).

### *Issues of scale*

The consumption and availability data that are collected in order to parameterise a consumption model should be collected as close together in time and space as is feasible, so that measured prey availability corresponds with that which is experienced by the predator while foraging. Satisfying

these criteria when collecting data for marine mammals and their fish prey in the field is a real challenge. However, some flexibility may be acceptable if prey and predator spatial distributions are constant or change only slowly over time, and if prey abundance does not vary significantly. The uncertainty associated with the estimates of prey availability should be quantified, and this should be taken into account during the model fitting process.

If a consumption model is fitted to data collected over a very short time scale, it is unlikely that the same model will be appropriate for other time periods (Hosseini 2003). A 'snapshot' of active foraging may provide valuable insights into the nature of predation by individuals, and it may be possible to use this information to construct a detailed biological model of foraging behaviour. However, extrapolating this model to the behaviour of an entire population or the entire life-span of an individual is questionable. Detailed information on the timing of foraging, life history traits, and individual and population movements would probably be required to make this extrapolation. In short-term laboratory experiments, satiation may simply represent the maximum rate at which predators can consume prey under the experimental conditions, and may not accurately reflect long-term satiation levels. In longer-term experiments or in the field, consumption should be averaged over a complex suite of behaviours that might include concentrated bursts of foraging, periods of travelling to foraging sites, and periods of rest. If consumption is viewed over a whole-year time scale, episodes of fasting associated with breeding or hibernation may also be involved. The meaning of

'satiation' in such studies will be quite different, and fitted parameters would be expected to reflect this.

One important point that should be mentioned is that what is eaten by a predatory species may vary over its geographical range. These differences may not be fully explained by prey availability alone but may be a consequence of genetic variation within the predator population: different 'races' of a given species such as killer whales may exhibit very different predation behaviour (Herman *et al.* 2005). The spatial scale over which FR models can be applied will therefore depend on the genetic structure of the population as well as the ecological context.

#### 1.2.5 Fitting a functional response to the data

Fitting FRs to consumption and availability data presents some particular difficulties. Most published work on FR fitting is confined to interactions between single predators and single prey species. This will be discussed first and then reviewed in the light of challenges that arise when consumption by generalists is considered.

The form of the FR (hyperbolic or sigmoidal) is central to our understanding of predator prey interactions, but this can only be determined reliably if measurements of consumption at very low prey availability are available. Values of consumption at high prey availability are also required to define the

asymptote of the FR. In laboratory systems it is possible to control prey density precisely and offer prey over a wide range of densities, but data covering the full range of prey availability in sufficient detail may be hard to obtain under field conditions, unless prey availability can be manipulated (Forrester and Steel 2004). Extreme values of prey availability may only be observed if there is significant spatial variation in prey availability within the geographical range of the predator (Hammond *et al.* 1994a,b), or if there are large scale cycles in prey abundance (Redpath and Thirgood 1999).

Prey abundance may be difficult to estimate precisely. This uncertainty may be particularly severe when prey are scarce, and predators are probably better at finding prey than human observers at these densities. Prey availability to predators is also likely to be more uncertain than absolute prey abundance, since the uncertainty in prey abundance will generally be confounded by uncertainties in our understanding of the use of space by predators. Any model-fitting technique should therefore recognise and incorporate this uncertainty, as well as the uncertainty in consumption measurements which is normally taken into account.

Most predators consume discrete prey items. As a result, consumption data often consists of counts: direct observations of predation events or the number of prey remains found in scats or pellets. Uncertainty in consumption is therefore rather poorly modelled as a Gaussian process. Different authors have addressed this problem in different ways, by re-arranging equations to

linearise them (Williams and Juliano 1985, Livdahl and Steven 1983) and log-transforming the data prior to analysis (Rindorf 2005). However, these approaches can pose problems if it is important to quantify parameter uncertainty.

Maximum likelihood approaches to fitting FRs enable the use of more realistic error distributions for the consumption data, and they have been successfully applied to the results of laboratory studies (Skalski and Gilliam 2001).

McCallum (2000) used maximum likelihood techniques to fit single-species FR models to field data collected by Pech *et al.* (1992) and Messier (1994).

However, this approach has yet to gain universal acceptance. Instead, the method of Trexler *et al.* (1988), in which a logistic function is first fitted to the data to indicate whether the FR is likely to be linear or hyperbolic, is more widely used (e.g. Schenk and Bacher 2002, Pervez and Omkar 2005).

In this study I used Bayesian statistics, following the approach described in Asseburg *et al.* (2006).

Bayes formula can be used to determine the distribution of a set of parameters from a set of data, given an error model that can be used to compare the data with model predictions and a set of expected distributions for the model parameters - known as priors (Hilborn 1997, Gelman 1995):

$$p(\text{Parameters} | \text{Data}) = \frac{p(\text{Data} | \text{Parameters})p(\text{Parameters})}{p(\text{Data})} \quad (18)$$

The posterior distribution,  $p(\text{Parameters} | \text{Data})$ , is a joint distribution in which any covariance between the parameters is represented. Various algorithms, such as the Metropolis Hastings Monte Carlo Markov Chain (MCMC), can be used to generate parameter sets at random which can then be tested against the data and priors. This process produces a posterior distribution which can be sampled to provide parameter sets. These parameters sets can then be used to make inferences based on the model (Gilks *et al.* 1999). In the case of a FR model, draws from the posterior distribution can be used to produce a range of predictions of consumption, for any given value of prey availability, so that the uncertainty in the predictions of the model can be explored. Therefore one significant benefit of the Bayesian approach is that the resulting posterior distribution gives a thorough exploration of parameter uncertainty and can be used to calculate the uncertainty in inferences that are made, based on the model.

Another advantage, which is unique to the Bayesian approach, is that priors based on data from other studies can be used to restrict the parameter space that is explored. This makes it possible to fit a model to sparse data, where a maximum likelihood approach would be likely to fail (O'Hagan 1998).

However, the form of these prior distributions can have substantial influence on the posterior distribution, and it is necessary to choose them with care using evidence, expert opinion, or *a priori* knowledge. Where there is no

information available to set a prior for a given parameter, 'broad' priors may be used, but the sensitivity of the results to the form of these priors should be carefully examined.

Three additional advantages of the fitting methods adopted here are:

- software is freely available for implementing MCMC (Speigelhalter *et al.* 2003);
- it is easy to code a model involving multiple dependent and independent variables, something that is not conveniently done in many standard packages;
- uncertainty in the independent variables can be easily incorporated into the fitting process.

### 1.3. Two marine mammal generalists: the minke whale *Baleanoptera acutorostrata*, and the grey seal *Halichoerus grypus*

In this section, I briefly discuss the background to conflicts between marine mammals and fisheries in order to point to the importance of understanding predation by generalists. Two marine mammal case studies will be introduced: consumption of fish by grey seals around the UK and by minke whales in the Barents Sea. Both predators are potentially in conflict with commercial fisheries, and data sets that could be used to parameterise consumption models were available. The issues of prey availability and modelling approaches discussed in the previous sections are then examined for each species. Finally, I identify some questions and challenges posed by these two case studies that have a wider application.

### 1.3.1 Marine mammal/fisheries conflicts

Marine mammals may compete directly with human fisheries for the available harvest of fish. This can result in commercial difficulties for the fishery, especially if the effects of marine mammal predation on the dynamics of fish stocks are significant (Harwood and Croxall 1988, Schweder *et al* 2000). A generalist may drive a prey species to extinction, or prevent the prey population from recovering after some event - such as over-fishing - that has caused a population crash. Such a scenario is suggested for the collapse and subsequent non-recovery of the Newfoundland-Labrador cod stock, where predation on cod by harp seals may be an important factor (Bundy, 2001). According to Tamara (2003), cetaceans worldwide consume a larger quantity of fish than that taken by commercial fisheries. However, many of these fish are not targeted by fisheries and the spatial distribution of fisheries and cetaceans do not overlap completely, so that the conflicts may be much less serious than this figure suggests (Trites *et al.* 1997).

One case in which a marine mammal predator has been implicated in the failure of a fish stock to recover is that of NorthWest Atlantic Harp Seals, preying on arctic and Atlantic cod (Stenson *et al.* 1997). Cod stocks were reduced to very low levels as a result of over-fishing during the 1980s but they have failed to recover despite almost complete protection. A model of harp seal prey consumption would be powerful tool in managing the cod and harp

seal harvest appropriately, and Bayesian methods have recently be applied to this problem (Asseburg 2005).

Another case of pinniped-fisheries conflict involved the South African fur seal *Arctocephalus pusillus pusillus*, preying on hake *Merluccius capensis* and *M. paradoxus*. Punt and Butterworth (1995) have shown that detailed modelling of trophic links in the local ecosystem is necessary to determine the impact of seals in this system. When indirect interactions were accounted for, the effect of seals on the fishery was more likely to be positive than negative.

Marine mammals themselves may themselves be adversely affected by human fisheries: deliberate harvesting and incidental bycatch may present significant risks to marine mammal populations in some cases (Northridge 1991).

Competition for food with fisheries can reduce the availability of prey for cetaceans and pinnipeds, and this may have an important adverse effect in populations which are experiencing other difficulties e.g due to pollution (Bearzi 2004). It is possible to compare the diet of marine mammals, the species known to be taken by fisheries, and the state of fish stocks, but it is difficult to use this information to obtain reliable predictions of the likely consequences of different management actions. The quantitative consequences of changes in food availability for consumption by the marine mammals must be known and, ideally, the link between food intake and life history parameters (i.e. the numerical response) for the predator should be understood. Detailed data are currently scarce, but negative impacts of

fisheries on populations of short beaked common dolphin (*Delphinus delphis*) in the Mediterranean (Bearzi *et al.* 2003), Steller sea lions (*Eumetopias jubatus*) in Western Alaska (Trites 1997), and fin whales (*Balaenoptera musculus*) off Eastern Canada (Whitehead and Carscadden 1985) have been suggested by some authors.

The populations of minke whales in the Barents Sea and of grey seals around the UK are not currently under threat. However, both species have been implicated in conflicts with fisheries (Stefansson *et al.* 1995, Matthiopoulos *et al.* 2006, Fedak *et al.* 1985, Hall *et al.* 2000). Fully parameterised models of consumption for these marine mammals may prove useful in quantifying the importance of marine mammal predation for Barents and North Sea fisheries if the impact of predation can be assessed at the appropriate spatial scale. It may also be that the techniques of modelling consumption for these animals will find a wider application and prove useful in illuminating conservation questions for other, threatened, marine mammal species.

In order to resolve questions concerning marine mammal conflicts with fisheries, multi-species models are required which take into account all important trophic interactions. Priorities for such models must be to determine what the relevant interactions are, to incorporate consumption models that capture the important features of consumption such as switching, and to include spatial effects such as migration and changes in predator prey overlap, where these are relevant. Models of consumption which have been

parameterised using consumption and availability data can be incorporated directly into ecosystem simulation models. These ecosystem models can be used to explore system properties such as stability and the potential for predators and prey to co-exist (Bogstad *et al.* 1997, Yodzis 1998, Yodzis 2000). Alternatively, the parameters of consumption models can be used as starting values or as priors to assist with fitting multi-species models to time series data sets.

### 1.3.2 Minke whales

The Barents Sea is a relatively simple ecosystem and one of the first for which multi-species models were implemented (Bogstad *et al.* 1997). One aim of such models has been to clarify the role of minke whales in the Barents Sea and in particular to determine their impact on the capelin and herring fisheries. Schweder *et al.* (2000) suggested that minke whales may have a significant impact on the cod and herring fisheries, but the model of Bogstad *et al.* differs in its predictions, suggesting that the most significant competitors with the fisheries are fish predators. The consumption sub-models used in these two studies are different, and new modelling of the minke whale MSFR based on new field data might play an important role in reconciling them. Appropriate data on minke whale consumption and local prey abundance has been collected for a study of preference, which appears to vary with prey availability, indicating that some form of switching occurs (Lindstrom and Haug 2001).

### 1.3.3 Grey seals

Grey seals are generalist predators, which consume more than 80 species of prey in UK waters, foraging close to the seabed (Prime and Hammond 1987 and 1990, Hammond and Prime 1990, Thompson *et al.* 1991, Hammond *et al.* 1994a,b, Hall *et al.* 2000). Their diet is known to vary seasonally and spatially (Pierce *et al.* 1991c), possibly in response to local prey densities (Hammond *et al.* 1994a,b). Commercially exploited fish, such as cod, plaice (*Pleuronectes platessa*) and whiting (*Merlangius merlangus*), form an important part of their diet, leading to repeated calls from fishermen for a seal cull.

A model of seal consumption would enable managers to predict how seals may alter their diets in response to changes in fish stocks. Together with estimates of seal population size and seal distribution, such a model could be used to estimate the level of predation mortality on commercial fish stocks, to indicate whether grey seals are important competitors with the fishery, and to predict whether grey seal predation might prevent a recovery of stocks such as cod from their present low levels. This would then assist in providing a rational basis for management decisions concerning the management of seals and fish stocks.

Seal diet was estimated from scat samples collected at UK sites in the 1980s and 1990s (Hammond and Prime 1990, Hammond *et al.* 1994a,b, Hall *et al.* 2000). The complexity of the consumption model was limited by choosing a

subset of prey, based on the importance of prey classes in the diet of the seals, in order to make it possible to fit the model using the available data.

Prey distribution was estimated from research catches collected as part of the annual International Bottom Trawl Survey, coordinated by the International Council for the Exploration of the Seas. These cover most of the area used by foraging seals around the UK. In order to calculate prey availability to seals, and the uncertainty associated with these availability estimates, spatial models of prey abundance were combined with existing maps of grey seal distribution, (Matthiopoulos *et al.* 2004).

#### **1.4. Aims of this thesis**

The principle aim of this work was to develop methods for parameterising and interpreting MSFRs for minke whales and grey seals. The following questions had to be addressed:

- 1) Is it possible to obtain sufficient field data to parameterise the FR of a generalist? Issues of spatial and temporal scale, and details of predator and prey behaviour, suggest that MSFRs should be parameterised using field data rather than laboratory experiments.
- 2) How can the availability of prey be calculated for a mobile predator (the minke whale) and a central-placed-forager (the grey seal)?

- 3) Can the uncertainties in consumption and prey availability be modelled appropriately?
- 4) If FR models can be fitted, what conclusions can be drawn from them about the role of a generalist predator in a complex food-web?
- 5) How can the fitted consumption models be incorporated into such multi-species models, which may operate over different spatial and time scales?

## Chapter 2. The Multi-Species Functional Response Of Grey Seals:

### Estimating Prey Availability

#### Summary

The main prey species and size classes consumed by seals were identified by examining the composition of seal diets, which were estimated from the analysis of scat samples. This process is described in Chapter 4.

In this chapter I describe how maps of the spatial distributions of these species and size classes of fish were obtained, using GAMs fitted to IBTS data. The fish distributions were then combined with existing models of the availability of space to grey seals, in order to obtain indices of prey availability to the seals. Bootstrap re-sampling of the trawl data was carried out to obtain an indication of the uncertainties in these predictions.

## 2.1 Introduction

In order to parameterise a multi-species functional response model (MSFR), a mathematical form for the model is needed, and appropriate information on prey availability and predator consumption rates are required. In this chapter I describe how prey availability for marine predators can be calculated using models of prey distribution and the availability of space to predators. I use UK grey seals (*Halichoerus grypus*) and their fish prey as an example.

Ideally, all prey species that are known to be consumed by a predator should be incorporated into the MSFR. Prey species which grow to large size, such as Atlantic cod *Gadus morhua*, should be represented by multiple size classes, because predators may show a size-based preference for prey, (Hoover 2005). Also, there may be significant changes in the behaviour of fish during their life history which will affect their availability to predators. For example, the migratory behaviour, use of habitat, prey and schooling behaviour of small juvenile fish may be quite different from that of older fish (Verdoit *et al.* 2003, Floeter and Temming 2005, Duffy-Anderson *et al.* 2003). Changes in spatial distribution of fish on a large scale may result in fish moving in or out of areas used by seals. For example, ling (*Molva molva*) may move into deep waters as they get larger, taking them out of the normal diving range of grey seals. On a local scale, use of refuges by young fish (Gotceitas and Brown 1993) may strongly affect their availability to predators.

The diet of UK grey seals includes more than 80 prey species. Depending on how size classes are chosen, the number of possible species/size classes is very large. The available data on fish abundance covers only some of the species in the grey seal diet in a satisfactory way. Fish such as bullrout (*Myoxocephalus scorpius*) and blennies (*Lipophrys pholis*) that are known to be important for seals in some areas and seasons (Hall *et al.* 2000, Prime and Hammond 1990) are poorly represented in these data, and so their availability cannot be estimated reliably.

One possible simplifying approach to the problem of selecting prey types would be to group prey according to size alone. There is some evidence that size is the main factor affecting prey choice in some marine fish predators (Floeter and Temming 2005) and size-based approaches to ecosystem modelling show some promise (Jennings *et al.* 2002). However, differences in the biology of equivalent-sized fish suggest there are difficulties with this approach. A pelagic fish and a flatfish of the same length or mass inhabit different parts of the water column, move in different ways, and have significantly different nutritional content. A modification of the pure size-based approach would be to divide fish into broad categories based on phylogeny or behaviour, and then divide these categories into size classes ('all flatfish between 0 and 10cm' for example). However, as more is learned about the movements and habits of different fish (Temming *et al.* 2004) it seems increasingly clear that species which resemble one another phylogenetically may yet have very different behaviour. I therefore chose to

focus my attention on those prey species which appeared to be of particular importance in the diet of UK grey seals and for which comprehensive data on prey availability were available. All prey types which contributed more than 10% to the diet of grey seals at two or more of the individual sites sampled in the studies described by Prime and Hammond (1990), Hammond *et al.* 1994a,b and Hall *et al.* (2000) were included.

Regular scientific surveys, targeting all size classes of fish, are carried out each year in the Northeast Atlantic as part of the International Bottom Trawl Survey (IBTS) co-ordinated by the International Council for the Exploration of the Sea (ICES). Coverage was limited in two important respects: local and contemporaneous trawl survey data were not available for every haul-out from which diet information was collected, and the spacing of the trawl surveys was relatively coarse by comparison with the foraging range of seals from a given haul-out. Both these problems were addressed by using Generalised Additive Models (GAMs) to provide interpolated estimates of prey abundance in space and time. It was hoped that the inclusion of the environmental covariates, such as water depth and sediment type, would improve the reliability of the spatial interpolation. By interpolating in time, fish abundances could be estimated for any time of interest within the 1980s and 1990s, so that all the available seal diet data could be used.

The availability of prey to a predator is determined not only by prey abundance but also by its accessibility. Seals return to land regularly between

foraging trips to haul out. Therefore the area over which they can forage is limited by the duration of these foraging bouts and their mean swimming speed. However, some areas within a seal's foraging range are used more intensively than others that are equally accessible i.e. there is strong habitat selection. Matthiopoulos *et al.* (2004) developed the concepts of accessibility and usage of space by seals and they describe how information on these two variables can be extracted from telemetry data.

Telemetry data (McConnell *et al.* 1999) also suggest that, while seals occasionally make long journeys from one site to another, most grey seal foraging trips begin and end at the same haul-out. Therefore, diet information obtained by analysis of scats collected from a given haul-out (Prime and Hammond 1987) can reasonably be assumed to represent the diet of seals that are resident in the area provided that potential biases, such as digestion effects and the loss of otoliths at sea due passage through the seal gut, are carefully accounted for.

Given that most seals forage in the vicinity of their haul-outs and that the distributions of their prey species around the British Isles are not uniform, the availability of prey to seals is likely to vary among haul-outs. In order to obtain a realistic estimate of the availability of prey to seals we need to estimate the abundance of prey in the area that is accessible to seals from each haul-out for which we have diet data.

## 2.2 Methods & Results

### 2.2.1 IBTS data

Seven prey classes were identified

	common name	latin name	length in cm
1	immature cod	<i>Gadhus morhua</i>	0-50
2	mature cod	<i>Gadhus morhua</i>	50+
3	whiting	<i>Merlangius merlangus</i>	all
4	plaice	<i>Pleuronectes platessa</i>	0-70
5	saithe	<i>Pollachius virens</i>	0-60
6	ling	<i>Molva molva</i>	all
7	sandeels	all species, mainly <i>Ammodytes marinus</i>	all

Around the UK, the Centre for Environment, Fisheries and Aquatic Sciences (CEFAS) and the Fisheries Research Service of the Scottish Executive are responsible for the IBTS, and have kindly made their data for the 1980s and 1990s available to me in a detailed form. The IBTS are conducted in a standardised way with consistent gears, and are regularly distributed in time and space covering all ICES statistical rectangles in quarter 1 (January-March) and/or quarter 3 (July-September) every year. Additional, more irregularly

spaced surveys, using similar or identical gear, have been conducted during quarters 2 and 4. The locations of the IBTS trawls for 1985, 1997, and 1998 are shown in Figure 2.1.

The British IBTS surveys are carried out using the standard Grande Ouverture Verticale (GOV) gear: a demersal trawl fitted with a cod-end of 20 mm stretched mesh which is designed to improve the catch of small size-classes of fish (Daan 2005). Based on the estimated horizontal net opening and prescribed towing speed (3-4 knots), an average 150 000 m<sup>2</sup> are fished during a 1-h haul (Knijn *et al.* 1993).

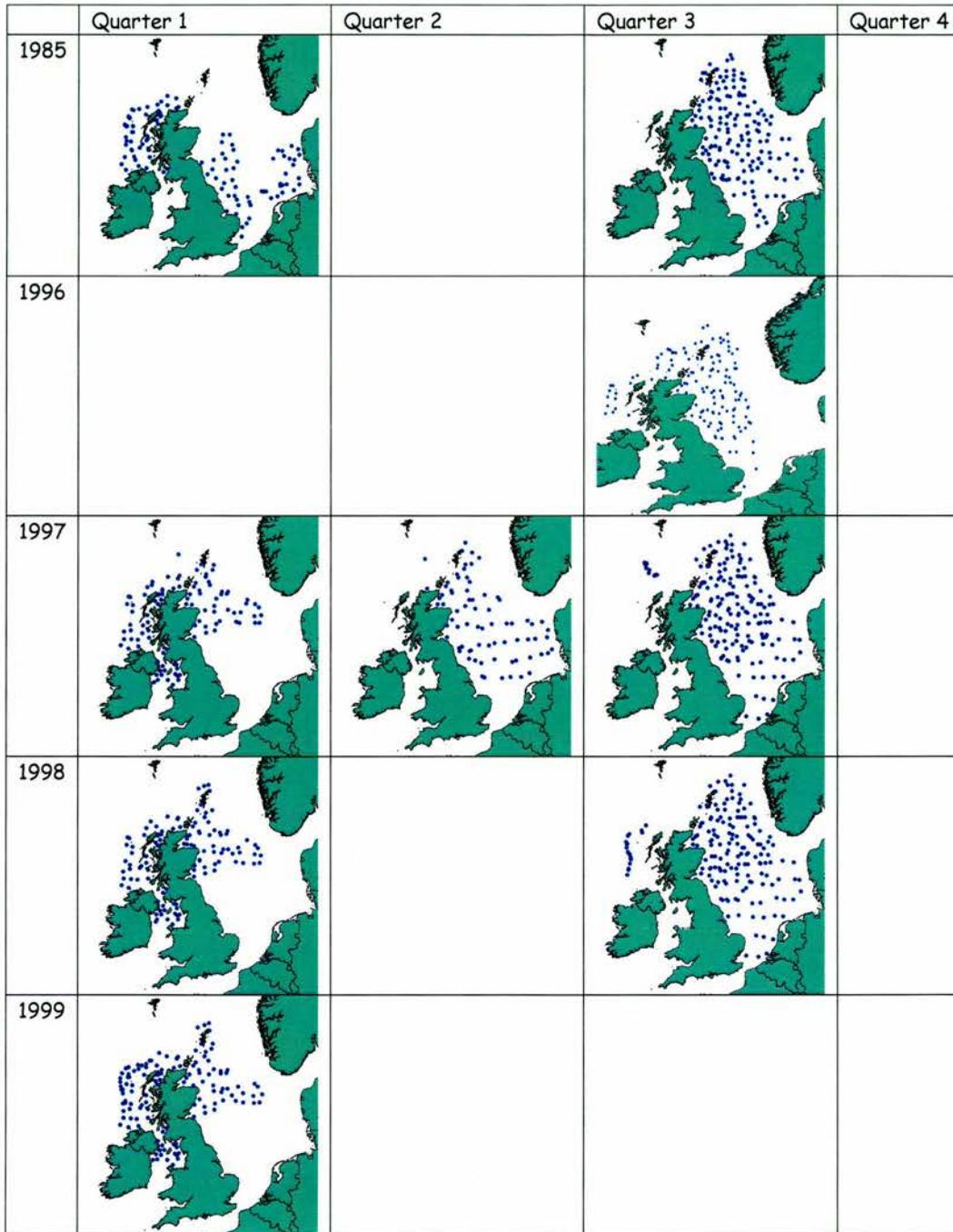
The IBTS data sets from CEFAS and FRS recorded the date, time, longitude and latitude of trawl start and end points, and counts of all species caught during the trawls, grouped into 1cm size classes. These data could then be used to calculate Catch per Unit Effort (CPUE) for a given prey class. The duration of the trawls was small, compared with scale of the area around each haul-out, and route followed during the trawls varied (some were straight and some were circular). I therefore used the latitude and longitude of the final haul as the point location for each trawl.

### 2.2.2 GAMs

GAMs (Wood and Augustin 2002) offer a useful method whereby environmental correlates can be used to enhance spatial smoothing of point estimates of

**Figure 2.1: Locations of the IBTS surveys**

Locations of all the IBTS trawls that were carried out during the years when scat collections took place. Blue points indicate the end point of each trawl.



abundance. In a GAM, it is assumed that the value of interest (in this case, CPUE) can be described as the sum of a number of smooth functions of suitable covariates (in this case, spatial co-ordinates and environmental variables). The form of the smooth functions is determined during the fitting process. Cross-validation is used to estimate the value of a smoothing parameter which limits the ‘wiggleness’ of the functions by imposing a penalty on their 2<sup>nd</sup> derivatives in order to avoid over-fitting (Wood and Augustin 2002).

The covariates used were:

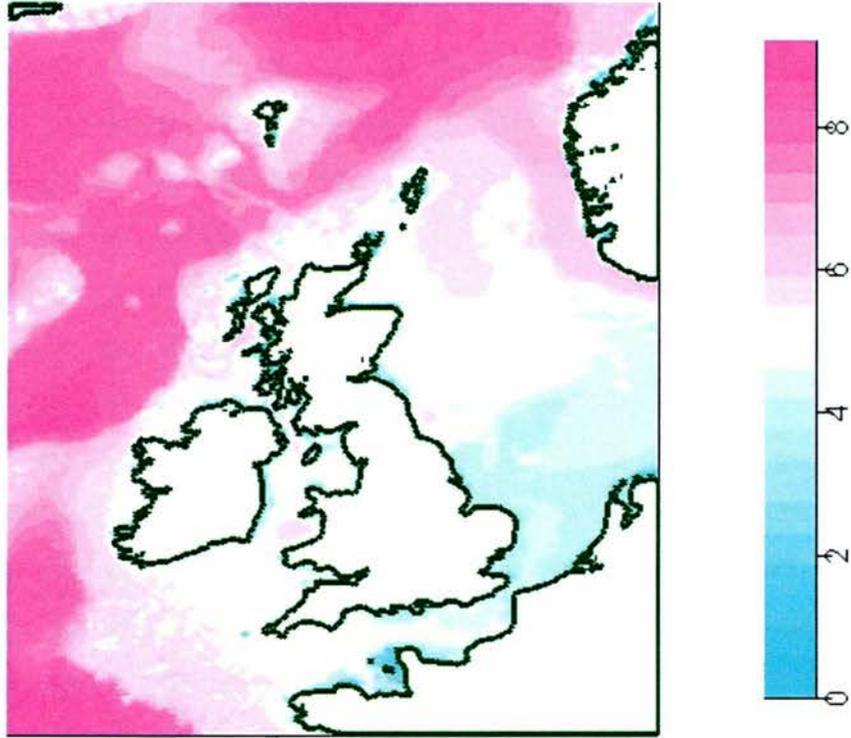
- ❖ the Cartesian co-ordinates of each haul, calculated using the British National Grid projection (a transverse Mercator projection), which allow for isotropic spatial smoothing;
- ❖ water depth (NGDC 2005), which is known to be relevant to the distribution of many fish species and size classes;
- ❖ bottom sediment type, based on kriging of BGS sediment surveys: this is most likely to be relevant for bottom-living species such as plaice and sandeels;
- ❖ year: it is expected that fish distributions will show some stability over time, and the inclusion of this covariate enables smoothing over time;
- ❖ season was also included as a covariate, since habitat use and recruitment are both likely to show seasonal effects.

Maps of the values of these covariates are shown in Figures 2.2-2.5.

## Figure 2.2: Bathymetry Of The Seas Around The British Isles

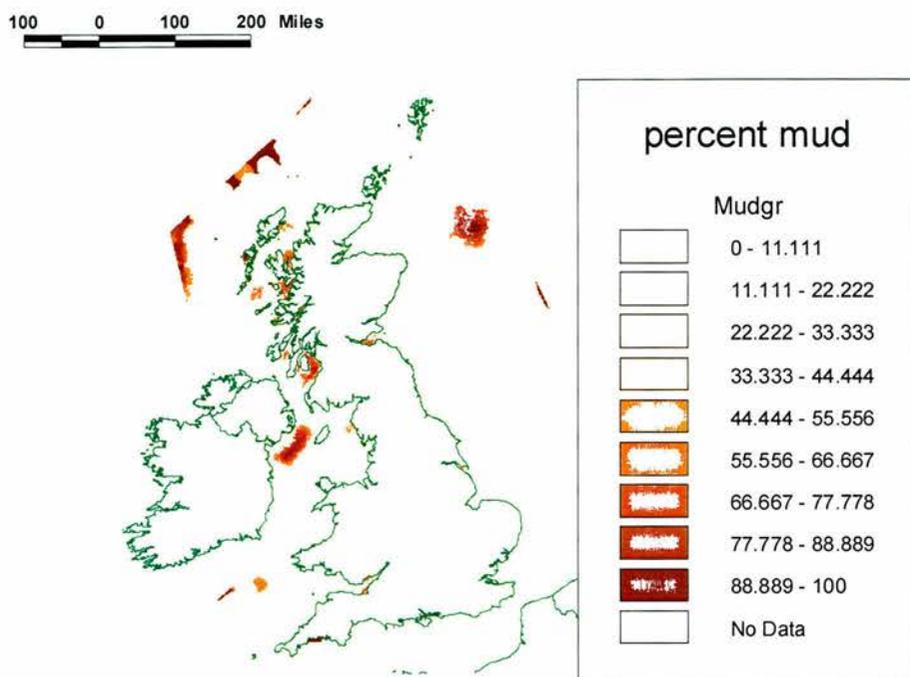
depth is measured in metres, and plotted on a log scale

(Data are from NOAA (NGDG 2005))



## Figure 2.3: mud on the seabed around the UK

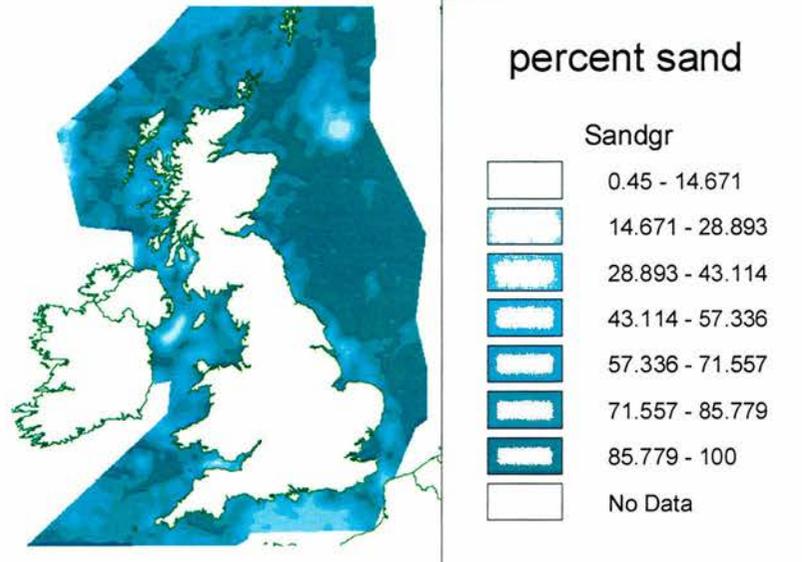
The colour ramp shows the percentage of mud in seafloor sediments



## Figure 2.4: sand on the seabed around the UK

The colour ramp shows the percentage of sand in seafloor sediments

100 0 100 200 Miles



## Figure 2.5: gravel on the seabed around the UK

The colour ramp shows the percentage of mud in seafloor sediments

100 0 100 200 Miles

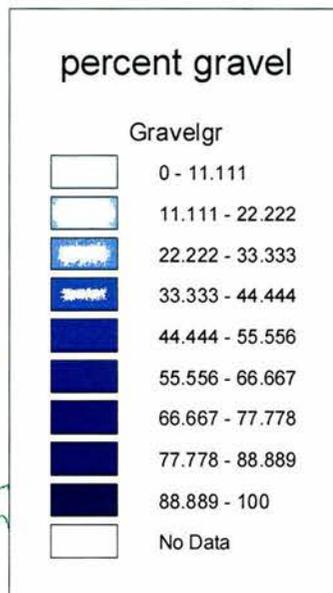
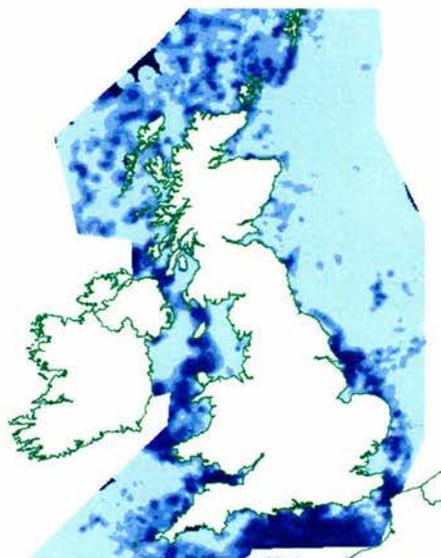
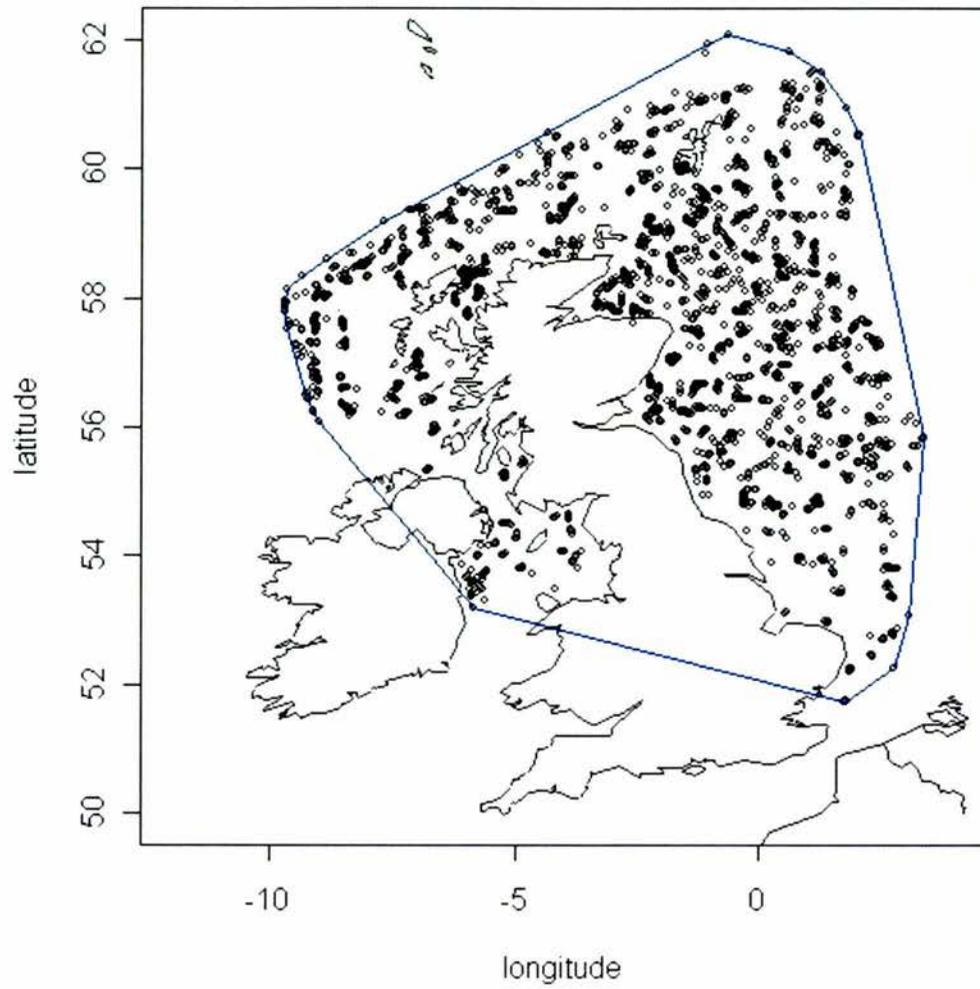


Figure 2.6: data points from the IBTS surveys for the 1980s and 1990s, and the convex hull for these points



Sediment data were only available for the continental shelf and the western parts of the North Sea. Therefore, only those IBTS trawls falling within the range of these data were included in the analysis. Abundance surfaces for the fish species of interest were only calculated within the convex hull of the data points. The total spatial coverage of survey points and the convex hull of these points are shown in Figure 2.6.

GAMs were fitted in R (R Development Core Team 2004) using the MGCV package (Wood and Augustin 2002).

The trawl data consisted of counts of individuals, and were over-dispersed compared with a Poisson distribution due partly to the clustering of fish into schools. The presence of zero counts creates some difficulties for GAM fitting - for example, a negative binomial distribution cannot then be used to account for over-dispersion (Venables and Ripley 2004). The following approaches were therefore considered:

- a) The data could be transformed into a continuous form, e.g. by calculating  $\log(\text{count} + e)$  where  $e$  is a (possibly random) number less than 1, representing a 'background count' of fish not picked up during the 1 hour trawls. This enables  $\log(\text{count} + e)$  to be calculated. A normal error distribution could then be applied to the log-transformed data. This method produced plausible predictions for one species for which it

was tried but it was difficult to justify the specific value of  $e$  that was chosen, e.g. to objectively judge how small  $e$  should be.

- b) A presence/absence model could be fitted, based on a binomial error distribution and a logistic model of the probability of presence ( $P(\text{fish})$ ). A model representing the abundance of the non-zero data could then be fitted using a Poisson error distribution and log link, or a normal error distribution (Piet 2002). Predicted fish abundance could then be calculated as

$$\text{fish abundance} = P(\text{fish}) \times \text{number}(\text{fish})$$

This method is described in more detail by Barry and Welsh (2002).

However, it was not implemented for this study because of the potential difficulties in implementing bootstrap re-sampling of data for such a model.

- c) An over-dispersed Poisson distribution could be assumed for the data (Venables and Ripley 2002), and a square root link function used. This link function was the only one available that would allow for count data that included zeros. The model relating the response variable  $c$  to the covariates ( $x_i$ ) then takes the form:

$$c = (s(x_1) + s(x_2) + s(x_3) + \dots)^2 \quad (1)$$

There was no biological reason to assume such a model, though it was considered reasonably well able to capture the most plausible forms of the relationships between the response variables and the chosen environmental covariates.

Terms to include in the GAM for each prey class were then chosen by a process of forward selection based on the AIC (Stratoudakis *et al.* 2003). This procedure was carried out manually in R. Only a limited number of interaction terms were explored. These were:

(x,y)

(x,y, year)

(depth, season)

(sand, mud, gravel) plus all single and pair-wise combinations of these

GAMs can sometimes produce extreme values at the edges of the prediction area or even inside it, if there are ‘holes’ in the spatial distribution of the data. If absurd values (i.e. CPUEs that were orders of magnitude greater than any in the data set) were predicted by the model, then the model was rejected, even if the values of GCV score and explained deviance (DE) had been optimised, and the best alternative model was sought.

Some caution was required when examining the model outputs. The form of the linear predictor itself was difficult to interpret directly, since negative values correspond to positive values of the response variable when a square

root link function is used. Therefore, I examined how CPUE predictions calculated from the GAM model were influenced by changes in covariates, before making any interpretation of the model.

Table 2.1 shows details of the fitted GAMs, including the smoothed terms included in each model and the deviance explained (DE), which varied between 35% and 69%. The lowest values of DE were for sandeels.

Plots of the predicted relationship between CPUE and depth are shown for selected species in Figure 2.7. All other variables (quarter, year, sediment type) were held constant at typical values in order to demonstrate this relationship.

Figure 2.8 shows a selection of maps of predicted CPUE for all prey classes, based on the GAMs and calculated on a grid of 5km squares.

Seasonal and between-year effects were examined by plotting prey distributions for different years and seasons. For the years 1985 and 1997, and for quarters 1 and 3 where the GAM included a seasonal term, I predicted CPUE values over a grid within the convex hull of the data points. I then compared these maps with the original data and with existing maps of nursery areas, spawning grounds, and general fish distributions (Knijn1993) to check that predictions were reasonable throughout the region).

**Table 2.1: GAM models**

P-values are shown for each smoothed term in the GAM for each prey class. % deviance explained is shown for each GAM.

species	Age/years	Length/cm	Terms in the model, with associated p-values	% Deviance Explained
cod	0-3	0-50	s(Xx, Yy, Year) s(Depth, Season) s(Sand, Mud, Grave1) p < 2.22e-16 p < 0.00054601 p < 1.3688e-05	45
cod	3+	50+	s(Xx, Yy, Year) s(Depth) s(Season) p < 2.22e-16 p < 2.22e-16 p < 4.47e-09	40
plaice	0-5	0-30	s(Xx, Yy, Season) s(Sand, Mud, Grave1) s(Year) s(Depth) p < 2.22e-16 p < 2.2595e-08 p < 2.22e-16 p < 0.0013280	62
Ling	all	All	s(Xx, Yy) s(Year) s(Depth, Season) p < 2.22e-16 p < 4.1141e-12 p < 2.22e-16	69
Sandeels	all	All	s(Xx, Yy, Year) s(Depth) s(Season) s(Mud, Grave1) p < 1.1513e-12 p < 3.8556e-09 p < 3.2461e-08 p < 0.0026025	34
whiting	all	all	s(Xx, Yy) s(Year) s(Depth, Season) p < 2.22e-16 p < 2.22e-16 p < 1.0108e-14	63
saithe	all		s(Xx, Yy, Year) s(Season) s(Depth) p < 2.22e-16 p < 1.2213e-09 p < 2.22e-16	60

**Figure 2.7: the variation in CPUE with bathymetry**

GAMs for each prey class were used to predict CPUE values (an index of abundance) at a range of sea-bottom depths corresponding approximately with the depth range available to seals (Thompson, pers com).

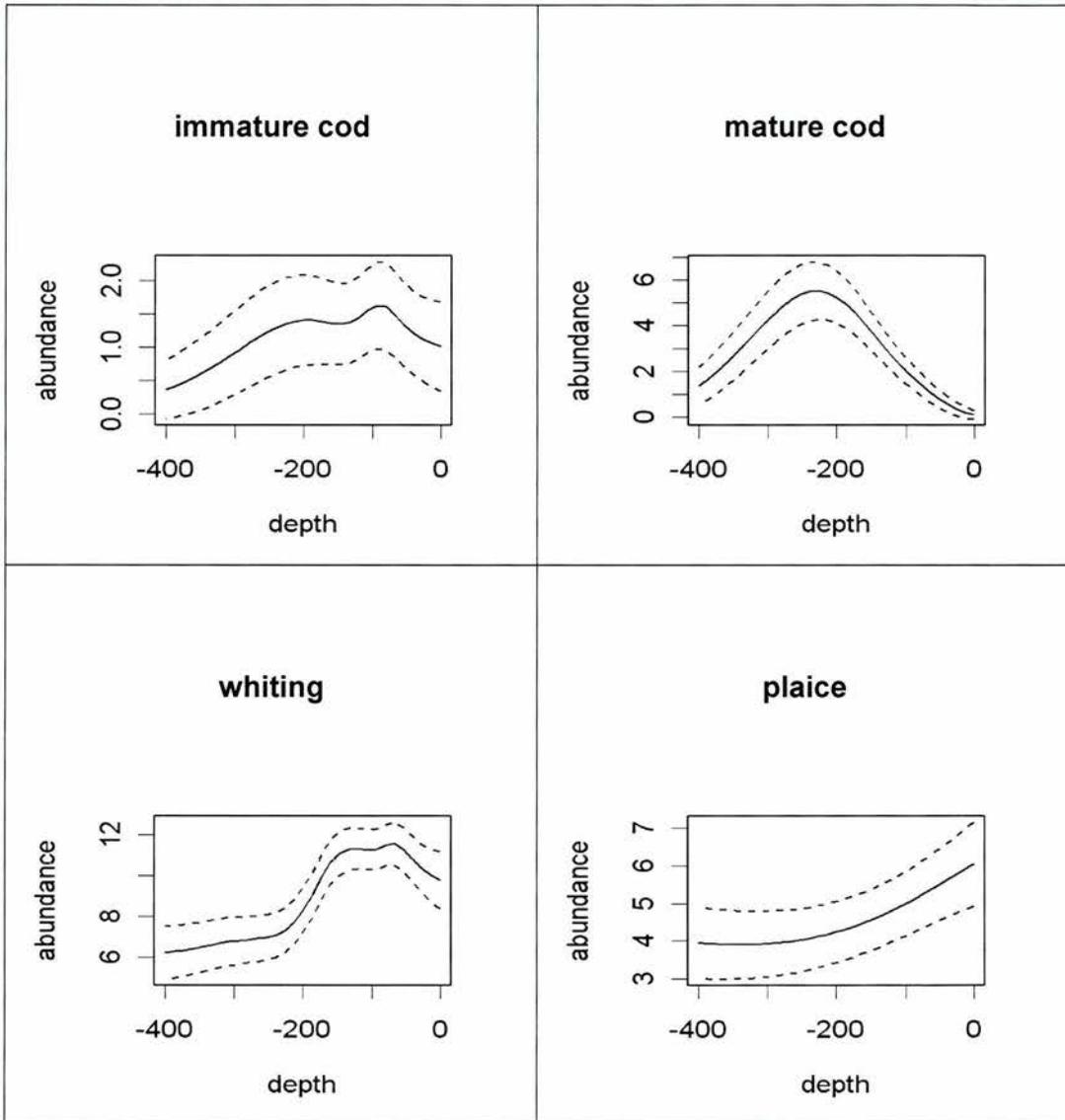
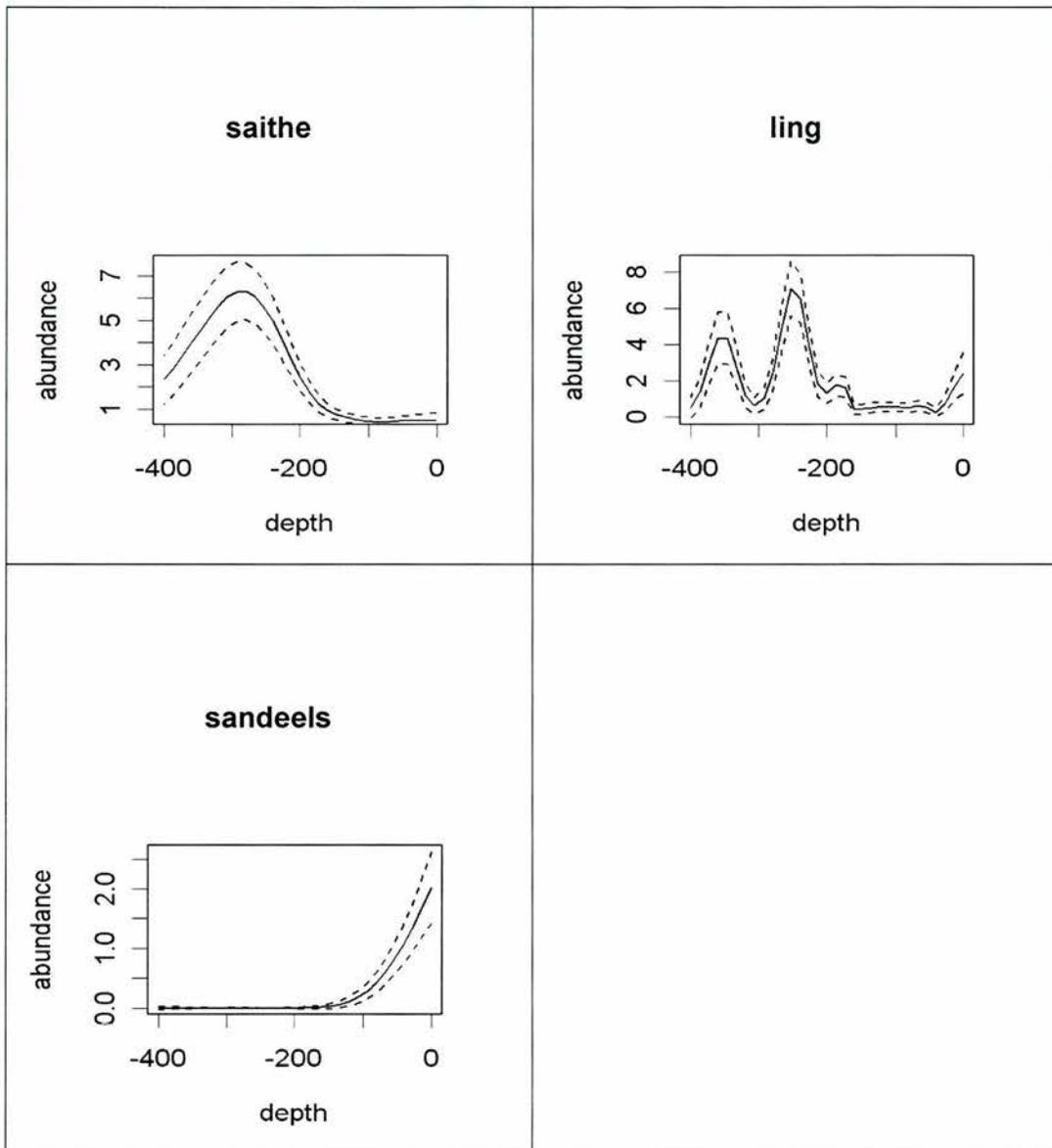


Figure 2.7 continued: the variation in CPUE with bathymetry

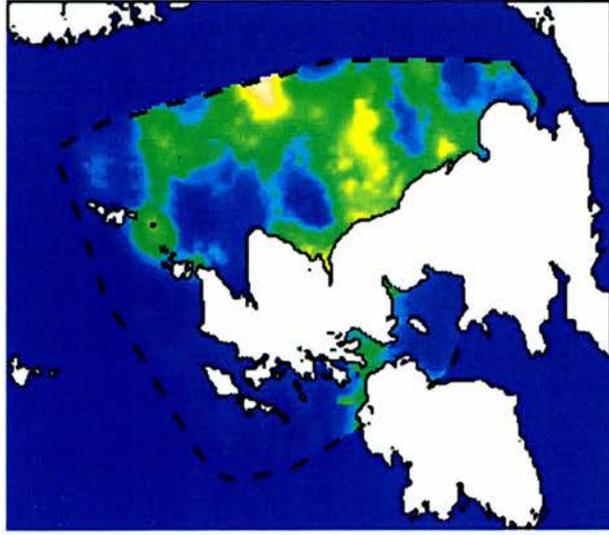


## Figure 2.8: Predicted Fish Distributions, based on GAMs

Predictions are made over a grid of squares, each with side length 5km, within the convex hull of the original data points. For all prey types, the colour scale represents the predicted CPUE (the number of individuals caught during a single IBTS trawl).

**immature cod**

1985 quarter 1



**immature cod**

1997 quarter 1

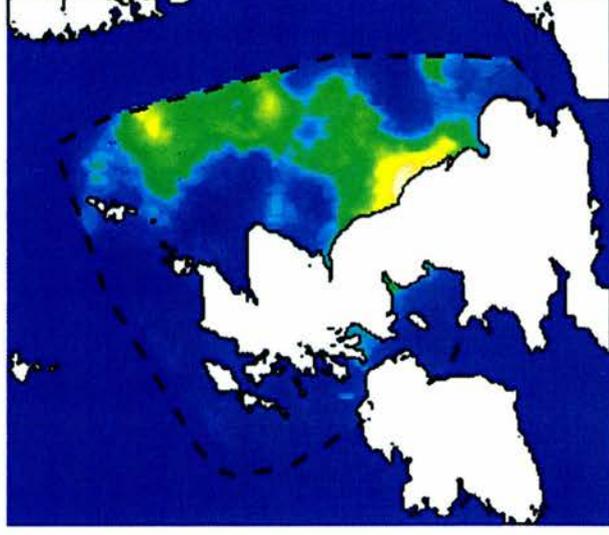
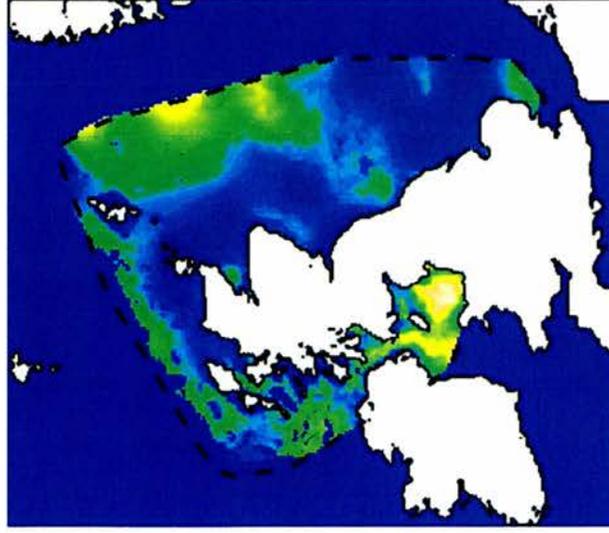


Figure 2.8.2

**mature cod**

1985 quarter 1



**mature cod**

1997 quarter 1

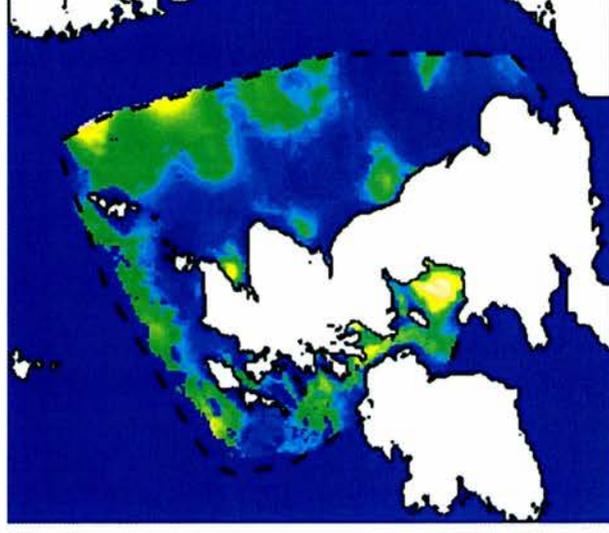
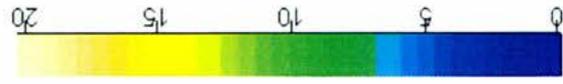
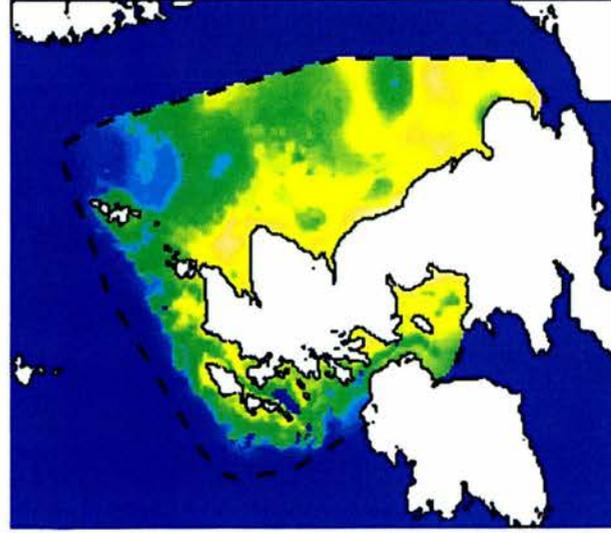


Figure 2.8.3

**whiting**

1985 quarter 1



**whiting**

1997 quarter 1

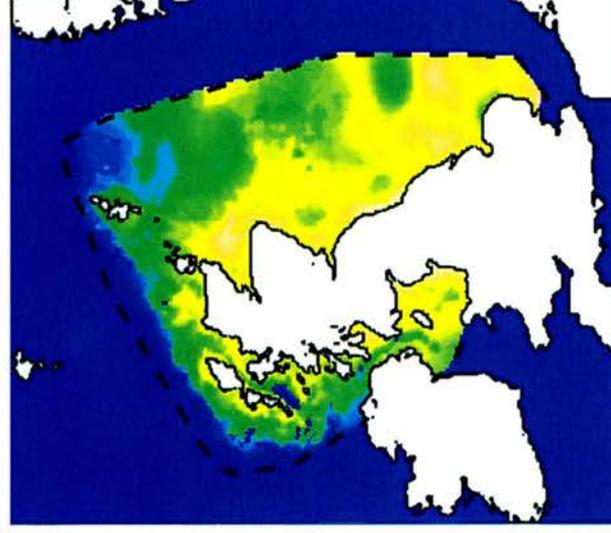
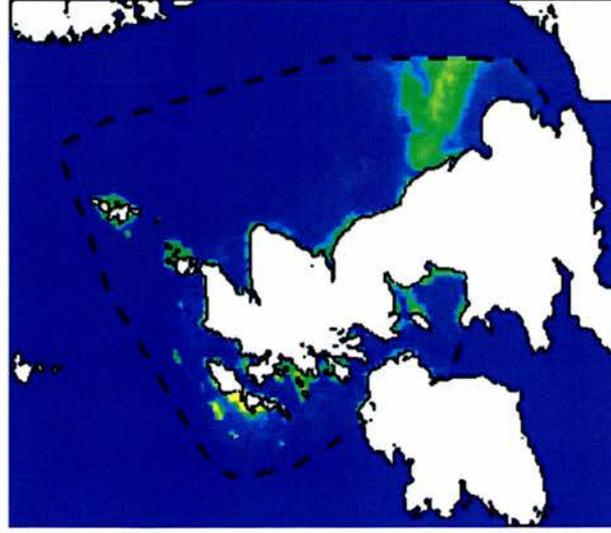


Figure 2.8.4

**plaice**

1985 quarter 1



**plaice**

1997 quarter 1

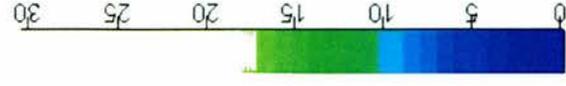
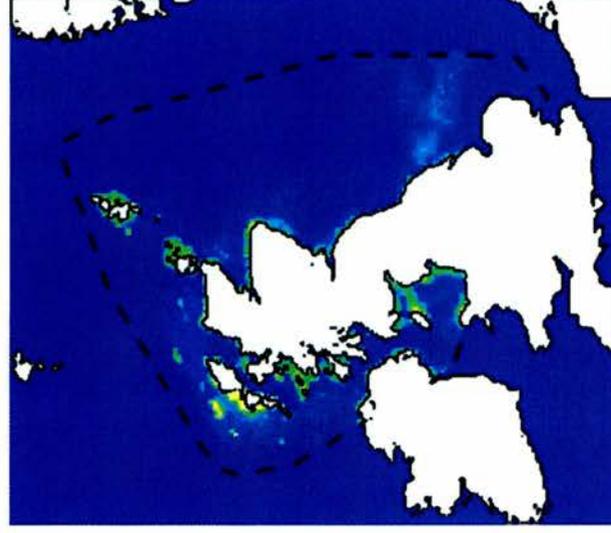
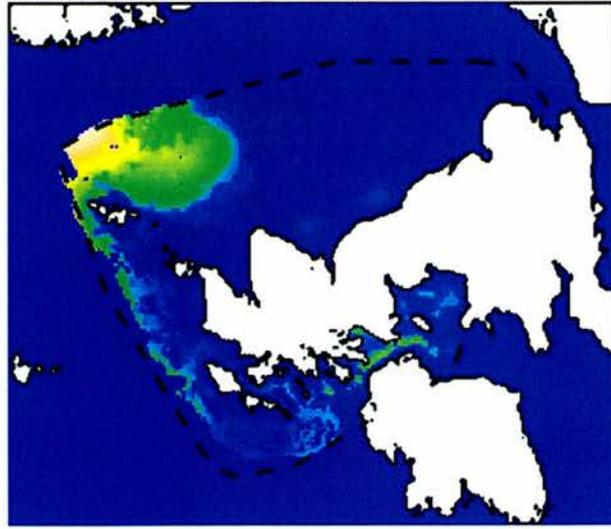


Figure 2.8.5

**saithe**

1985 quarter 1



**saithe**

1997 quarter 1

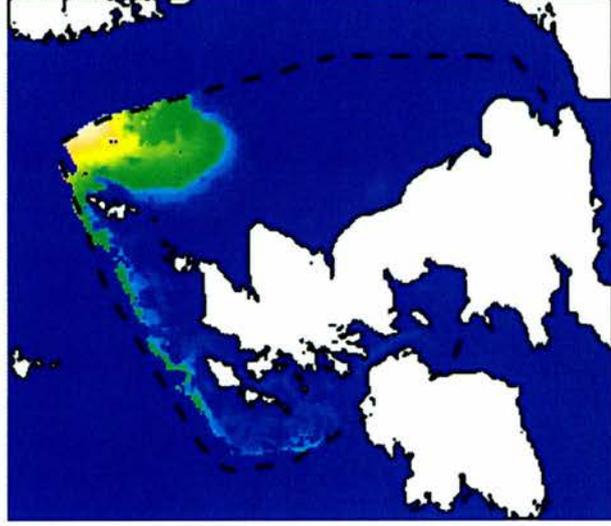
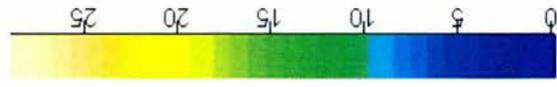
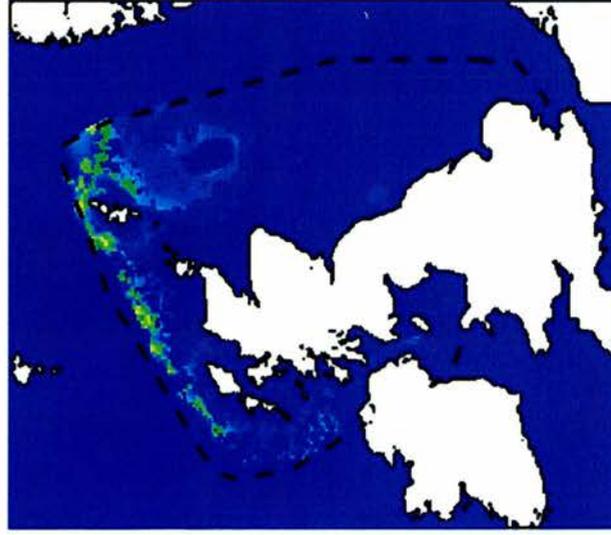


Figure 2.8.6

ling

1985 quarter 1



ling

1997 quarter 1

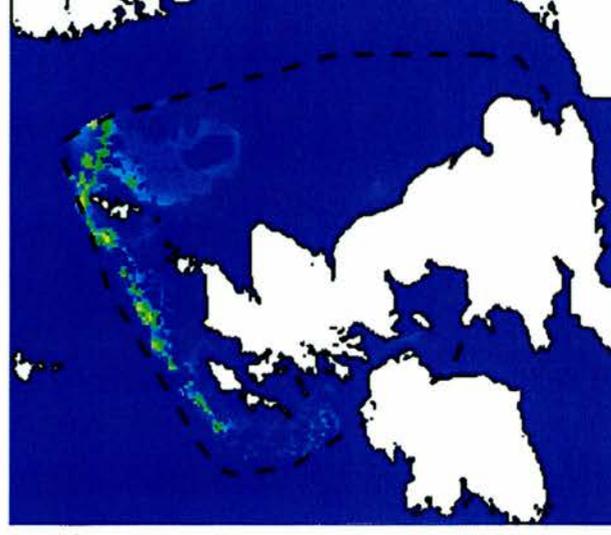
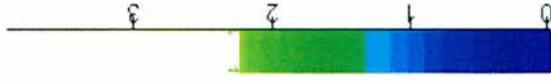
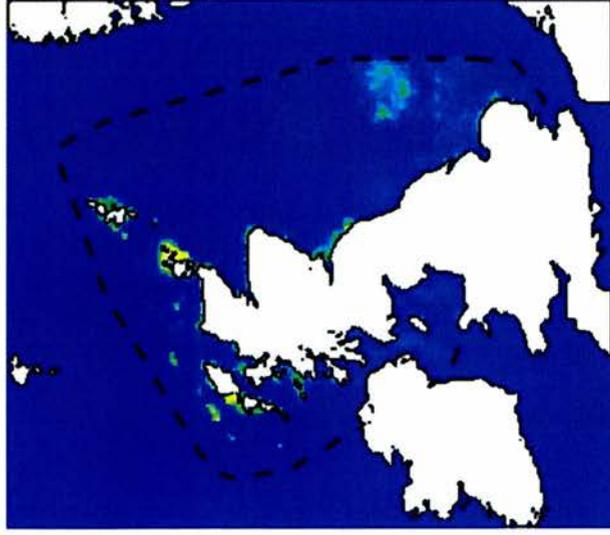


Figure 2.8.7

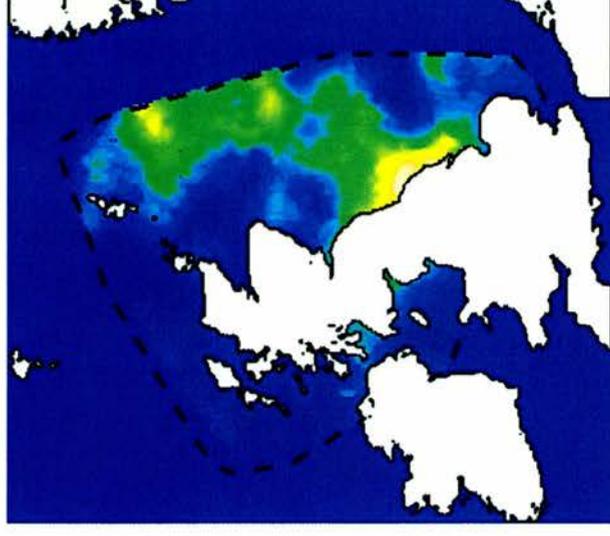
**sandeels**

1985 quarter 1



**sandeels**

1997 quarter 1



For those prey classes for which good North Sea VPA estimates of total abundance were available, I compared the time-dependence in the abundance of the stock as predicted by the GAMs with the annual VPA estimates (Piet 2002). An abundance surface for quarter 1, based on a 5km square grid, was predicted using the GAM for that part of the North Sea which was enclosed by the convex hull of the data points. Predicted CPUE values within this hull were then integrated numerically over the grid. This process was repeated for each year between 1980 and 1999. Estimates of numbers-at-age for each prey class based on VPA (ICES 2004c) were then calculated for the same region and years. Plots of these time series are shown in Figure 2.9.

The smoothed GAMs tended to predict less short-term variation than the VPA models, but there was some correspondence in the long-term for some species. The correlation coefficient for the comparison between the two time series for immature plaice was 0.44 ( $P = 0.065$ ). For immature cod, it was 0.54 ( $P < 0.01$ ), and for mature cod it was 0.79 ( $P < 0.00005$ ). For whiting, however, the correlation coefficient was -0.1 ( $P = 0.4$ ), and for saithe it was 0.142, ( $P = 0.7$ ). The relationship between VPA and GAM time series was therefore not strong, even for those species where a significant correlation was observed, and it should be noted also that no attempt was made to account for temporal autocorrelation within these time series in this simple analysis.

**Figure 2.9: time series of abundance predicted by the GAM models and VPA for cod**

An index of annual total stock size was predicted from each GAM model by numerical integration of predicted CPUE, over a surface of 5km squares. VPA estimates were obtained from ICES (ICES 2004).

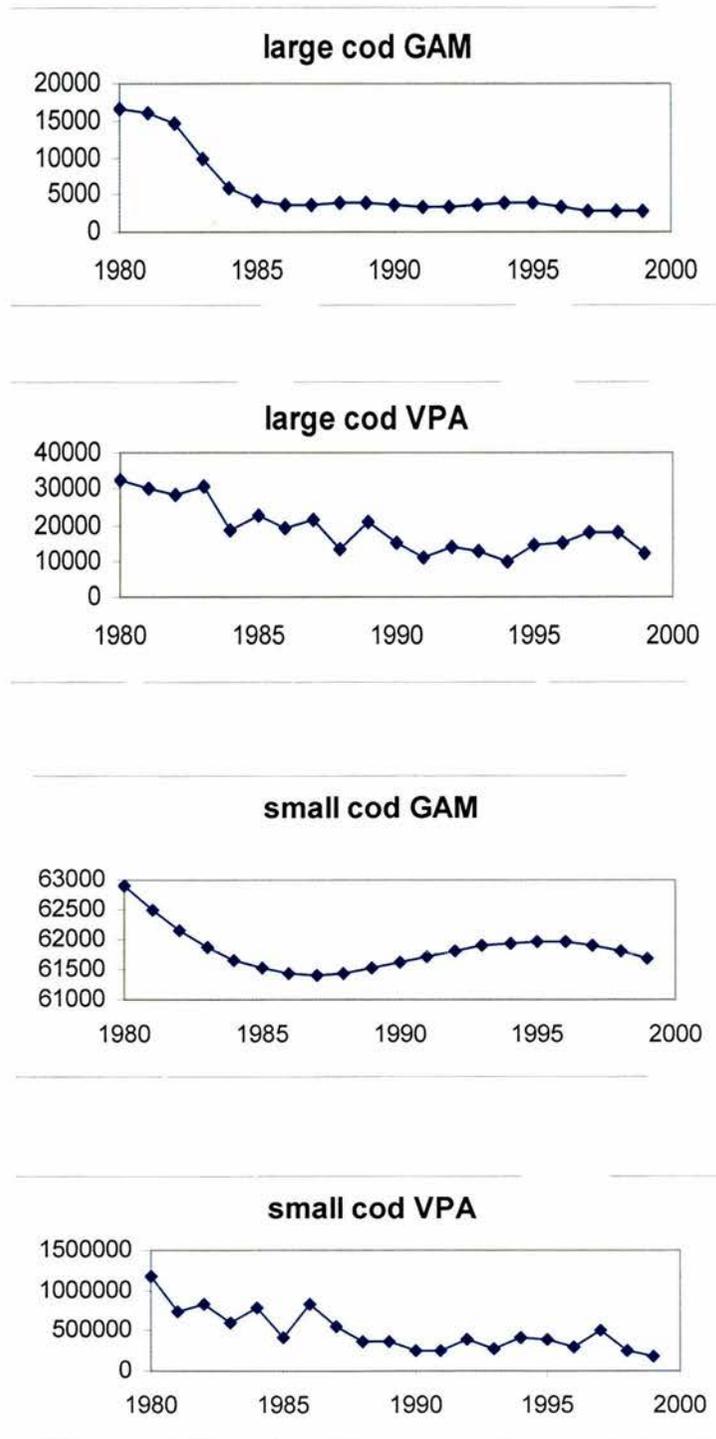
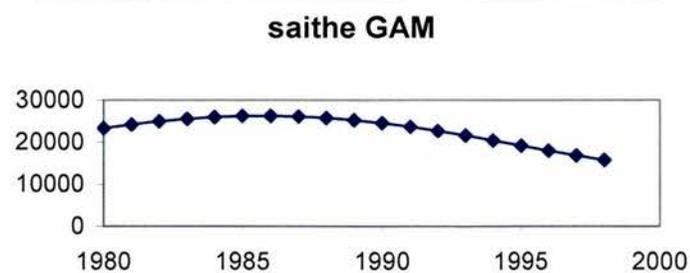
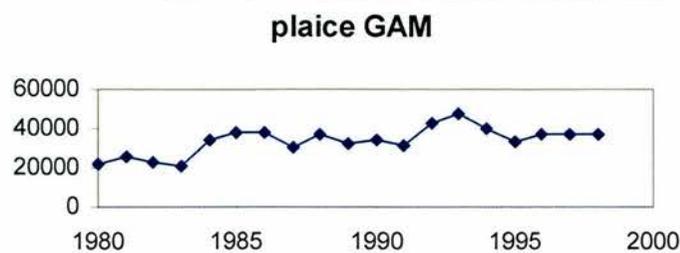


Figure 2.9 continued: time series of abundance predicted by the GAM models and VPA for plaice and saithe



### 2.2.3 Prey availability

Maps of the accessibility of space to seals around six UK regional haul-out groupings were supplied by J Matthiopoulos. The locations of these haul-outs are shown in Chapter 4 (Figure 4.1). Accessibility  $a$  at distance  $d$  from the centre of each haul-out group (where  $d$  is measured in kilometres) was calculated using the following relationship, the derivation of which is given in Matthiopoulos *et al.* 2004:

$$a = \left(\frac{d}{5}\right)^{-1.98} \quad (2)$$

Prey availability was calculated as follows.

Predicted CPUE values were calculated from the GAM for each prey class, for each 5km grid cell  $i$  within the convex hull of the data points. For a given haul-out  $k$ , the predicted CPUE value in each cell  $c_i$  was multiplied by the accessibility  $a_{i,k}$  of that cell to grey seals from the haul-out. These values were then summed over the entire surface.

$$\alpha_k = \sum_i c_i a_{i,k} \quad (3)$$

Availabilities for each haul-out group, site and quarter are shown in Table 2.2.

**Table 2.2: Prey availability**

Indices of prey availability based on overlap between accessible space for seals, and fish distributions calculated from GAMs. Upper and lower confidence intervals were calculated from bootstrap re-sampling of the IBTS CPUE data that was used to fit the GAMs.

bootstrap iterations	immature cod			mature cod			whiting			plaice			saithe			ling			sandeels				
	year	quarter	location	mean	lower CI	upper CI	mean	lower CI	upper CI	mean	lower CI	upper CI	mean	lower CI	upper CI	mean	lower CI	upper CI	mean	lower CI	upper CI		
1985	1	ork	3.92	3.15	4.48	2.31	1.72	2.70	10.60	9.37	10.90	5.89	5.10	6.78	1.27	0.99	1.51	1.32	0.80	1.73	1.00	0.64	1.21
1985	1	fm	7.90	5.98	9.12	2.58	2.27	3.27	14.80	13.80	15.50	6.50	5.55	7.24	0.78	0.44	0.85	0.49	0.26	0.58	0.73	0.35	0.80
1985	1	dn	7.32	5.95	9.27	2.92	2.09	3.77	14.40	13.00	15.80	10.30	8.23	13.30	0.22	0.16	0.23	0.42	0.18	0.45	0.33	0.17	0.50
1985	1	ih	2.26	1.49	2.79	4.13	2.93	4.98	10.30	9.11	10.90	8.73	6.36	9.96	2.43	1.75	3.04	1.09	0.59	1.54	0.61	0.39	0.75
1985	1	ohn	1.51	0.95	1.81	6.24	3.89	8.14	9.23	8.12	9.84	7.16	6.05	8.72	1.92	1.43	2.25	1.65	1.17	2.33	0.40	0.25	0.57
1985	1	ohs	1.55	1.10	2.07	4.37	3.07	5.43	9.96	9.14	10.80	9.70	8.16	11.10	1.41	1.00	1.67	0.98	0.66	1.41	0.56	0.30	0.60
1985	3	ork	3.65	2.88	4.27	2.26	1.77	2.60	9.75	8.59	9.96	5.58	4.59	6.30	1.80	1.49	2.17	1.25	0.75	1.67	1.14	0.67	1.37
1985	3	fm	7.50	5.56	8.63	2.52	2.21	3.11	13.80	12.70	14.40	6.14	5.01	6.60	1.28	0.87	1.48	0.45	0.23	0.55	0.83	0.42	0.88
1985	3	dn	6.94	5.50	8.94	2.85	2.10	3.77	13.40	12.00	14.70	9.81	7.26	12.00	0.37	0.27	0.45	0.39	0.15	0.42	0.41	0.18	0.59
1985	3	ohn	2.06	1.26	2.61	4.05	2.84	4.90	9.45	8.31	10.00	8.33	5.86	9.06	3.28	2.30	3.98	1.03	0.55	1.42	0.69	0.43	0.85
1985	4	ork	3.52	2.74	4.14	1.64	1.23	2.01	9.33	8.20	9.59	5.15	4.27	5.87	1.40	1.18	1.81	1.22	0.73	1.63	0.66	0.35	0.70
1985	4	fm	7.31	5.46	8.49	1.74	1.39	2.25	13.30	12.20	13.90	5.64	4.69	6.19	0.90	0.41	1.10	0.44	0.21	0.51	0.48	0.24	0.50
1985	4	dn	6.75	5.29	8.73	1.88	1.25	2.54	12.90	11.40	14.20	9.16	6.49	11.40	0.25	0.18	0.33	0.37	0.14	0.41	0.18	0.10	0.30
1985	4	ih	1.96	1.16	2.51	2.96	1.93	3.74	9.05	7.88	9.66	7.77	5.21	9.08	2.64	1.92	3.43	1.00	0.53	1.38	0.40	0.23	0.55
1985	4	ohn	1.26	0.74	1.59	4.67	2.86	6.49	8.05	6.94	8.60	6.28	5.14	7.49	2.09	1.61	2.55	1.54	1.10	2.20	0.22	0.13	0.29
1996	4	fm	6.91	5.34	7.94	1.03	0.71	1.32	15.90	14.70	16.60	3.48	2.61	3.96	0.32	0.22	0.43	0.32	0.17	0.36	0.51	0.22	0.57
1997	1	fm	7.49	5.81	8.90	1.61	1.29	2.04	17.80	16.80	18.50	3.82	3.03	4.56	0.16	0.14	0.22	0.32	0.16	0.38	0.76	0.29	0.91
1997	3	fm	7.10	5.49	8.34	1.57	1.24	1.92	16.60	15.60	17.30	3.55	2.69	4.09	0.42	0.30	0.50	0.29	0.15	0.34	0.88	0.34	0.99
1998	1	fm	7.50	5.66	8.99	1.61	1.28	2.04	17.90	16.90	18.80	3.51	2.73	4.27	0.20	0.15	0.27	0.29	0.16	0.36	0.72	0.27	0.87
1998	3	fm	7.12	5.41	8.44	1.57	1.23	1.95	16.70	15.70	17.70	3.26	2.44	3.84	0.35	0.24	0.42	0.27	0.15	0.33	0.83	0.31	0.94
1998	4	fm	6.93	5.25	8.23	1.01	0.71	1.34	16.20	15.10	17.00	2.92	2.18	3.43	0.17	0.15	0.23	0.26	0.14	0.32	0.47	0.21	0.53

The uncertainty associated with these availability estimates was calculated using bootstrap re-sampling of the IBTS data. GAMs, maps and availabilities were recalculated at each re-sampling step. The number of bootstrap iterations was limited by the CPU time required, each iteration taking approximately 10 minutes running under Windows on a Pentium M 1.70 GHz machine. The confidence intervals resulting from the bootstrapping process are shown in Table 2.2.

Some bootstrap iterations failed when the GAM-fitting algorithm was unable to converge on a solution. The number of successful bootstrap iterations that was performed each time is shown in Table 2.2. No attempt was made to take account of uncertainty in the values of accessibility, because these were considered to be relatively small.

Examples of the distribution of availability for two prey classes at two sites are shown in figure 2.10.

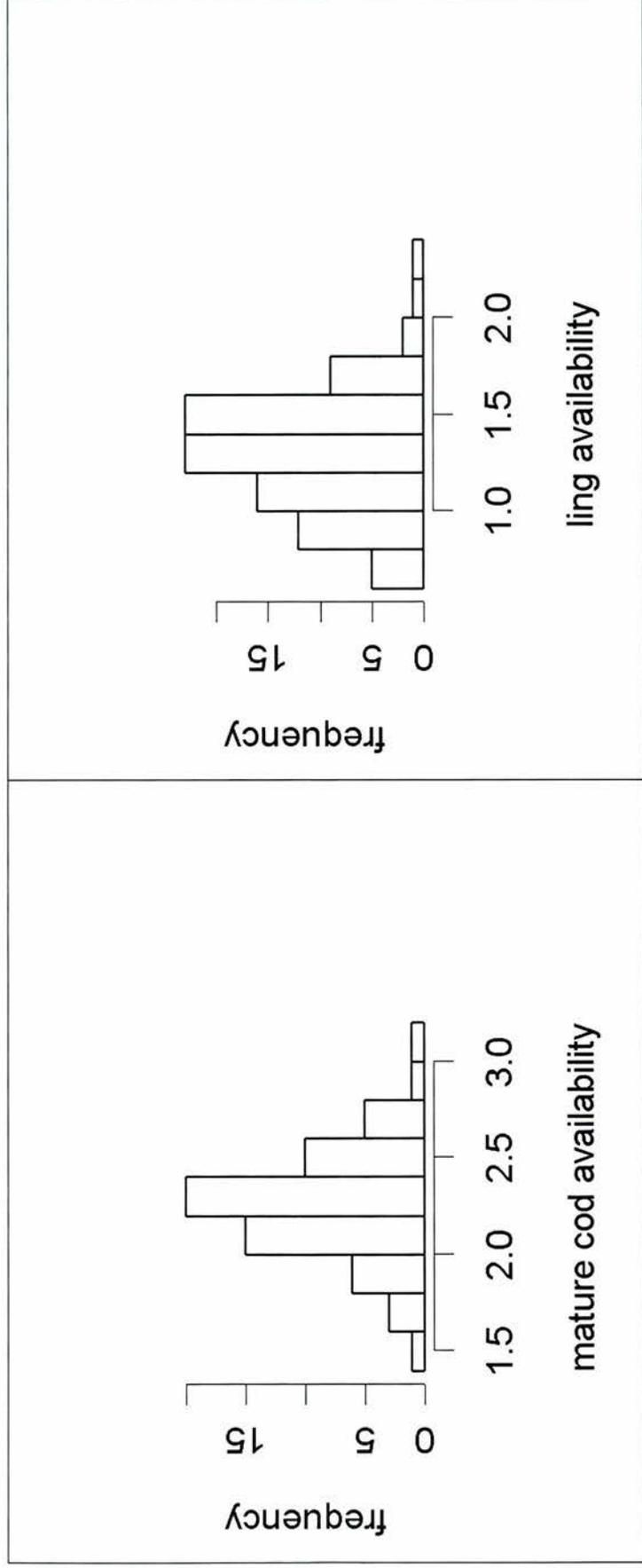
## **2.3 Discussion**

### **2.3.1 Abundance and CPUE**

In this study, I used CPUE estimates to predict fish distributions. However, trawls only sample from a fraction of the available water volume. Absolute

**Figure 2.10: Uncertainty in estimates of availability**

Uncertainty in the estimates of availability of mature cod and ling in the Orkneys, Quarter 1, 1985. Distributions were obtained from bootstrap re-sampling of the IBTS data. 'Best estimates' based on the complete data set were 2.31 for mature cod, and 1.32 for Ling.



abundance can only be measured from CPUE if the dimensions, speed and time of the trawl are recorded, and the catchability of a given fish species and size class is known (Jennings *et al.* 2002, Sparholt 1990). An important factor that influences catchability is the mesh-size of the net, because small fish may escape through a wide mesh. Catchability will also vary according to the depth of the trawl and the depth band in the water column that is normally occupied by a given fish species. Catchability may also depend on detailed fish behaviour (Wardle 1983). As a result, converting counts of the number of fish collected in a trawl into estimates of abundance is not straightforward, (Sparholt 1990, Maunder and Langley 2004, Harley and Myers 2001).

CPUE data cannot be assumed to indicate even the relative numbers of different species that are present in a single haul, because catchability varies among species and size classes. However, provided that CPUE data are collected in a consistent way between sites (Adlerstein and Ehrich 2003, Hjellvik *et al.* 2002), and that catchabilities do not vary in time or space (Alderstein *et al.* 2002, Petrakis *et al.* 2001), CPUE values can be used to compare the abundance of individual species and size class among sites.

Fortunately, absolute measures of abundance are not needed to fit an MSFR, provided that the relationship between CPUE and abundance is linear, and does not vary between surveys. For the purposes of the present study, I assumed that the standardised methods used in the IBTS survey ensured that

trawls are carried out consistently (Alderstein and Ahrich 2002), so that CPUE can be used as a satisfactory index of abundance. I also assumed that abundance is linearly related to CPUE - a strong assumption, but one that is commonly used in fisheries modelling (Jennings *et al.* 2002).

### 2.3.2 GAMs and fish

#### 2.3.2.1 Immature cod, *Gadhus morhua*

Immature cod are known to inhabit shallow inshore nursery areas (Munk 2002). The predictions of the GAM for immature cod (Figures 2.8 and 2.7) are consistent with this, although there is also an indication that some use is made of deeper water. This probably arises because fish have been allocated to size rather than age classes, and some fish in this size class may be mature. The fitted relationship between CPUE and depth confirms that these fish prefer shallow areas, though it should be noted that IBTS data were not available for the shallowest waters close to shore.

Cod stocks are currently at very low levels, and reached a historic minimum during the 1990s, probably as a result of over-exploitation (Daan *et al.* 2005, Hislop 1996, Hutchinson *et al.* 2003). Most cod stocks in the northeast Atlantic are considered to be outside safe biological limits (ICES 2004c). The signature of this population decline is seen most clearly among larger fish, because the highly variable level of recruitment causes considerable variation in the

numbers in younger cohorts, and the larger size classes appear to be most strongly impacted by exploitation (Jennings *et al.* 2002, Law 2000). The GAM fitted in this study however was still able to detect a decline in the abundance of immature cod in the North Sea (Figure 2.9) that is consistent with the long-term trend in VPA estimates, suggesting that the north-western part of the cod stock was following the whole-North-Sea downward trend in abundance during this time period.

The combined effect of trawl location and year was selected for inclusion in the final model, suggesting that there has been a change in the distribution of immature cod over the study period. Such a redistribution might be a response to the decline in the whole stock, with cod concentrating in areas where growth is optimised (Blanchard *et al.* 2005). Alternatively, the effect might be seen due to different population dynamics occurring in different areas: it is now known that there are several genetically distinct stocks within the North Sea (Hutchinson *et al.* 2001). Hedger *et al.* (2004) drew similar conclusions about changes in the distribution of mature cod in the North Sea.

### **2.3.3.2 Mature cod, *Gadhus morhua***

No significant effect of time of year was detectable when fitting the GAM model, although tagging studies suggest that individual cod may undertake considerable seasonal migrations (Solmundsson *et al.* 2005, Righton and

Metcalfe 2002). This might indicate that individual migrations are not representative of whole-population behaviour, but it is more likely to be an artefact of the spatial selection of data. Spawning areas off the south-west Norwegian coast, where significant movements of adult fish are known to occur, were not included. The GAM does predict a relationship between abundance and depth, with mature cod inhabiting a wider range of depths than immature cod, and preferring deeper waters (Magnussen 2002). The general distribution is consistent with other spatial models of cod distribution that make use of the same survey data sets (e.g. Hedger *et al.* 2004, Perry *et al.* 2005), showing concentrations of fish to the north and east of the UK coast, and towards the Norwegian coast.

There was a positive linear relationship between the VPA predictions of North Sea cod stock size and the predictions of the GAM, with both models showing a strong decline during the 1980s and 1990s, though details of these time series are different (Figure 2.9). It is interesting that the general reduction in the North Sea cod stock is detectable in the north-western area modelled by the GAM, even though the redistribution of cod shows a northwards trend: this trend is therefore most likely to be due to a more severe decline in southern stocks, rather than a northwards movement of fish (Cook, 2002).

#### ***2.3.3.3 Immature plaice, *Pleuronectes platessa****

The GAM for immature plaice suggests that they prefer shallow waters, and this is consistent with observations from other studies, where young plaice were found inshore, right up to the surf zone (Beyst *et al.* 2002, Gibson *et al.* 2002). Immature plaice are known to winter offshore (Rinsjodorf 1995). The GAM showed a slight trend for smaller catches during the summer period, perhaps resulting from fish moving inshore in the summer, making them less available to the trawl. The GAM did not capture the complexity of migrations observed during individual tagging studies, however (Hunter *et al.* 2003).

The highest densities of immature plaice are generally observed in the south-western North Sea (Knijn 1993). Only the north-west edge of this region was represented in the IBTS hauls used in this study (Figure 2.8).

The North Sea plaice stock was heavily exploited during the later part of the twentieth century. Since the 1970s, the population appears to have been considerably depleted, resulting in reduced genetic diversity (Horau *et al.* 2005), and effects on age and size at maturity (Kell and Bromley 2004). The North Sea plaice VPA estimates show significant fluctuations in the size of the immature cohort during the 1980s and 1990s, resulting from several particularly strong year classes, but there is no general time trend (ICES 2004c). There was some support (at the 90% level) for a linear relationship between the VPA results and those from the immature plaice GAM, even though most of the North Sea plaice stock is outside the area used to construct the GAM.

#### **2.3.3.4 Sandeels, *Ammodytes marinus* and other species**

The abundance of sandeels is particularly difficult to measure. They are small and difficult to catch using ordinary fishing gear. During the winter, they are generally buried in sediment. Intensive local surveys of sandeel populations have been made using grabs, trawls and acoustic methods, but the results from different techniques are not always easy to reconcile with one another, though progress has recently been made in predicting sandeel populations from the results of grab surveys, acoustics and trawls (Greenstreet *et al.* in press). Studies in Shetland (Wright *et al.* 2000) suggest that sandeel population density can vary considerably over small spatial scales.

ICES stock assessments for sandeels are based on CPUE data collected by the Danish sandeel fishery which operates mainly in the south-eastern North Sea. Rindorf (pers com) has used Generalised Linear Models to investigate spatial variation in sandeel abundance in this region, but the modelled area is not accessible to most UK grey seals.

Catchability for sandeels in the IBTS is low and the data contain many low values and zeros, even in areas where sandeel abundance is thought to be high. CPUE in IBTS trawls may also be an inconsistent measure of sandeel abundance because their distribution in the water column is known to be highly variable (Jensen *et al.* 2003). However, for all its shortcomings, the

IBTS is the only data set based on a consistent survey technique that is currently available and which covers the time period and geographical area of the seal diet studies.

The GAM that was fitted to the IBTS data did explain a significant amount of variation (DE= 39%), but the poor quality of the data is reflected in the wide confidence intervals obtained when bootstrapping.

Previous studies have indicated that local abundance of sandeels is strongly related to environmental factors, with shallow depths and gravely sediments being preferred (Wright *et al.* 2000). Depth and sediment type have been used to predict the occurrence of sandeels in particular areas (e.g. MacLeod *et al.* 2004), so it is therefore not surprising that sediment type and depth were significant variables in the GAM and that predicted abundance was highest in shallow waters (Figure 2.7).

Pederson *et al.* (1999) suggests that the sandeels around the UK form a number of sub-populations. If this is the case, the annual ICES stock assessments for sandeels (Lewy *et al.* 2004), which are based mainly on Danish CPUE data collected outside the area covered by the present study, are unlikely to be related to the predictions of the GAMS reported here. No attempt was therefore made to compare the two time series. It was also difficult to compare the results of the GAM analysis with historical local

studies (Greenstreet *et al.* in press ) because these have not provided time series of abundance estimates that match the time scale of the present study.

#### **2.3.3.5 Whiting, *Merlangius merlangus***

Whiting were predicted to be widespread and generally abundant throughout the North Sea (Zheng *et al.* 2001, Zheng *et al.* 2002).

The GAM detected an interaction between season and depth (see Table 2.2) in the distribution of whiting. The preferred depth range was 0-200m, with the highest abundance predicted to occur in the more shallow areas in winter. Verdoit *et al.* (2003) detected similar seasonal and age-related effects in research and commercial catch data from the Celtic Sea (though this is not within the area of the current study). Zheng *et al.* (2002) note that the effect of environmental variables on whiting distribution change with season. This highlights the importance of testing for interaction terms in GAMs (Venables and Dichmont 2004).

No significant relationship was found between the GAM predictions and VPA estimates of whiting stock size in the North Sea. It appears that IBTS hauls of whiting in the north-western North Sea remained relatively large throughout the 1980s and 1990s, while catches in more southerly areas decreased (ICES 2004c).

### 2.3.3.6 *Ling, Molva molva*

Adult ling are large fish, inhabiting waters between 100m and 1000m, though habitats between 100m and 400m are preferred (Bergstad 1991, Husebo *et al.* 2002). Younger individuals may inhabit shallower areas, and it is largely these young fish that are taken by seals (Hammond *et al.* 1994a,b). The GAM predicts a rather complex depth-abundance relationship, suggesting that depth may be acting as a surrogate for another environmental covariate, or that several age classes of ling may be represented, each of which has a different depth preferences. The deeper parts of potential ling habitat were not explored by IBTS. However, these would not be accessible to diving seals, so this is not an important limitation for this study.

The greatest densities of ling are predicted to occur around the northwest of the UK, where the continental shelf drops away towards deeper waters. Some commercial fishing for ling takes place in this area, and the predicted distribution of ling is consistent with known habitat and spawning grounds (Gordon 2001, Gordon 1999). This area is also known to be visited by seals monitored during telemetry studies (Aarts, pers com).

### 2.3.3.7 Saithe, *Pollachius virens*

The GAM showed saithe concentrated in the waters north and east of the British Isles, consistent with known distributions (Knijn 1993) and the main fishing areas for this species (CEFAS 2005). A predicted preference for deeper water (Figure 2.7) probably reflects the behaviour of larger saithe as reported by Cotter *et al.* 2004, since younger saithe are known to inhabit shallower areas (CEFAS 2005). A seasonal effect was also predicted, with CPUEs being higher during summer months (FRS 2005).

Saithe in ICES areas IV and VI (North Sea and Western Scotland) is treated as a single stock in the ICES VPA, so the GAM was used to predict an index of total abundance for the whole area within the convex hull of the data, for the 1980s and the 1990s. This index was not well correlated with the VPA stock assessments, however (correlation coefficient=0.142, p-value 0.8), and the plot appears over-smoothed (Figure 2.9).

It is likely that the poor correspondence of VPA and GAM time series is a result partly of excessive smoothing occurring within the GAM fitting process, and this might be circumvented by fitting the GAM in a different way (i.e. not relying solely on the AIC as a criterion for choosing between models). It is also possible, however, that there is some feature of the IBTS data that was used to fit the GAM which partly accounts for the differences between the GAM and VPA time series. Future work will look in more detail at the age and size

structure of the IBTS catch, and at the corresponding VPA age classes. The effect of the limited spatial area that was included in the GAM, compared with the VPA, will also be examined.

#### **2.3.4 Modelling fish distributions in time and space using GAMS**

When a GAM is fitted, some spatial detail may be lost during the smoothing process. Small-scale variations may not be detected if data are collected from widely-spaced locations, as in the IBTS data set. Significant variations which may escape observation are likely to occur where habitats lie close to the shore, or where the substrate is rocky and inaccessible to trawling. In certain areas (the Minch, for example) coverage by the IBTS trawls is poor in all years. In addition localised concentrations of prey may go undetected if the prey species are relatively immobile, such as buried sandeels. However, such localised concentrations may be readily detectable to predators and could be very important to them.

The ability of the GAMS to predict detailed spatial distributions depends on the predictive power of the covariates that are used. However, it is also important that these covariates are mapped with sufficient precision and spatial resolution. In practice, this is rarely the case and this often prevents a modeller from including factors that are known to be important into a working GAM. Lack of covariate information is a particular problem for marine

systems, where remote sensing can generally only provide useful information about the properties of surface waters.

Some of the abiotic variables which have been shown to influence the distribution of fish are: time of day, (Alderstein *et al.* 2003, Petrakis *et al.* 2001, Wieland and Rivoirard 2001, Hjellvik *et al.* 2004); sea bottom temperature, (Hedger *et al.* 2004, ); sea surface temperature and temperature effects mediated by the North Atlantic current (Zheng *et al.* 2002); and tidal streams (Arnold 1994). Biotic variables that appear in other studies include plankton distributions (Corten and Lindley 2003); primary productivity (Munk and Wright 2002); the presence of weed (Laurel *et al.* 2003); the presence of deep-sea corals (Husebo *et al.* 2002); general population density (Arnott and Ruxton 2002, Bergstad *et al.* 2002, Hjellvik *et al.* 2004); and the presence of predators and prey (Cianelli *et al.* 2002, Beare *et al.* 2003, Gotceitas and Brown 2003).

The choice of covariates to include in a GAM must be based on biological knowledge, but it is usually difficult to include all the likely covariates for computational reasons. It is also preferable not to include covariates that are highly correlated with one another - something which can easily occur, for example, when depth and distance-from-shore are both included in a model. Moreover, no purely habitat-based model, however detailed, can predict the spatial distributions of an organism perfectly. Dynamic processes including migration and local population dynamics may be powerful forces in shaping

fish distributions, and these factors may create complex patterns of abundance even within areas of habitat that appear uniformly suitable.

In this study, I used only two environmental covariates (depth and sediment type) to predict fish distributions. I assumed that the spatial modelling would ‘absorb’ any effects on the distribution due to unknown variables that had not been included in the model. It might be possible to improve the confidence with which abundances can be predicted by including other predictive variables in future work. Likely candidates would be sea bottom temperature, which has been shown to be a useful indicator for gadoids (Hedger *et al.* 2004, Zheng *et al.* 2002), sea surface temperature which may be a crucial factor in the survival and recruitment of year 0 sandeels in any given year, (Arnott and Ruxton 2002), and primary and secondary productivity which vary considerably within and between years (Schrum *et al.*, 2006). There is some evidence that changes in productivity can control the growth and settlement of sandeels, and may thereby influence the behaviour and distributions of their predators (Daunt *et al.* 2003).

### **2.3.5 Time and space**

To include time as an extra ‘dimension’ in the GAMs seemed an attractive option, because it allowed for spatial distributions in the years of interest to be informed by data collected during other years. It also offered the possibility of interpolating between time points in order to obtain estimates

of fish distributions for quarters in which seal diet data, but no IBTS data, was available (for example, quarter 4 in 1996).

Previous studies (Piet 2002, Fox *et al.* 2000) have incorporated time-variation into GAM models with some success. No comparable time-series of abundance indices were available for sandeels and ling, and the time series predicted by the GAMs for these species could not therefore be compared with any known 'standard'. However, for both size classes of cod and for plaice, the time series predicted by the GAMs corresponded fairly well with VPA stock estimates. Though the two time series are not entirely independent, because the North Sea VPAs also make use of the IBTS data as well as commercial catches, this does provide some evidence in support of the GAM predictions of temporal trends. The stock trajectory calculated from the GAM is more smooth than that predicted by the VPA. This may be a consequence of the smoothing that is incorporated in GAM estimation and it appears to be a problematical effect in the case of Saithe. However, it is also possible that the size-based IBTS data themselves are somewhat less 'spiky' than the VPA estimates, because growth and size-at-age are not constants and they may be density-dependent, and the timing of recruitment into the catchable population of fish is variable.

### **2.3.7 Calculating prey availability for a central placed forager**

In the present analysis, the availability of space to seals, rather than the usage of space by seals, was used to calculate prey availability (Matthiopoulos *et al.* 2003). The detailed usage of space by foraging animals was considered to be part of the process of prey choice, which could be adequately represented by a fitted functional response. This reasoning assumes that seals have some knowledge of the general availability of prey that is within reach of their haul-out, and can adjust their usage of space in response to changes in local prey distributions.

An important assumption of the present study is that seal foraging behaviour has not changed significantly during the past two decades, and the availability of habitat around haul-outs can be considered to have remained constant during the period of the study. It is perhaps more justifiable to assume that habitat availability (which emerges from general properties of seal movement) is stable over time, than to assume that detailed spatial usage is stable. It is however difficult to test either hypothesis because of the limited amount of telemetry data that is available.

### **2.3.8 Estimating uncertainty**

A potential difficulty with non-parametric re-sampling for spatial data is that uncertainty may be underestimated if errors are spatially auto-correlated (Stratoudakis *et al.* 2003). However, for fish CPUE data where errors are most likely to arise as a result of very localised behaviour such as shoaling and

predator avoidance, spatial correlation of errors is not likely to cause difficulties on the scale of the IBTS survey.

## **2.4 Conclusions**

Estimates of prey availability for UK were made by interpolating CPUE estimates from research survey data using GAMs to produce spatial models of fish distributions over the time period of the study. The resulting spatial distributions and relationships with environmental covariates corresponded well with known fish behaviour and distributions, and provided a good fit to the data. Prey availability was then calculated using an existing model of habitat accessibility for UK grey seals. Uncertainty in the estimates of availability was explored using bootstrap re-sampling from the fish survey data.

## Chapter 3. Spatial bias in estimates of the diet of a marine predator: the grey seal *Halichoerus grypus*

### Summary

In order to determine the diet of grey seals, scats are collected from haul-outs. Otoliths, paired small bones from the skulls of fish, are extracted from the scats, and these are measured and identified in order to determine the size and species of fish from which they came. The proportion of each prey in the diet can then be calculated.

A key assumption of scat analysis is that each scat is a representative sample of the seals' diet. Previous studies have taken account of two possible sources of bias in the process of estimating diet: the effects of digestion, which reduces the size of otoliths; and the complete loss of otoliths due to digestion. In this chapter, I examine a third source of bias: unrepresentative sampling of the space over which seals forage.

Only scats that are deposited on land can be collected. These will only provide a representative sample of the seals' diet if the location where the prey was consumed by the predator does not affect its chances of being found in the scat samples collected at the haul-out. However, the time taken for prey items to be processed in the seal's digestive tract and

excreted (the 'passage time') is of the order of days - the same time scale as a typical foraging trip. If the spatial distributions of prey species differ and some prey are more likely to be taken at a greater distance from the haul-out, or if the transit time of food through the gut varies substantially between prey species, then estimates of diet based on scat samples might be biased. The nature and significance of this bias will depend on seal behaviour, i.e. the duration of foraging trips and subsequent hauling-out.

In order to evaluate the extent of this potential 'spatial bias' for British grey seals, I analysed experimental and telemetry data and used the results to run simulations in which fish remains were returned to shore in seal scats. The results indicate that prey which is consumed far from shore and/or passes through the gut in a short time may be under-represented in the scats. However, for UK grey seals which generally forage close to shore, the analysis suggest that any bias that emerges from these effects is not likely to be significant.

This methodology may be applicable to other central-placed predators whose diet is estimated using scat analysis.

### 3.1 Introduction

In order to determine the diet of grey seals, scats are collected from coastal haul-outs. Otoliths, paired small bones from the skulls of fish (Harkonen 1986) are extracted from the scats. These are then identified and measured in order to determine the size and species of fish from which they came. The proportion of each prey in the diet can then be calculated (Prime and Hammond 1987, 1990).

A key assumption of scat analysis is that the contents of each scat provide a representative sample of the diet of the seals using that haul-out. In previous studies, one source of bias in the process of estimating diet from scats was taken into account: the effects of digestion, which reduces the size of otoliths (Prime and Hammond 1987, Grellier and Hammond 2005). Estimates of the digestion coefficients, which are used to correct for this effect, have recently been improved as a result of experimental work with captive seals at SMRU (Grellier and Hammond 2005). Another source of bias - the complete loss of otoliths due to digestion - can be addressed by measuring the recovery rate of otoliths when a known number of otoliths are fed (Bowen 2000). In this chapter, a third effect that could result in significant bias is investigated.

Diet is estimated from scats found onshore, and scats that are deposited at sea are not found. Each scat is only a representative sample of the seals' diet if the location where the prey was consumed by the predator does not

affect its chances of being found in the scat samples collected at a particular haul-out. Two ways in which the locations at which prey items are consumed might effect the estimates of seal diet composition are:

- (a) if large quantities of prey are consumed far from the haul-out, and the near-haul-out diet is significantly different from the diet consumed in locations that were remote from the haul-out, and passage rates are such that otoliths are lost at sea before a seal returns to its haul-out. This might result in an important bias if seals spend significant time foraging both near and far away the haul-out, and if prey distributions are very different in these locations.
- (b) even if prey is uniformly distributed, items that pass through the seal's gut quickly may be under-represented in scats compared with items that pass through more slowly, due to the loss of otoliths at sea before hauling-out takes place.

### 3.2 Methods

I used simulation modelling to explore the expected relationship between the distance ( $d$ ) from a haul-out where a fish is eaten, and the probability  $P$  that otoliths from this fish will be found in a scat sample.

For a given prey type,  $P$  was expected to depend on the time( $S$ ) taken for an otolith to pass through the gut of a grey seal after the prey has been eaten, and the nature of the seal's movement. In particular, the duration of

foraging trips and haul-outs, and any dependency that might exist between these, were thought likely to affect *P*.

Haddock, plaice and sandeels from which one otolith had been extracted were fed to a captive seal held within a small pool at the Sea Mammal Research Unit. Faecal material was collected at 24-hour intervals by draining the water from the pool through a filter. Recovered otoliths were identified, counted and measured (Grellier and Hammond 2005, Grellier pers. com.).

The passage-rate data for each prey species were interpolated by fitting a logistic curve to the data, with the proportion of otoliths passed as the dependent variable and time as the only covariate. The analysis was carried out in R using the function `glm` (.).

Telemetry data were collected by means of Argos satellite tags, glued to the fur of seals (McConnell *et al.* 1999). Data are returned to the experimenter via a satellite, which receives signals from the tag when the tag is exposed above the water at an appropriate time. Information on the current location of the seal, previous dives, and the state of the tag (wet or dry) is transferred. Significant errors occur in some satellite tag locations, due to refraction of electromagnetic waves in the Earth's atmosphere.

Tags were deployed on 110 individual British grey seals between 1997 and 1999 (Matthiopoulos *et al.* 2004, McConnell *et al.* 1999). On average, 104

days of data were collected for each individual seal, with an average of 6.5 location fixes per day. Locations were interpolated and smoothed using an algorithm developed by J. Matthiopoulos (pers com) to provide tracks with locations calculated at 2 hourly intervals. The state of the tag (wet or dry) at each location was also recorded. For the purposes of the present analysis, seals were defined as 'hauled out' if their location was within 10km of the nearest haul-out grouping, and the tag sensor also recorded a dry reading.

The probability  $P(D)$  that an otolith ingested at a distance  $D$  from shore was deposited in a scat while a seal was hauled out was assumed to depend on:

- I. passage time ( $s$ )
- II. the time ( $t$ ) taken for the seal to return to its haul-out
- III. the duration of the haul-out ( $u$ )

An initial approach was to model  $P(D)$  analytically as :

$$\int_0^{\infty} f_{TID}(t) \left\{ \int_t^{\infty} f_S(s) ds - \int_0^{\infty} f_U(u) du \int_{t+u}^{\infty} f_S(s) ds \right\} dt \quad (1)$$

(Matthiopoulos, pers com), evaluated for a representative range of distances away from the haul-out. The distributions of  $T$ ,  $S$ , and  $U$  were estimated empirically. I assumed that  $T$ ,  $S$  and  $U$  were independently distributed. A further assumption was that prey was equally likely to be consumed at all locations visited by the seal.

I used this model to explore the probability of scat deposition on the first return visit that the seal made to shore after a foraging trip. However, it is

not obvious how to adapt equation (1) to incorporate the possibility of return-visits to the same haul-out during which a scat might be deposited. In order to incorporate the possibility of further visits, and to take advantage of information that may be contained in the data about any dependency between journey time and haul-out time, a simulation approach was adopted, using code written in R (R Development Core Team 2004).

I aggregated haul-out locations into the same regional groups as were used in chapter 3 because this was consistent with the scale over which scats were pooled in order to calculate diet composition. Any scat deposited on a haul-out belonging to a particular regional group was assumed to be recoverable.

The simulation was carried out separately for each of the three prey species (plaice, haddock, and sandeels). The steps in the simulation were as follows.

1. Pick a point  $x$  at random from the database of satellite locations for all seals.
2. Record the haul-out group used by the seal at its subsequent haul-out, and the distance to the centre of that grouping ( $d$ ).
3. Assume that a fish was consumed at  $x$ .
4. Chose a random passage time  $S=s$  from the empirical distribution of  $S$ .

5. Decide whether the seal will be hauled out or in the water at time  $t=s$  after the original foraging event, by picking the appropriate time-point from the interpolated track of the seal, and noting the wet/dry state and proximity to the haul-out.
6. If the seal was in the water at this time, assume that the scat was lost.
7. If the seal was hauled out, assume that the scat was recoverable.
8. Return to step 1.

The simulation was repeated 1000 times for each of 23 haul-out groups.

Data from all haul-out groups were then pooled.

A scaled logistic function was fitted to the binomial data

$$P(D) = \frac{ke^{(a_0 + a_1 D)}}{1 + e^{(a_0 + a_1 D)}} \quad (2)$$

where  $k$ ,  $a_0$  and  $a_1$  are parameters to be estimated.

The fitting was carried out using a Bayesian approach in WinBugs (Speigelhalter *et al.* 2003) with uniform priors

$$k \sim u(0, 1)$$

$$a_0 \sim u(0, 100)$$

$$a_1 \sim u(-2, 0)$$

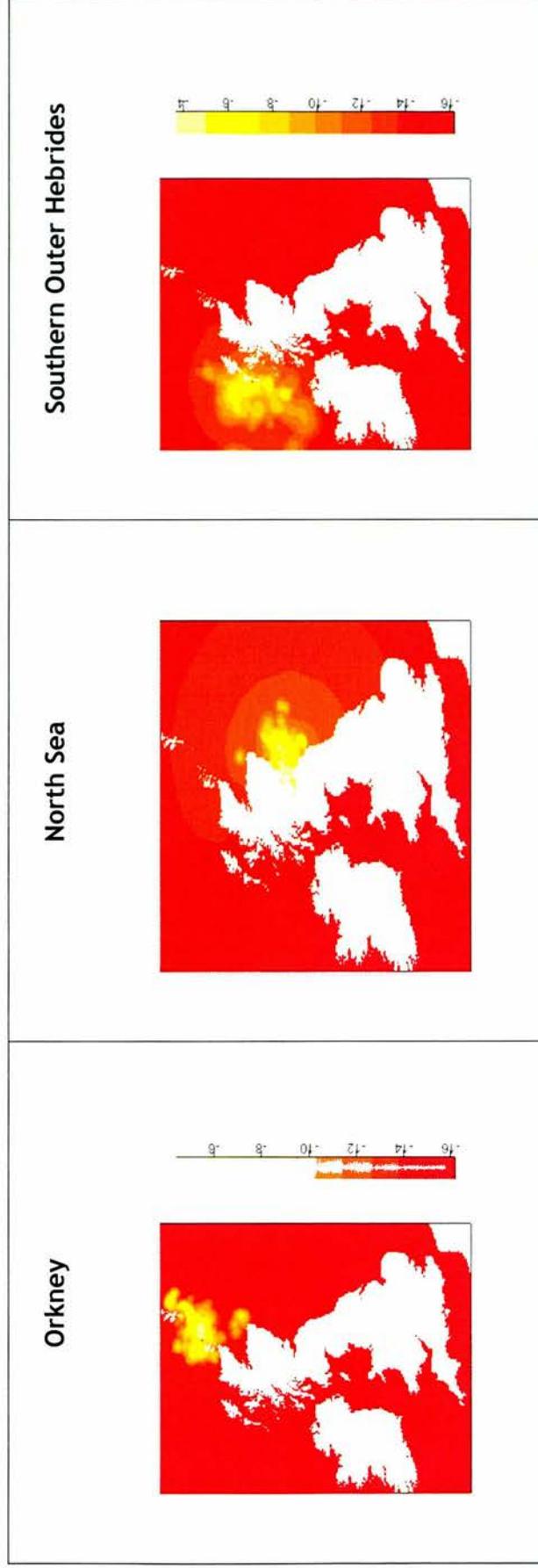
The locations at which prey items were consumed were expected to have a significant effect on estimates of seal diet composition if large quantities of prey were consumed sufficiently far from the haul-out, and the near-haul-out diet was significantly different from the diet consumed in locations that were remote from the haul-out. It was therefore necessary to investigate the spatial overlap between predators and prey in order to assess the bias that might be caused. Maps of the usage of space by grey seals around the haul-out groups, calculated over a grid of 5km squares, derived from model-supervised kernel smoothing of satellite locations (Matthiopoulos 2003, 2004) were provided by J. Matthiopoulos (Figure 3.1).

Distributions of the three prey species were simulated in three different ways:

- a) assuming prey were uniformly distributed
- b) assuming one prey was concentrated in a single patch either close to or distance from a haul-out group
- c) using the models of prey distribution developed in Chapter 2, together with a new GAM fitted for haddock. A prey distribution surface was produced for 1995, on a grid of 5km squares.

The foraging behaviour of grey seals varies according to the type of prey sought (Thompson *et al.* 1991, Bowen *et al.* 2002). Fish are therefore not accessible to seals in the same ways as they are to trawling gear. That is,

Figure 3.1: Predicted usage of space around three haul-out groupings used by British grey seals, based on telemetry data.



the ‘catchability’ of prey is different for seals and research vessels. The prey distribution maps were therefore used as indicators of fish distribution rather than absolute measures of fish abundance, and for convenience, all fish distributions were normalised such that total fish abundance summed over the grid was identical for all species.

The availability of fish to seals was then calculated by multiplying seal spatial usage and normalised fish abundance for each grid cell, and integrating this quantity numerically across the whole prediction surface.

The diet of seals was expected to depend on their multi-species functional response (see Chapter 1). However, no such functional response was available. I therefore assumed that grey seals would consume prey in direct proportion to their availability.

The estimated diet was then calculated by weighting predicted consumption in each grid square by the probability that otoliths from prey consumed in that square would be deposited and recovered at the nearest haul-out group

$$\text{prey collected} = \Sigma(\text{prey abundance} \times \text{seal usage} \times \text{probability of recovery}) \quad (3)$$

This was then compared with the un-weighted diet of the simulated seals (i.e. the diet that the simulated seals consumed).

Simulations were carried out for haul-out groups in Orkney, the North Sea and the southern Outer Hebrides. The output of a typical simulation is plotted in Figure 3.2.

### **3.3 Results**

The mean passage times for otoliths of the three different prey species are given in Table 3.1. No attempt was made to quantify the uncertainty in the estimates because they were based on results from a single individual.

Figure 3.3 shows the fitted logistic functions representing the distribution of passage times for each species.

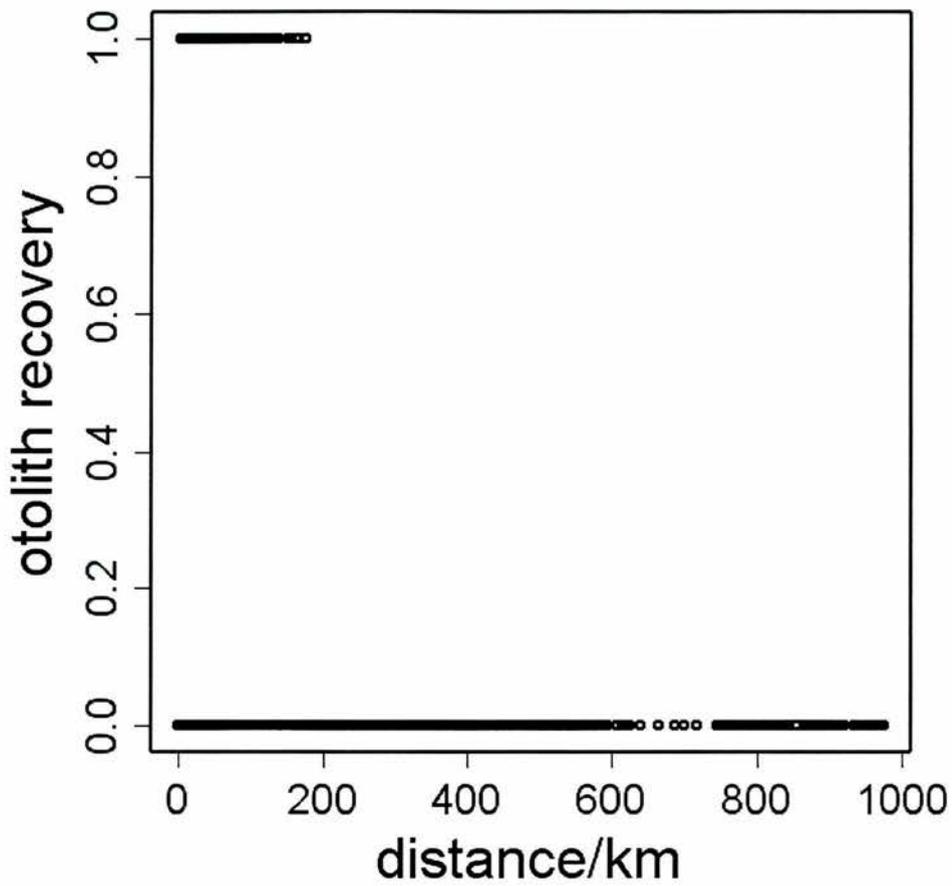
The differences in otolith passage times among species were probably related to the size and mass of the prey fish and their otoliths. For example, sandeels, being significantly smaller than haddock or plaice, might be expected to pass through the stomachs of seals more quickly leading to earlier recovery of their otoliths.

A seal foraging trip was defined as a segment of track joining two episodes of hauling-out. The distribution of the durations of these trips for the satellite-tagged seals is shown in Figure 3.4a. Most trips were less than 10 hours long. The distribution of haulout durations is shown in Figure 3.4b. Very short haul-out episodes (less than five minutes in duration) were considered unlikely to represent true haul-outs on land, and were excluded from the analysis (McConnell pers. com.).

### Figure 3.2: Output of simulation

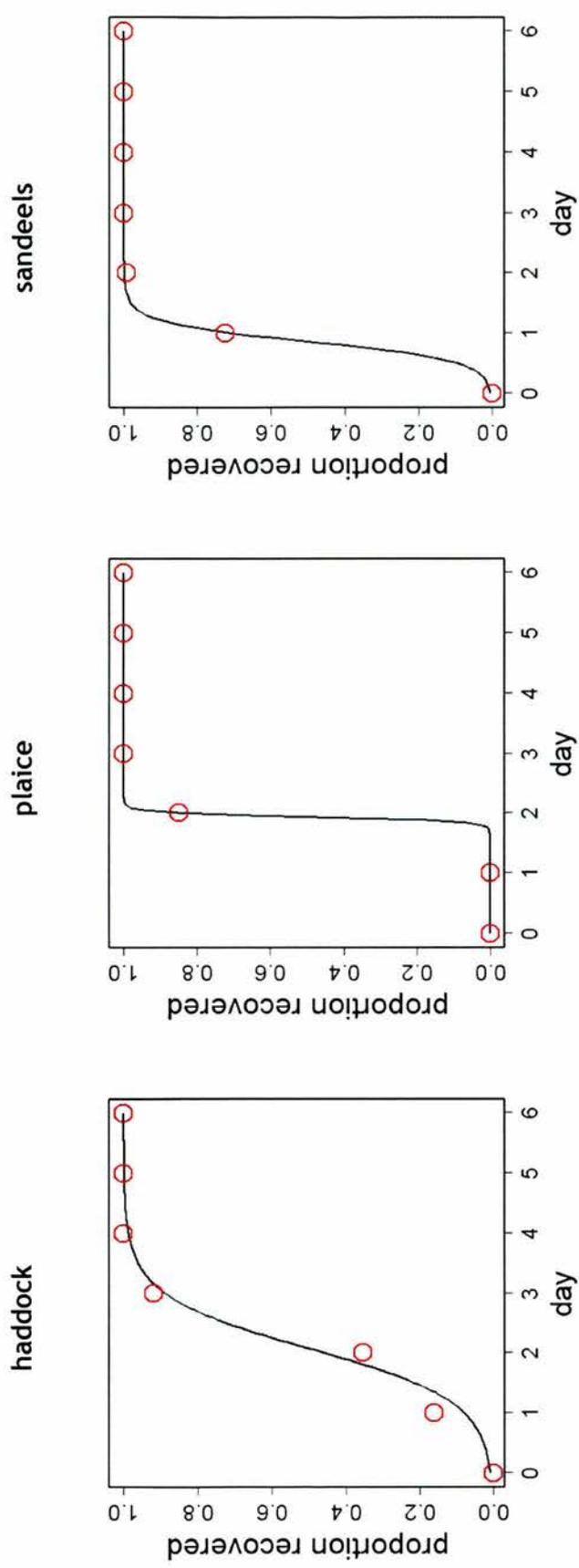
The relationship between the distance of a foraging location from a grey seal haul-out group and the probability that sandeel otoliths consumed at that location by a grey seal will be recovered from a scat deposited at the nearest haul out group.

For each iteration of the simulation, 1 corresponds to an otolith deposited onshore, and 0 corresponds to an otolith deposited at sea. This run of the simulation represents recovery of plaice otoliths.



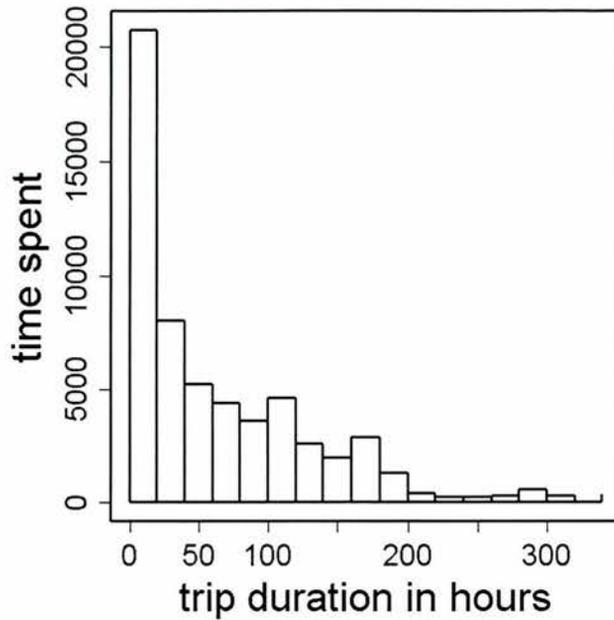
**Figure 3.3: Variation in the total number of fish otoliths recovered at different times after fish had been fed to a captive grey seal.**

Local polynomial smoothing was used to generate the curves.

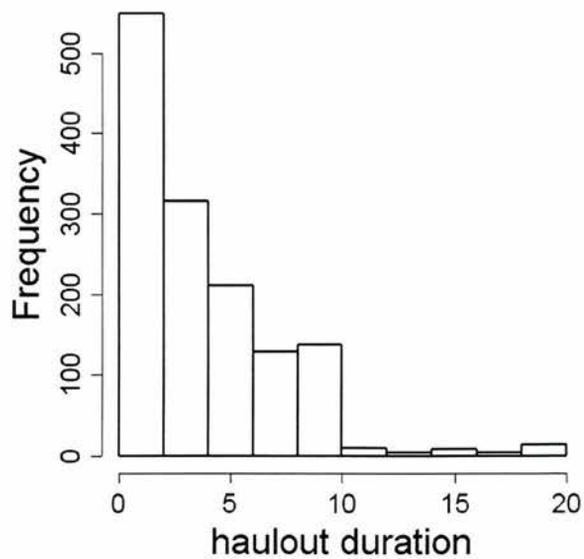


**Figure 3.4: the duration of seal journeys and haulouts**

(a) Distribution of duration of trips away from haul-out groups made by satellite-tagged British grey seals.



(b) distribution of haul-out duration for satellite-tagged British grey seals. Very brief haul-outs (less than five minutes long) were excluded from the analysis (McConnell, pers. com.).



**Table 3.1: Mean passage time for each prey species**

Passage rates were determined experimentally using a captive seal (Grellier, pers. com.)

species	time (days)
haddock	2.56
plaice	2.15
sandeels	1.28

**Table 3.2: Parameters of  $P(D)$** 

Mean values of the individual parameters of the scaled logistic were calculated from the Markov chain. Standard deviations are shown in brackets

	haddock	plaice	sandeels
k	0.279 (0.0860)	0.130 (0.0144)	0.114 (00.0140)
a <sub>0</sub>	0.845 (0.766)	10.4 (1.96)	67.6 (17.4)
a <sub>1</sub>	-0.279 (0.00561)	- 0.115 (0.0198)	- 1.00 (00.248)

**Table 3.3: GAMs**

GAMs fitted to 1990s IBTS data were used to model the spatial distribution of prey.

species	terms included	significance of each term (P-value)	%deviance explained
haddock	Xx, Yy Year Depth Season	$2 \times 10^{-16}$ $2 \times 10^{-16}$ $2 \times 10^{-16}$ $2 \times 10^{-8}$	60%
plaice	Xx, Yy, Season Sand, Mud, Gravel Year Depth	$2 \times 10^{-16}$ $2 \times 10^{-8}$ $2 \times 10^{-16}$ 0.001	62%
sandeels	x,y year quarter depth mud,sand,gravel	$2 \times 10^{-16}$ $4 \times 10^{-6}$ $4 \times 10^{-5}$ $4 \times 10^{-16}$ $2 \times 10^{-16}$	54%

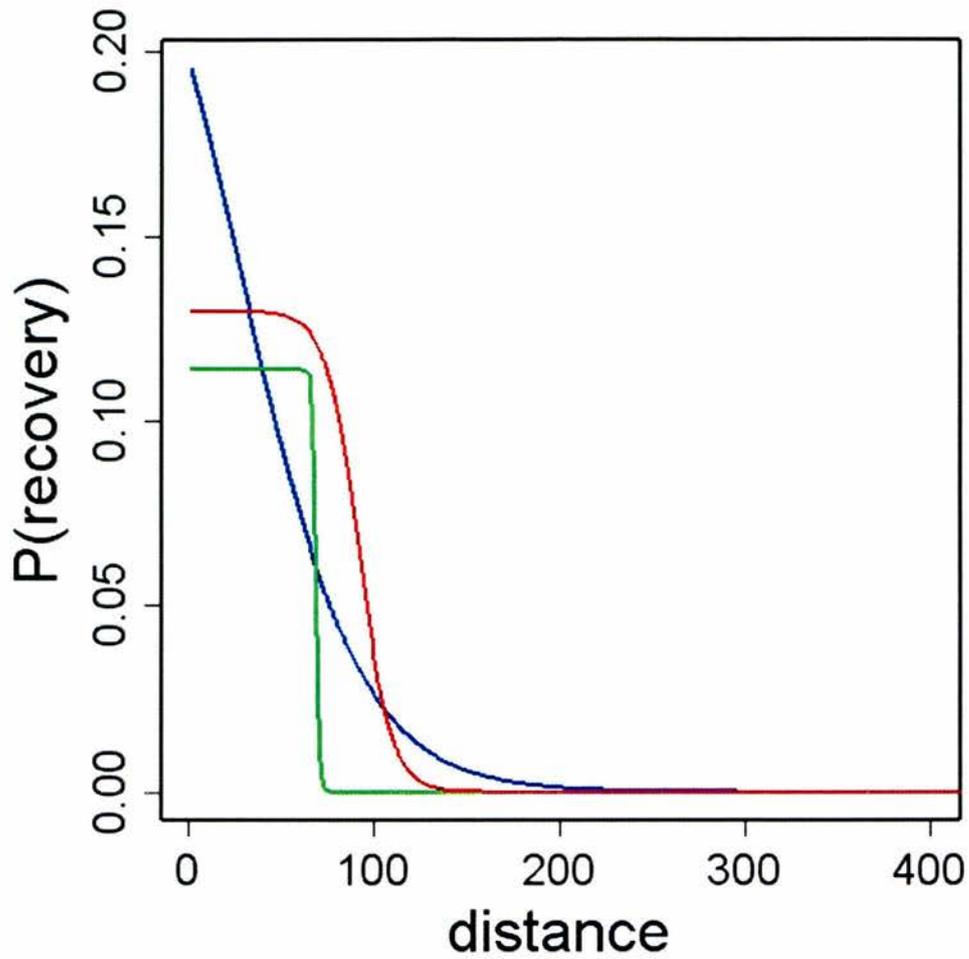
Simulations ran in approximately 10 minutes on a PC with an Intel Pentium M 1.7GHz processor. When fitting equation (2) to the simulation results using Winbugs, convergence was obtained in 5000 iterations, which took approximately 30 minutes to run (machine specifications as above). The mean posterior parameter values for  $k$ ,  $a_0$  and  $a_1$  are shown in Table 3.2. There was little overlap between the distributions of these parameters for the three prey species, apart from the  $k$  parameter for plaice and sandeels (this parameter represents the y-axis intercept, i.e. the probability of recovering an otolith from prey consumed very close to the haul-out). The relationship between probability of detection and distance from the haul-out groups therefore appears to vary among prey species.

Figure 3.5. shows the fitted form of  $P(D)$  for each prey species, based on these parameter estimates. There is a clear decline in the probability of otolith recovery with distance from the haul-out group. The range of distances shown corresponds with the range of locations found in the data set. There is, therefore, a possibility of spatial bias occurring in scat data collected from seals foraging in the wild.

Figure 3.6 shows the predicted seal diet when prey were uniformly distributed and the diet that would have been estimated from scat samples. The proportion of sandeels is slightly underestimated and the proportion of plaice slightly overestimated, indicating that even where prey are not

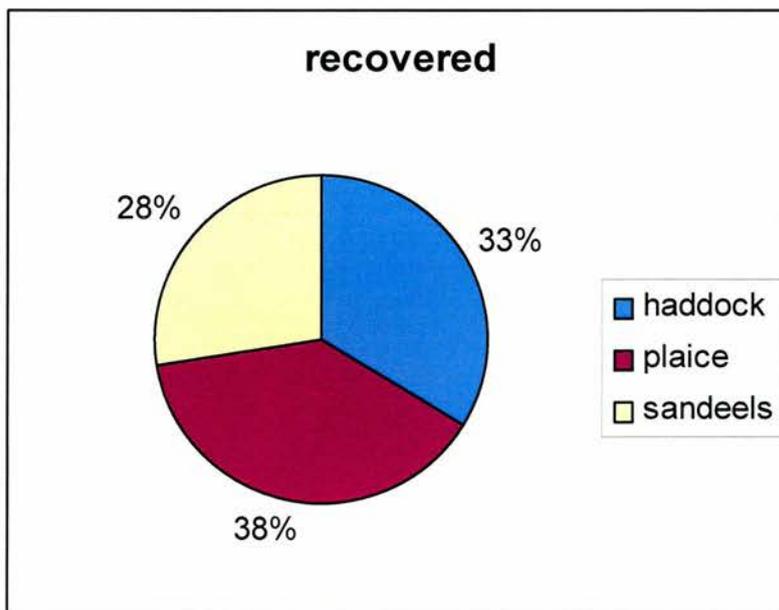
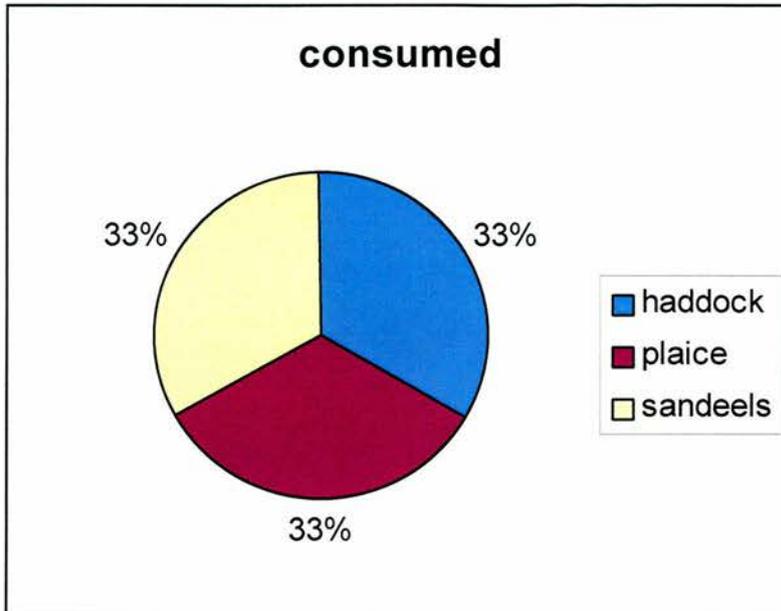
**Figure 3.5:**  $P(D)$

The estimated relationship between the probability of recovering otoliths from sandeels (green), plaice (red) and haddock (blue) in grey seal scats at a haul-out, and the distance of that haul-out from the foraging location used by the seal.



**Figure 3.6: the effects of spatial bias for uniformly distributed prey**

Comparison of predicted diet consumed by grey seals foraging on uniformly distributed prey and the diet estimated from scats recovered at a nearby haul-out.



localised, the effects of differences in otolith loss at sea between prey species can produce a small bias in diet estimates.

Figure 3.7 shows the simulated distribution of aggregated prey around the North Sea haul-out group. Sandeels were assumed to be highly aggregated in a single patch, either close to the haul-out (Figure 3.7a), or distant from it (Figure 3.7b). Other prey were assumed to be uniformly distributed. The predicted and estimated diets of seals from this haul-out grouping are shown in Figures 3.8 and 3.9. Actual and estimated diets were similar when the sandeel aggregation was close to the haul-out grouping, but sandeel consumption was severely underestimated if the aggregation was far away.

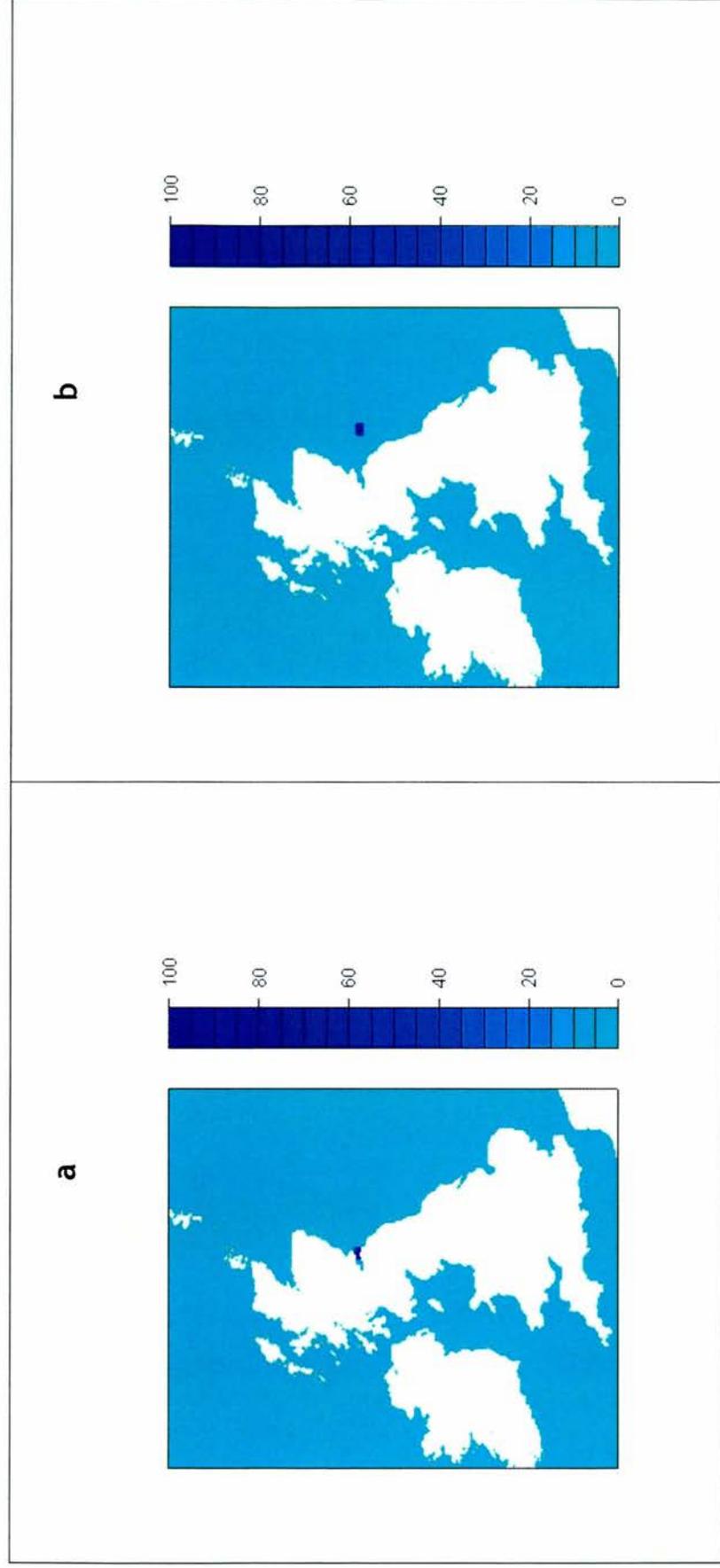
The GAMs for haddock, plaice and sandeels are summarised in Table 3.3. The smoothed terms included in the GAMs are shown, with their significance. The deviance explained is also given for each model.

Maps of the predicted spatial distributions predicted by the GAMs for 1995 for each of the three prey species are shown in Figures 3.10-3.12.

The prey distributions are clearly non-uniform, and they are very different from one another. Differences in prey availability at locations around the UK have previously been linked to differences in the diet of seals at different UK haul-out sites - e.g. between sites in Orkney, and on the east and west coasts of the UK (Hammond *et al.* 1994a,b, Hall *et al.* 2000).

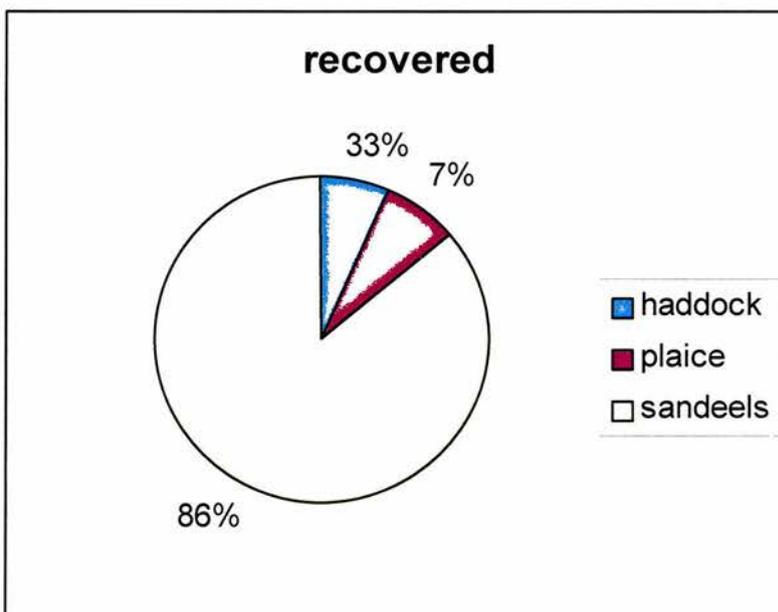
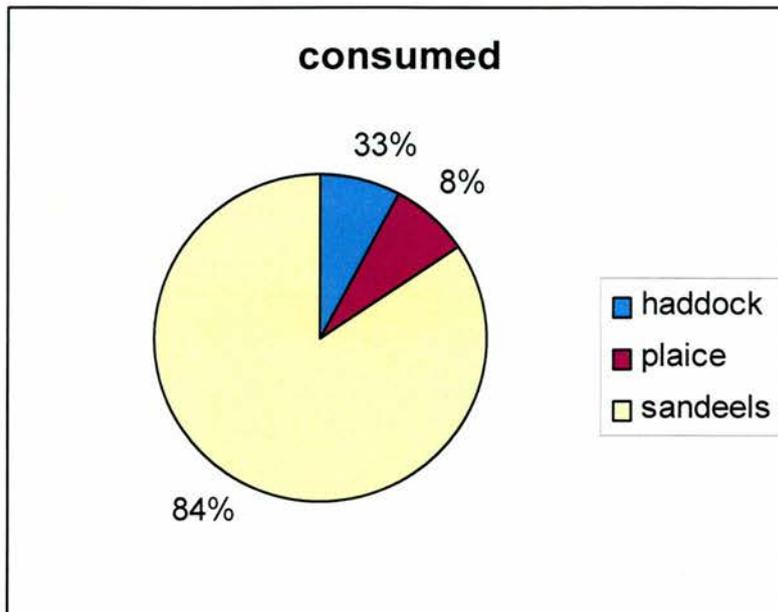
**Figure 3.7: Simulated distribution of sandeels around a grey seal haul-out grouping in the North Sea.**

- a. close to the haul-out grouping
- b. far from the grouping.



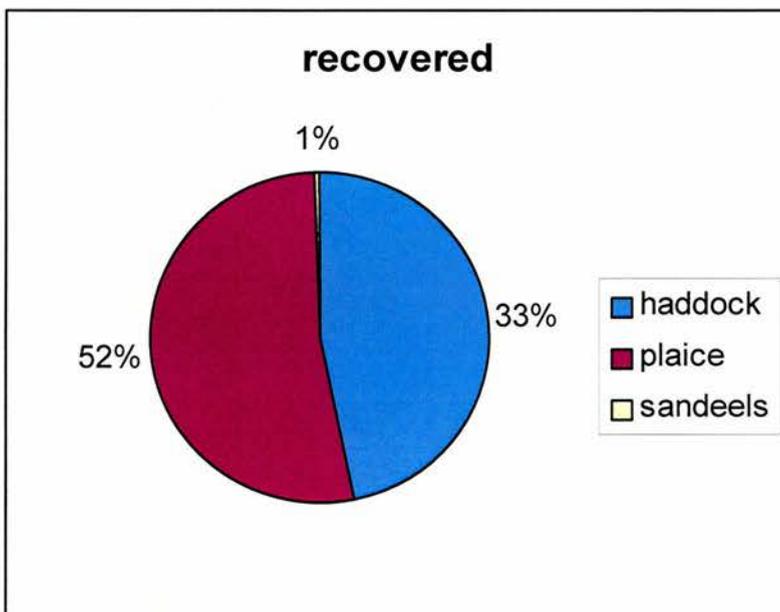
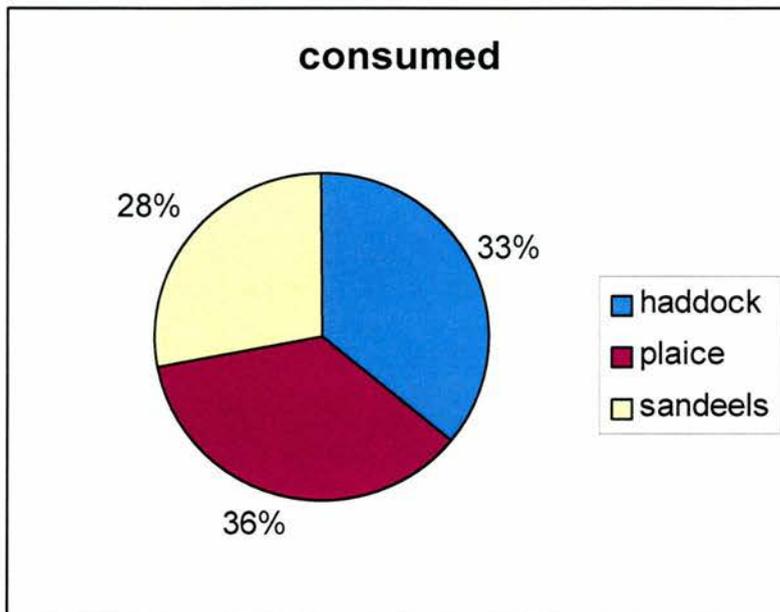
**Figure 3.8: the effects of spatial bias when prey is highly aggregated close to the haul-out**

Predicted diet consumed by grey seals feeding in a situation where sandeels are aggregated close to the haul-out and all other prey are uniformly distributed, and the diet that would have been estimated from scats recovered at that haul-out.



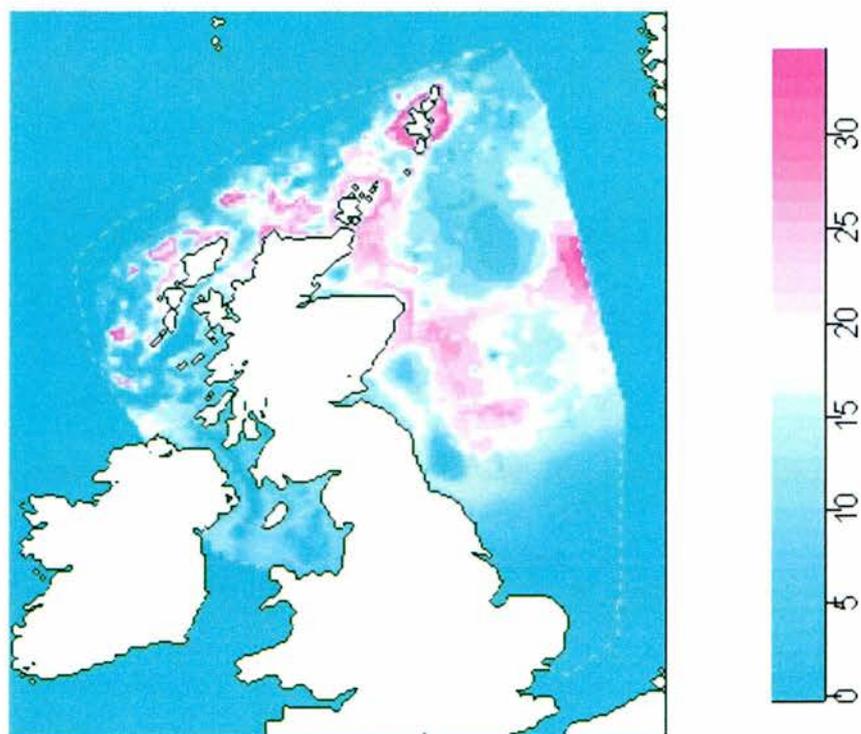
**Figure 3.9: the effects of spatial bias when prey is highly aggregated far from the haul-out**

Predicted diet consumed by grey seals feeding in a situation where sandeels are aggregated far away from the haul-out group and all other prey are uniformly distributed, and the diet that would have been estimated from scats recovered at that haul-out.



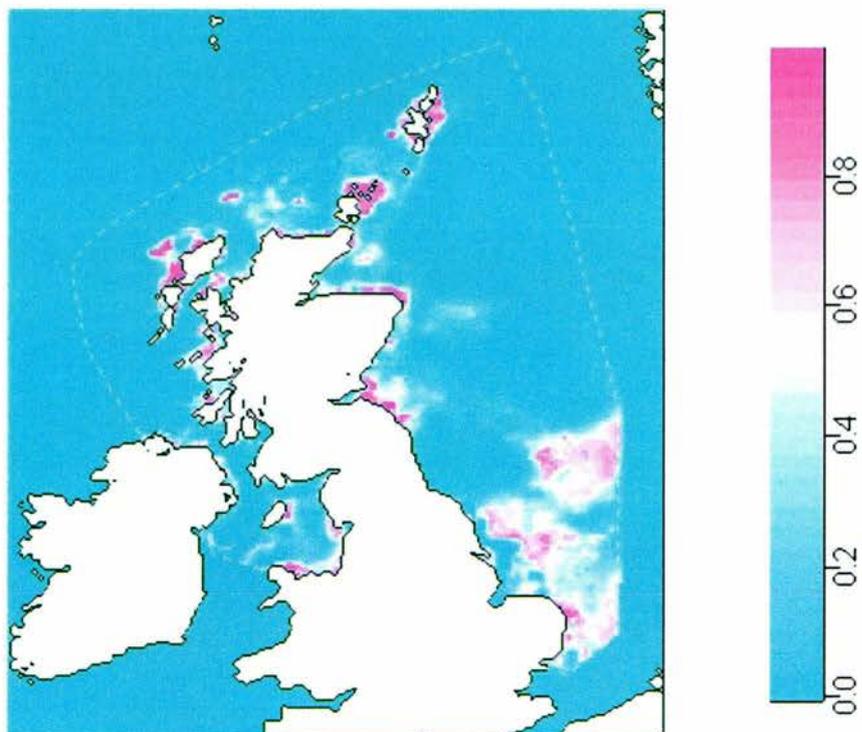
### Figure 3.10: Predicted distribution of haddock around the UK

A Generalised Additive Model was fitted to IBTS data. The colour scale represents predicted CPUE. The prediction surface was calculated from the GAM for a grid of 5km squares, for 1995.



**Figure 3.11: Predicted distribution of sandeels around the UK**

A Generalised Additive Model was fitted to IBTS data. The colour scale represents predicted probability of presence. The prediction surface was calculated from the GAM for a grid of 5km squares, for 1995.



### Figure 3.12: Predicted distribution of plaice around the UK

A Generalised Additive Model was fitted to IBTS data. The colour scale represents predicted CPUE. The prediction surface was calculated from the GAM for a grid of 5km squares, for 1995.

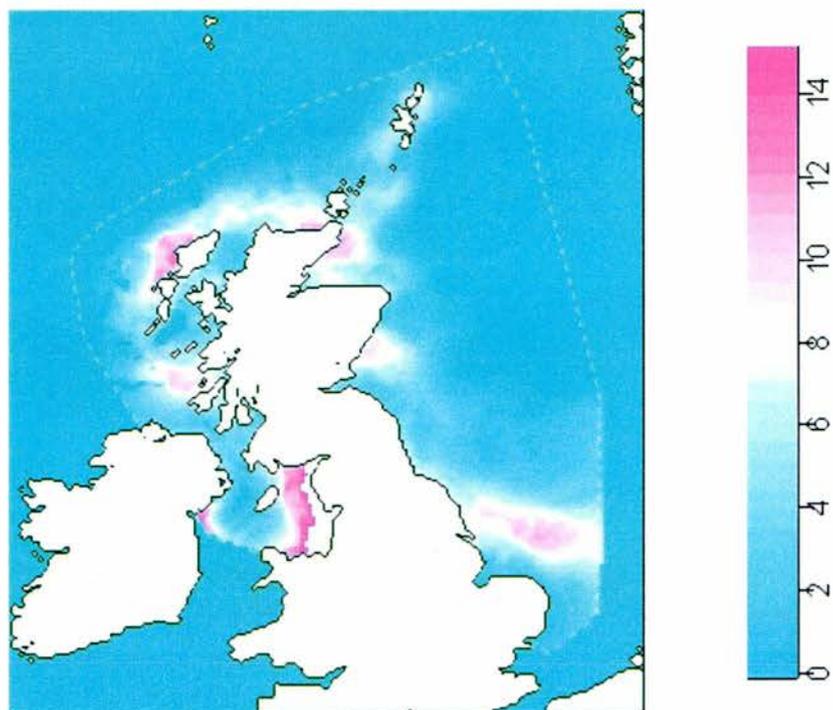


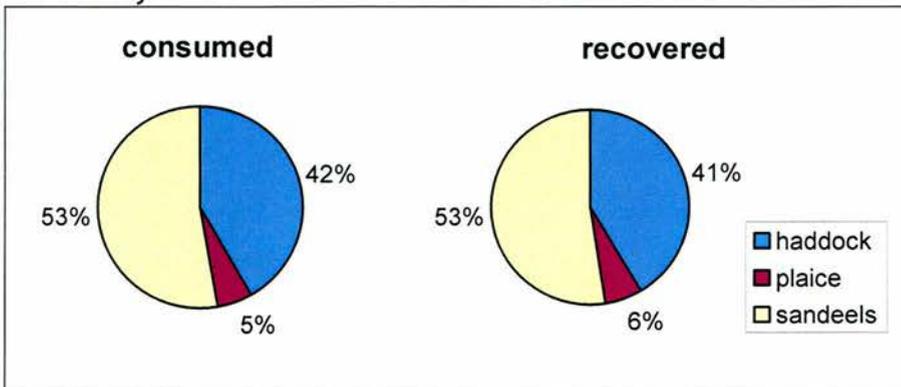
Figure 3.13 compares the composition of diets inferred from recovered scats with the composition of the diet consumed, for seals that were foraging on prey whose distribution was estimated from fisheries research surveys.

Although prey distributions and patterns of spatial usage are unique to each site, so that the composition of the diet is different for each haul-out grouping, the effects of spatial bias appear to be small in all cases, so that the inferred and 'true' diet were similar.

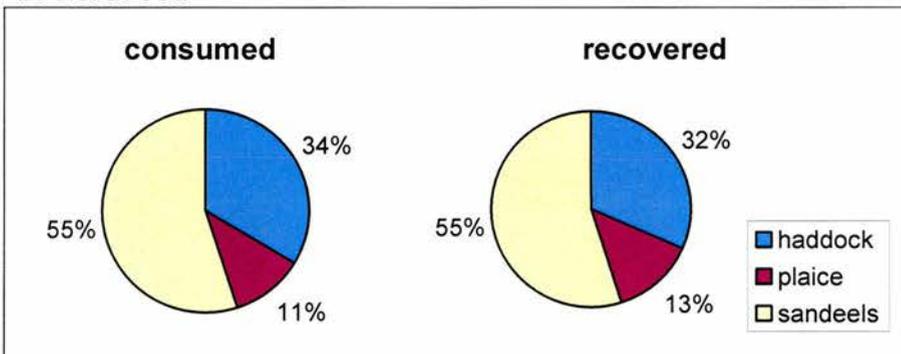
**Figure 3.13: the effects of spatial bias when prey distributions are realistic**

Predicted diet consumed by grey seals based at haul-out groups in Orkney, the North Sea and the southern Outer Hebrides when prey were distributed as shown in Figures 2-4. These predictions are compared with the diet that would have been estimated from scats recovered at the haul-out groups.

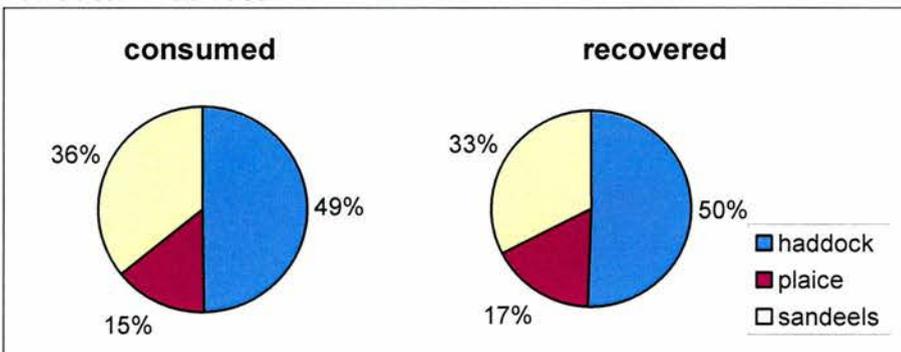
a. Orkney



b. North Sea



c. Outer Hebrides



### 3.4 Discussion

The impact of foraging location on the recovery of otoliths from seal scats, and the implications of this for estimating diet composition, were investigated using a combination of data from telemetry studies and experiments. The results suggest that the probability of recovering an otolith from a meal eaten at sea does depend on where the meal was consumed. The precise form of this relationship varies among prey species, depending on their passage rate through the gut. There is, therefore, potential for a significant spatial bias in estimates of diet based on scat samples.

However, when this approach was applied to realistic predator and prey distributions, the effect of spatial bias was small, and otoliths recovered from scats provided a reliable indication of actual diet composition. The value of passage rate, (or retention time), and the statistical distribution of this value for each prey type, was a crucial input to the analysis and determined the nature of spatial bias that emerged. Passage rates were, of necessity, estimated for only one seal and three prey species and the uncertainty associated with these estimates was based solely on counts of recovered otolith collected at 24-hour intervals.

Passage rates for other prey species consumed by seals (for example for pelagic fish such as herring) are likely to differ, possibly significantly, from the three species investigated so far. They may also vary according to the

activity levels and foraging behaviour of seals, as has been observed for captive harbour seals, *Phoca vitulina* (Staniland *et al.* 2002, Trumble *et al.* 2003). This implies that passage rates for actively foraging grey seals could be quite different from those observed in captivity, e.g. the passage of food through the gut might be faster during active foraging and passage times might decrease. Alternatively, seals may defer the energetic costs of digestion by not processing food while foraging, (Sparling 2004). This would be expected to increase passage times, and reduce the effect of loss of otoliths from distant foraging locations.

Such effects could not be easily investigated using the current experimental facilities because animals must be held in small pools so that faecal material can be collected. However, probes attached close to the anus of seals could be used to detect defecation events (Ropert-Coudert and Wilson 2005) in the field. If the time of feeding could be also inferred from observations of behaviour or from stomach-pellets, then some indication of the effect of foraging in the field on passage times might be obtained. Alternatively, captive experiments might be performed in a larger experimental area that permitted more exercise.

The simulations used in this study assumed (i) that the nature of the relationship between the probability of recovering an otolith and the distance of a haul-out from the location where it was consumed was the same for all haul-outs around the UK, and (ii) that foraging is equally likely to occur everywhere within the seals' range.

Assumption (i) would be violated if the foraging behaviour of seals varies significantly between haul-outs (Aarts *et al.*, in prep), and if favoured foraging locations are closer to haul-outs in some regions than in others. In this case, the mean time between prey ingestion and the next haul-out event would depend on location. There is some evidence (Matthiopoulos *et al.* 2004) that foraging ‘hot-spots’ do exist. However, given the variation in the number of tagged individuals from each haul-out grouping, no attempt was made to incorporate the effect of haul-out into the model.

Assumption (ii) would be violated if seals are more successful in their foraging at some locations than at others. In this analysis, I assumed that the time spent in an area represented the amount of time spent foraging there. This may not be strictly true if, for example, seals rest at sea or if segments of the seal tracks represent purposeful journeys towards localised foraging sites (though such segments are not likely to represent a large part of the seal’s time budget). The amount of foraging that occurs close to haul-outs may well be over-estimated if it is inferred from the usage of space alone, because a proportion of the time that seals spend in this area will be devoted to commuting to and from the haul-out. More detailed analyses of telemetry data, making use of dive profiles and swim speed, may in the future lead to revised estimates of the usage of space by seals for foraging purposes.

The relationship between  $P$  and  $d$  differed among prey species in a way that is intuitively consistent with the observed passage times, (see Table 3.2 and Figure 3.5). For example, the probability of recovering sandeel otoliths drops off steeply with the distance of the foraging location from the nearest haul-out, because passage rates for sandeels are short. However, the relationship between  $P$  and  $d$  is also influenced by factors other than the relative values of passage times and journey times. Haul-out behaviour is particularly important. During the simulations, scats were often deposited at sea after a seal had visited its haul-out and left again (in 45% of cases for haddock and plaice, contrasting with 20% for sandeels). This suggests that spatial bias might operate in two ways. Otoliths may be lost at sea before a seal returns to the haul-out, causing 'distant' prey to be under-represented in scat samples. Those for which passage times are shortest would then be more under-represented than those with longer passage times (i.e. otolith loss resulted from 'defecating too soon'). Alternatively, otoliths may be lost at sea after an initial period of hauling out. Prey consumed close to the haul-out would be under-represented, and those for which passage times are longest would be less likely to be recovered (otolith loss resulted from 'defecating too late').

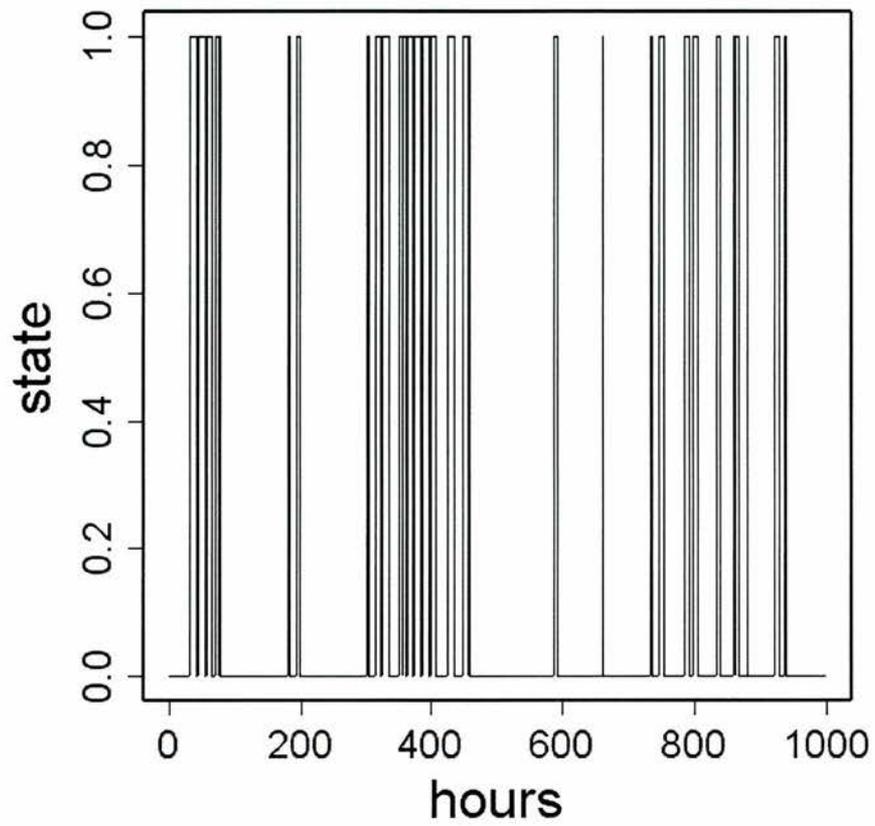
The relationships between haul-out time, passage time, and the nature of hauling-out behaviour therefore become very important in predicting how a spatial bias might operate in grey seals. For example, any dependency between the duration of hauling-out and the length and frequency of subsequent haul-outs, or between the duration of the preceding foraging

trips and haul-out behaviour, will affect the outcome. Episodes of hauling-out are often clustered in time (see Figure 3.14), possibly as a result of diurnal and tidal effects (McConnell pers. com.). One advantage of using the simulation-based approach developed here is that effects which emerge from correlations of this kind can be included in the analysis directly, because they are represented within the data set.

The results of these simulations indicate that the importance of spatial bias in estimates of diet from scat analysis depends on the spatial distribution of distributions of predators and prey in simplified theoretical cases (Figures 3.8 and 3.9). More realistic prey distributions were modelled based on data collected at a rather coarse spatial scale - ICES statistical rectangles. As a result, concentrations of prey that occur at a finer scale were not represented in the analysis. Given this limitation, however, it appears that the effects of spatial bias were not evident when realistic prey distributions were used. Seal foraging is concentrated close to haul-outs, and the impact of spatial bias is not important over this restricted spatial scale.

### Figure 3.14: hauling-out by an individual seal

Haul-outs for an individual seal based at Abertay in 1998. Where state=1, the seal is hauled out, where state=0, it is at sea.



### 3.5 Conclusion

It appears that, in realistic circumstances, the effects of spatial bias are likely to be small in comparison to the uncertainties arising from small sample size and uncertainties in digestion coefficients (Hammond and Rothery 1996). Hence, consumption estimates do not need to be revised to take account of spatial bias, and our present understanding of seal diets and their likely consequences of seal-fishery interactions appears to be robust to the effects of otolith loss at sea.

## Chapter 4: Modelling Prey Consumption by British Grey Seals

### Summary

The population of grey seals (*Halichoerus grypus*) around the British coast has approximately doubled over the last 20 years, and fishers are concerned about the quantities of fish, particularly cod, that seals consume. Seals are generalist predators, and so can potentially drive some of their prey species to extinction or trap prey at low abundance in a ‘predator pit’. The likelihood of these outcomes depends on the way in which predation responds to changes in prey abundance, and on the nature of density dependence in the prey population.

A model describing consumption by a generalist predator as a function of prey availability is therefore crucial if the relationships between predator and prey populations are to be understood. Bayesian statistical methods were used to fit a model of prey consumption to data on the diet and prey availability of grey seals. Grey seal diet was estimated from scats collected on haul-outs on the coast of Scotland, and the availability of fish to the seals was estimated using Generalised Additive Models applied to International Bottom Trawl Survey data, together with models of seal movement based on telemetry data. These results were used to predict the way in which prey consumption and seal-induced prey mortality might vary with prey abundance.

The biomass of fish removed by grey seals foraging in the North Sea was estimated for 1985, a year in which the two most important prey species - cod and sandeels - were relatively abundant, and for 2002 when stocks of both species were at low levels. The posterior distribution of model parameters was used to generate estimates of the uncertainty associated with these predictions.

#### 4.1 Introduction

The British grey seal population represents approximately 39% of the world population, and is protected by the Conservation of Seals Act (1970). Grey seals are also listed in Annex II of the EC Habitats Directive (Council Directive 92/43/EEC). The population has grown steadily from around 51,000 individuals in 1985 to around 99,000 in 2002. However, there is considerable uncertainty as to the true population size because only a part of the population, the pups, are easily accessible to surveys (Thomas and Harwood 2005, Hiby and Duck *unpublished*).

Fishers are concerned about the quantities of fish that seals consume, particularly in the context of the expanding seal population. Seals are generalist predators, and so can potentially drive some of their prey species to extinction or trap prey at low abundance in a “predator pit”, (Holling 1965, Hilborn and Walters 1992). The likelihood of these events depends on the way in which predators respond to changes in prey abundance, and on the nature of density-dependence in the prey population.

A model describing consumption by a generalist predator as a function of prey availability is therefore crucial to understanding the relationships between predator and prey populations.

If such a model can be parameterised for grey seals, it can be used to address two applied questions that are of particular interest:

1. What are the implications of prey availability for grey seal conservation? Given the current poor status of fish stocks, particularly sandeels (Furness 2002, Hislop 1996), will the survival or fecundity of seals will be reduced (Hall *et al.* 2000)?
2. What are the implications of grey seal predation for fish stocks, particularly cod? Is it likely that seals could prevent the recovery of fish stocks from their present low levels?

A model of prey consumption may in itself suggest some important properties of the relationship between grey seals and their prey. For example, if other parameters such as the background mortality and intrinsic density dependence of the prey are known, then the form of the functional response may indicate at what population levels stable equilibria are likely for this predator-prey system. A consumption model may also enable managers to pose and answer practical questions about seal predation. For example, it would be possible to predict the quantity of fish consumed under different levels of prey abundance which themselves would be the result of fisheries management decisions.

A particularly important application for a grey seal consumption model would be in multi-species modelling of the North Sea ecosystem. The interaction

between seals and their prey in the North Sea takes place in the context of a complex food web containing many other predators as well as commercial fisheries. The multiple trophic interactions within such a system may have consequences which are less than obvious (Yodzis 1998). It is likely that a realistic view of the behaviour of the system can only be produced if all significant interactions are modelled. Incorporating grey seal consumption into a multi-species ecosystem model such as SMS (Vinther *et al.* 2004) would allow the important properties of the whole food-web to be explored, and result in more informed management decisions with regard to seals and fisheries.

Previous studies of the diet of British grey seals have found significant regional and seasonal variations, which seemed to be related to prey abundance (Pierce *et al.* 1991, Prime and Hammond 1990, Hammond *et al.* 1994a,b, Hall *et al.* 2000, Walton and Pomeroy 2003). In the present study, scat data collected during the 1980s and 1990s are used to parameterise a model of the relationship between diet and prey availability, using prey availability estimates that were calculated from spatial models of prey abundance (chapter 2), and models of the usage of space by seals (Matthiopoulos, 2003).

Asseburg *et al.* (2006) showed that it is possible to estimate the parameters of a multi-species functional response using Bayesian methods and a Monte Carlo Markov Chain (MCMC) algorithm. The basic MCMC algorithm can be

conveniently formulated for such a model and an appropriate form can be developed for the likelihood function. The Bayesian approach allows prior information to be used to assist in fitting sparse and over-dispersed data, as is likely to be the case when a large number of potential prey species have to be included in the analysis (O'Hagan, 1998). Another important advantage of a Bayesian approach is that a full joint posterior distribution of parameter values is produced (Gilks *et al.* 1996, Hilborn 1997). This distribution can be used to explore the inferences that can be made from the model, and the nature of uncertainty in those inferences. Posterior distributions can also be used to inform other, even more complex models by providing appropriate prior distributions (Harwood and McLaren 2004, Harrison *et al.* in press). North Sea multi-species models that are currently under development (ICES 2004a, 2005) are not Bayesian, but Monte Carlo simulation could be used to provide information on the uncertainty in model outcomes that are of interest, (such as the recovery of fish populations) using random draws from the joint distribution of consumption model parameters.

Fitting a consumption model for grey seals presents some additional challenges to those faced by Asseburg *et al.* (2006).

1. Seals consume a large number of different prey species - more than 80 in UK waters. Prey size also varies considerably. An ideal model of consumption would include all the important prey classes, and a satisfactory model should represent all the strong trophic links between

predator and prey (Yodzis 1998). However, each prey species that is introduced into the model imposes a requirement for extra parameters, and a large amount of data is required to cover the full range of prey availabilities and combinations of availabilities. Because of the limited time scale covered by the diet data that were available for this analysis, a subset of the prey classes was chosen and some of the size classes were grouped together in order to reduce the complexity of the model.

2. The prey availability data was not perfectly matched in time and space with the prey consumption data, and there was considerable uncertainty associated with the estimates of prey availability.
3. It is difficult to observe predation by fish-eating marine mammals directly. Grey seal consumption is generally estimated by analysing scat samples that provide information on the composition of the diet in terms of mass or numbers of prey. Absolute consumption can then be inferred by considering the total energetic requirements of seals, (Fedak *et al.* 1985). Estimating consumption in this way requires the assumption that the energetic requirements of seals were always precisely met by their consumption of prey. For convenience, I will refer to this as ‘the constant energy assumption’. However, this assumption may not be correct in situations where the density of prey is low, and low-prey scenarios are of particular interest in determining the implications of predation for prey dynamics (Murdoch and Oaten, 1975).

In this chapter, I describe the development of methods for simplifying the consumption model by limiting the number of prey items considered, and for fitting a multi-species functional response model that takes account of uncertainty in availability. Absolute consumption of cod and sandeels in the North Sea was then calculated using the constant energy intake assumption, both for the levels of prey available in 1985 and also under a regime of low-cod and low-sandeel abundance that was more representative of the current state of the North Sea. Some approaches that could be used to link local predation by a central place forager with the population dynamics of fish stocks which may mix on a whole-ocean scale are also examined.

## 4.2 Methods

A multi-species functional response  $f$  relates the consumption  $c_i$  of all  $n$  prey classes to their availabilities  $N_i$

$$\begin{pmatrix} c_1 \\ c_2 \\ \cdot \\ \cdot \\ c_n \end{pmatrix} = f \begin{pmatrix} N_1 \\ N_2 \\ \cdot \\ \cdot \\ N_n \end{pmatrix}$$

### 4.2.1 Diet composition data

During the 1980s, (Prime and Hammond 1990, Hammond *et al.* 1994a,b) and 1990s (Hall *et al.* 2000), grey seal scats were collected from haul-outs visited

at low tide. For the purpose of the present analysis, scats from adjacent haul-outs (see Figure 4.1 for their locations) were combined into six groups.

Scat collections were only included in the data set used to fit the consumption model if more than one scat sample had been collected. The analysis was also restricted to samples collected in quarters 1, 3 and 4, because there was very little data on prey abundance for quarter 2 in any of the years between 1980 and 1999. Including quarter 2 would have been a particular problem for sandeels, which show significant seasonal changes in behaviour and vertical distribution, (Greenstreet *et al.* in prep.).

Twenty-one separate collections of scat samples, each corresponding to a unique combination of site and date (Table 4.1), were then available. Diet composition and prey consumption were estimated by pooling results from all the measured otoliths from all the scats in each scat collection.

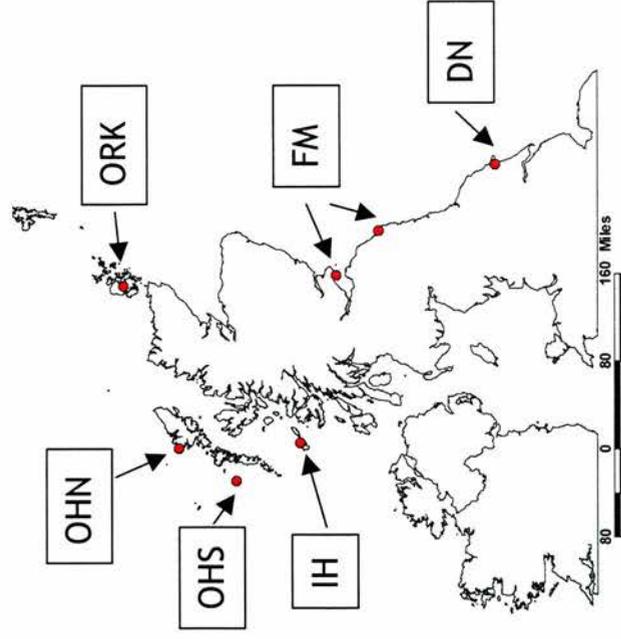
The procedure for estimating seal diet composition from scat samples is described in detail in Prime and Hammond (1987, 1990), so only a brief description is given here.

Scat samples were washed and sieved, and the hard parts they contained were identified to species where possible. Sandeel otoliths were not classified to species but were assumed to be *Ammodytes marinus*, the most abundant species of sandeel around the UK. Thickness, width or length of otoliths was

### Figure 4.1: Grey Seal haul-outs around the UK

Individual grey seal haul-out sites (shown in blue) from which scat samples were collected, and regional groupings of these sites (red).

DN = Donna Nook, FM = Farnes/Isle of May, ORK = Orkney, OHN = Outer Hebrides North, OHS=Outer Hebrides South, IH = Inner Hebrides



**Table 4.1: Collections of scat samples**

The location and date of each sample collection is shown, together with the number of scats that were collected on each occasion

Year	quarter	OHS	OHN	IH	ORK	FM	DN
1985	1	33	95	49	362	26	104
	2	0	21	0	129	69	92
	3	1	21	0	85	21	101
	4	1	82	45	295	278	63
1996	4					22	
1997	1					21	
	2					49	
	3					9	
	4						
1998	1					101	
	2					72	
	3					13	
	4					58	

measured as appropriate, and a correction was then applied to these measurements to allow for the effects of digestion in the seals' stomachs (Prime and Hammond 1990, Hammond *et al.* 1994a,b). The length or mass of each original prey fish could then be estimated using standard formulae (Harkonen 1986), and the total quantity of prey represented in the scats calculated. The energetic value provided by each prey species was then calculated using published energy densities. Net daily consumption of all prey species by mass was estimated using the constant energy assumption, (Sparling and Smout 2003). A one-day time scale was chosen.

Some otoliths, particularly small ones, may be completely digested so that they cannot be recovered from scat samples. This effect is likely to be particularly important for sandeels. Grellier (*pers. com.*) recently estimated recovery rates for sandeels fed to captive seals, and I applied their correction factors to the 1985 and 1990s otolith data to obtain revised estimates of consumption by prey class.

Fish known to be abundant in the seal diet, such as cod, were subdivided into 'mature' and 'immature' classes, based size-at-age data for the relevant years (ICES 2004c). I assumed that age at maturity did not change significantly during the 1980s and 1990s (Armstrong *et al.* 2004). The size of the immature classes were 0-35cm for plaice, 0-50cm for cod, and 0-30cm for whiting. Ling was an important prey species for the seals in the study, but ling - particularly young fish - are rarely caught in the research trawls used to estimate prey

availability (A. McLay, Fisheries Research Service *pers. com.*). Therefore, a single age class of ling was used in order to obtain reasonable estimates of abundance.

All prey classes that contributed more than 10% to the observed diet at two or more haul-out groupings were included in the analysis.

#### 4.2.2 Prey availability

Using the results of the analyses described in Chapter 2, fish distributions were predicted over a grid of 5km squares. The availability of each prey class to seals at each of the six haul-out groups was calculated as outlined in Chapter 2. Means and variances for these availabilities were obtained by non-parametric bootstrapping, although this may under-estimate the true variance if there is spatial correlation in the data (Borchers *et al.* 1997). The values for prey availability  $N$  were assumed to follow a gamma distribution whose shape and rate parameters were determined by the mean and variance of the sample obtained from bootstrapping.

#### 4.2.3 Modelling consumption

Consumption and availability were plotted separately for each prey class and Pearson's correlation coefficients were calculated to determine whether there were any simple single-species relationships. Bayesian methods were then used to fit multi-species models to these data using two closely related approaches.

**Model 1**

A multi-species version of the functional response model developed by Real (1975) was fitted to the data. This model is based on Holling (1959) and assumes that predators search for and attack all prey types simultaneously so that encounters with one species effect encounter rates with others. Here, however, encounter rates are allowed to vary according to prey availability (Yodzis 1994). This model has a been used in other studies of generalist predators (Rindorf 2004, Koen Alonso and Yodzis 2005, Asseburg 2006), and has the advantage of only requiring only 3 parameters per prey species. The model can be written:

$$C_i = \frac{a_i N_i^{m_i}}{1 + \sum_{j=1, \dots, n} a_j t_j N_j^{m_j}} \quad (1)$$

Where:

$C_i$  is the consumption rate of prey  $i$  by a single predator

$N_i$  is the availability of species  $i$

$t_i$  is the time taken to consume a single item of species  $i$

$a$  is the 'attack rate parameter', which predicts the relationship between attack rate and prey availability

$$\text{attack rate} = a n^{m-1} \quad (2)$$

Here, 'attack rate' is the reciprocal of the time between attacks on prey items, and attack rate would be equal to consumption rate if the handling time for prey was zero.

$m$  is a 'shape parameter'. If  $m=1$  for a given species, then the conditional functional response for that species is hyperbolic. If  $m>1$ , this functional response is sigmoidal, with an inflexion at low prey density.

The biological significance of these parameters is discussed in more detail by Real (1979).

The maximum value of consumption rate for a given prey item  $i$  that could ever be represented in the data, was given by

$$c_{max_i} = \frac{E_{tot}}{e_i} \quad (3)$$

where  $E_{tot}$  is the total daily energy requirement and  $e_i$  is the calorific density of food item  $i$ .

The asymptotic or maximum consumption rate,  $c_{max_i}$  for species  $i$  is related to the handling time  $t_i$  by

$$t_i = \frac{1}{C_{\max_i}} \quad (4)$$

and so for each species the value of  $t_i$  was set at

$$t_i = \frac{e_i}{E_{\text{tot}}} \quad (5)$$

### **Model 2**

I also wished to investigate the consequences of relaxing the constant energy intake assumption to take account of the fact that seals at different haul-out locations may not have been able to acquire all the energy they required. If this assumption is relaxed, it is not possible to calculate absolute consumption rates, but it is possible to predict the proportion of each prey class in the diet. Re-arranging equation (1) gives:

$$\frac{c_i}{\sum_{j=1}^n c_j} = \frac{a_i N_i^{m_i}}{\sum_{j=1}^n a_j N_j^{m_j}} \quad (6)$$

because the denominator of equation (1) is the same for all prey classes.

Equation (6) holds true, even if only a subset of all prey classes is included, provided that the same set of prey classes is used on both sides of equation (2). It also holds true if all the attack rate parameters are scaled by an identical arbitrary constant. Only the relative values of the  $a_i$  are needed in order to predict diet composition.

In order to calculate absolute consumption of any given prey class from equation 2, the total intake rate of all the prey species in the model must be known. The contribution of ‘other’ prey, (i.e. those not included in the model) to the diet was considered to be constant, both in terms of mass and energy, for this purpose.

#### 4.2.4. Fitting the models

Equations 1 and 6 were fitted to the data using Bayesian statistics and MCMC, coded in WinBugs. The WinBugs code is included in Appendix 1.

A continuous Poisson distribution (Speigelhalter *et al.* 2005) was used to compare model predictions with the data. This distribution was chosen because the data were derived from counts of the number of otoliths, i.e. the data were non-negative and contained zeros.

During the MCMC routine, random values of  $N$  were drawn from gamma distributions for each prey class, at each step in the Markov chain (Stephens and Dellaportas 1992).

#### ***Choice of priors***

To fit Model 1, prior distributions were required for  $a$  and  $m$  only, because the values of  $t$  were set according to the seals energetic requirements. To fit Model 2, priors were also needed for both  $a$  and  $m$ .

### Priors for $m$

Priors for  $m$  were derived from the results of experiments with captive seals that were offered sandeels at a range of densities (Sparling *et al. in prep.*). Prey density was kept constant during each experiment by replacing items that were taken by seals (Skalski and Gilliam 2001). Consumption rates were calculated using the number of sandeels consumed per dive and the length of time taken for the seal to dive to the feeder and rest at the surface in between feeding episodes.

A single species functional response based on equation 1 of the form

$$C = \frac{aN^m}{1+aN^m} \quad (7)$$

was then fitted to the experimental data, using WinBugs (Speigelhalter *et al.* 2005).

The following priors were used for the single species functional response:

- ❖ a gamma distribution with shape 1 and rate 1 for  $t$  (based on observations that handling times were considerably less than one minute);
- ❖ a gamma distribution with shape 1 and rate 0.1 for  $a$ ; (mean 10, variance 100);
- ❖ a gamma distribution with shape 2 and rate 0.1 for  $m$ .

The posterior distribution of  $m$  for the single species functional response was then used as a prior for the multi-species consumption models.

### Priors for $a$

There are few direct observations of grey seals foraging in their natural habitat (though see Bowen *et al.* 2002 for a description of how such measurements were made for harbour seals *Phoca vitulina* off the Newfoundland coast). It is thus difficult to obtain estimates of the relationship between attack rate and prey density for grey seals, or even to estimate attack rates. Therefore, when fitting Model 1, broad priors were used for  $a$ , and the sensitivity of the resulting parameter estimates to these priors was investigated.

The parameter  $a$  can be considered as a correction factor relating the absolute abundance of prey experienced by seals, to the indices of prey availability calculated in Chapter 2 based on the IBTS data. Using this interpretation, it was considered likely that the value of  $a$  for sandeels would be higher than that for other prey because the catchability of sandeels in research trawls is known to be low, while the abundance of sandeels is very high compared with that of fish such as whiting.

When fitting Model 2, only the relative values of  $a$  could be estimated, and so the value of  $a$  for sandeels was fixed at 1 while all other  $a$ 's were given uniform priors allowing them to take any value between 0 and 1:

$$a \sim U(0,1)$$

#### priors for t

For the MSFR model, the values of  $t$  were fixed according to the daily energetic requirements of the seals (Sparling and Smout 2003).

Markov chains were examined to check for mixing, and the convergence of two parallel chains was checked in each case. QQ plots, comparing quantiles for the data with theoretical quantiles based on the continuous Poisson distribution, were also constructed for the fitted models.

#### **4.2.5. Estimating consumption**

##### ***Consumption by individual seals***

The nature of the functional response of individual seals was visualised by plotting the relationships between estimated consumption and prey availability for all prey classes, while the availability of other prey was held fixed at some defined value (e.g. other prey were all scarce, or abundant).

For Model 2, consumption was estimated in the following way :

1. The mean energy  $E(\text{prey})$  contributed by the modelled prey classes was determined.  $E(\text{other})$ , the energy contributed by prey classes not included in the model, was then calculated.
2.  $E(\text{prey})$  was partitioned by prey class using Equation 6, the availabilities of all prey classes, the estimated parameters, and the estimated energetic value of each prey class. Consumption of each of the prey classes could then be estimated.

Two plots were constructed for each prey class. In one the availabilities of all other modelled prey species were set to very low, constant values. In the other, other (non-modelled) prey were held fixed at moderate availability. The availability of the prey of interest was then varied over the range represented in the data set.

Confidence intervals for the consumption estimates were calculated by repeating steps 1-2 100 times, taking random draws of parameters from the Markov chain.

Similar plots were created to illustrate the relationship between instantaneous predation mortality  $M_i$  for each prey class and prey availability with other modelled prey held at fixed, low levels of availability.

$$M_i = \frac{C_i}{N_i} \quad (8)$$

The absolute mortality rate for an individual prey class could not be calculated directly in this way, because there was no a clear correspondence between the prey availability index and absolute prey density, either in terms of biomass or prey numbers.

### ***Total consumption of prey by the entire grey seal population***

I also made predictions of the consumption of all prey classes by individual grey seals foraging in the North Sea (ICES area IV) in 1985 and 2002.

Predictions were made for seals using haul-outs in the North Sea (Donna Nook, Farnes Islands, Isle of May, and Orkney).

For 1985, I used the same prey availability estimates as those used for model fitting. Daily consumption was scaled up to annual consumption, and then annual consumption by individuals was multiplied by the estimated size of the populations associated with these haul-outs taken from SCOS (SMRU 2005).

The grey seal populations in the Orkneys, Farnes/May (East Coast), and Donna Nook were assumed to be 16457, 4783, and 153. These predictions were then compared with calculations based directly on the observed diets of grey seals at the same haul-outs.

Prey availability in 2002 was estimated by scaling the 1985 availability values according to changes in total North Sea fish stocks predicted by ICES working

groups. This approach assumes that the spatial distribution of prey did not change during the period 1985-2002. No stock assessments were available for ling, so I assumed that their abundance decreased by 70% over the period 1985-2002 (ICES 2004b).

The grey seal populations in the Orkneys, Farnes/May (East Coast), and Donna Nook were assumed to be 62775, 11871, and 2269 in 2002 (Hammond and Grellier *in prep.*). Predicted consumptions for the North Sea seal population in 2002 were compared with the ICES VPA estimates of biomass in the cod and sandeel stocks, and with the estimated biomass removed by fisheries (ICES 2004c). They were also compared with preliminary estimates of the diet of grey seals in the North Sea based on scats collected in 2002 (Hammond and Grellier *in prep.*).

### 4.3 Results

Seven prey classes were identified

	common name	latin name	length in cm
1	immature cod	<i>Gadhus morhua</i>	0-50
2	mature cod	<i>Gadhus morhua</i>	50+
3	whiting	<i>Merlangius merlangus</i>	all
4	immature plaice	<i>Pleuronectes platessa</i>	0-70
5	saithe	<i>Pollachius virens</i>	0-60
6	ling	<i>Molva molva</i>	all
7	sandeels	all species, mainly <i>Ammodytes marinus</i>	all

Figure 4.2 shows the estimated consumptions of these prey classes, for all sample collections, as a percentage of the total diet by mass.

Whiting, plaice and saithe did not make up 10% of the diet on 2 or more occasions, when they were grouped into size classes. However they did meet this criterion when size classes were aggregated and they were grouped by species only. They were therefore included in the analysis as single species classes. The range of sizes for these species in the consumption data set was determined, and this size range was used to select the research trawl data used to calculate prey distributions in Chapter 2.

Table 4.2 shows, for each of the 21 sample collections, the total biomass of prey that was represented by all the otoliths that were identified, the mass of

Figure 4.2: prey species in the diet of seals

Prey species in the diet of seals, inferred from scat analysis. Scat collections were made various sites and dates (see x axis labels, where the year is printed in full, 'Q' refers to quarter of the year, and site codes are as given in figure 4.1). The estimated contribution of the species to the diet is shown as a percentage by mass. Only those species which were estimated to contribute 5% or more of the diet in at least one collection are included.

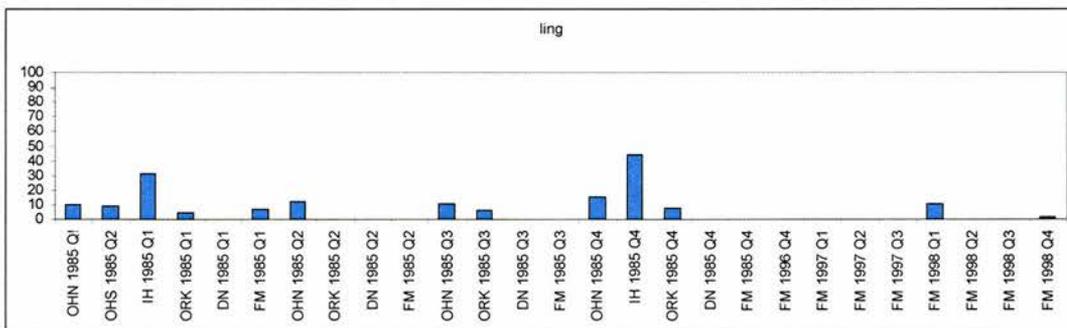
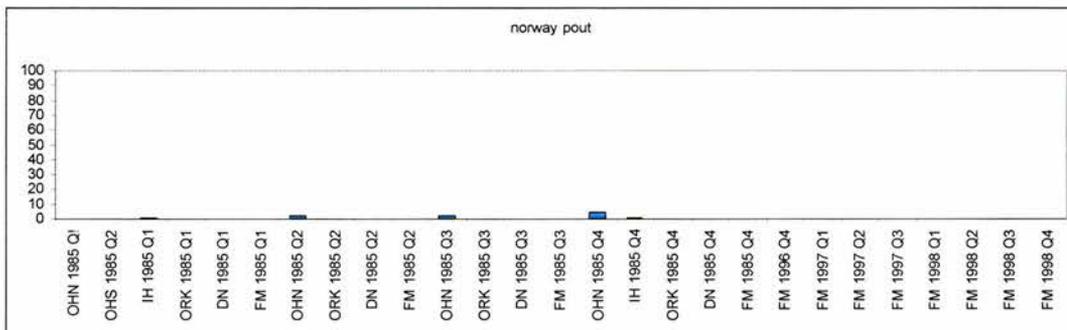
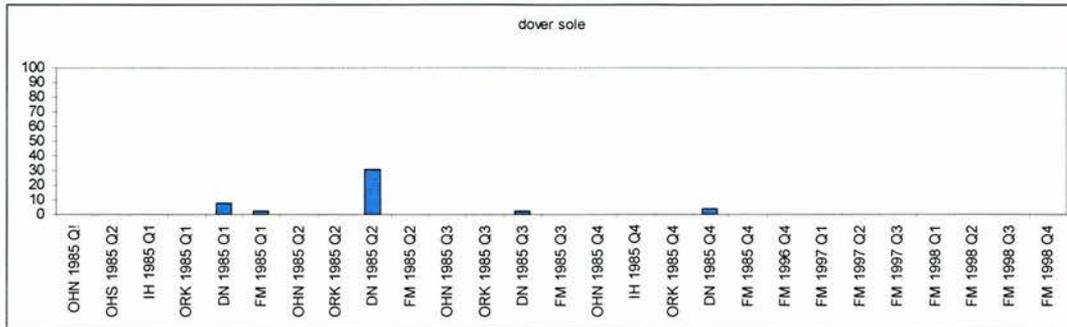


Figure 4.2 cntd.

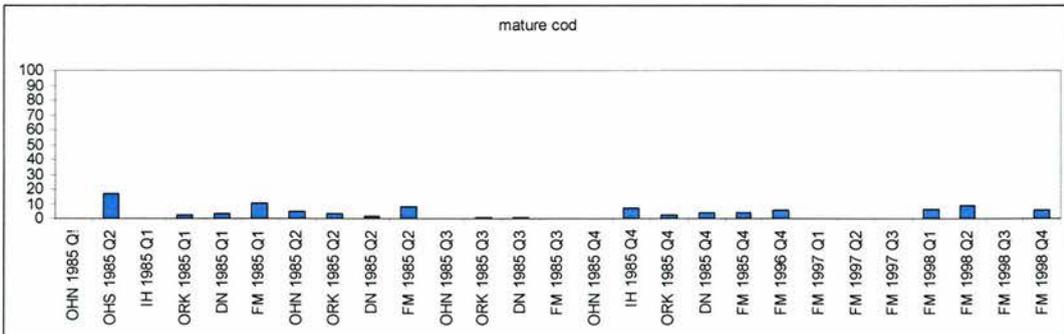
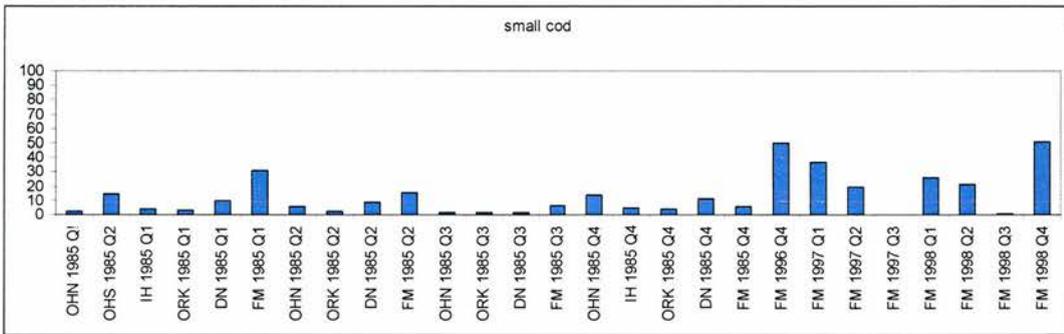
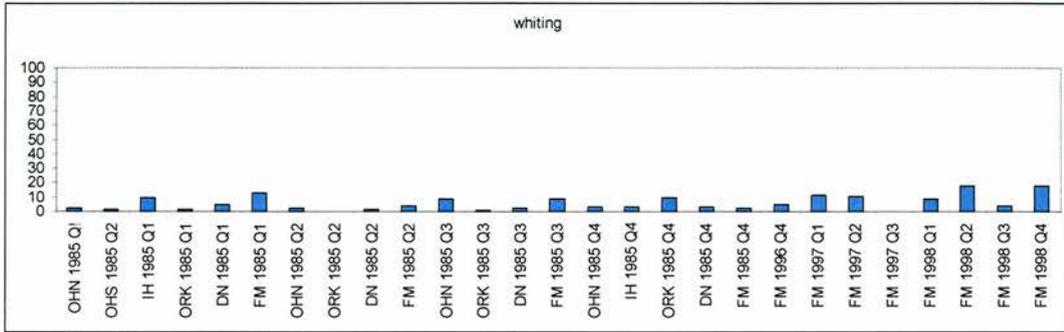
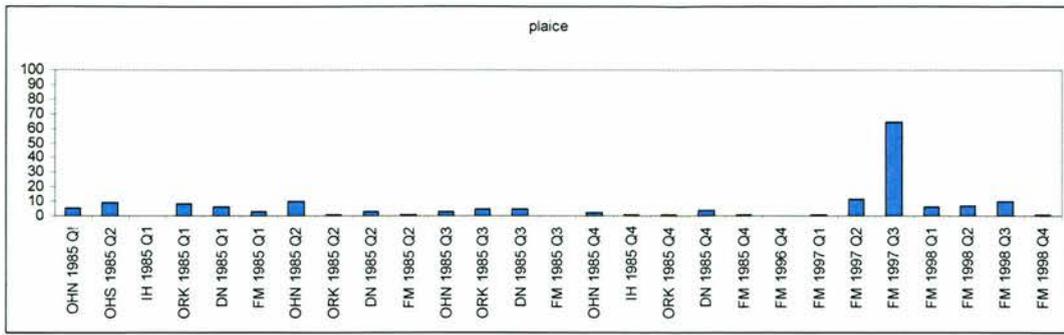


Figure 4.2 cntd.

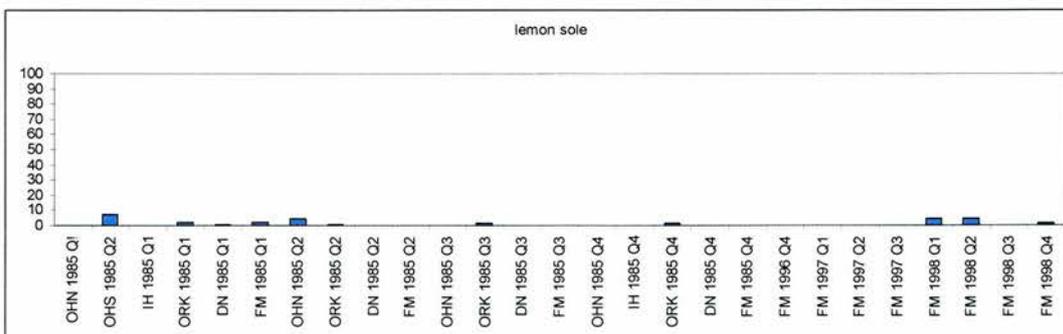
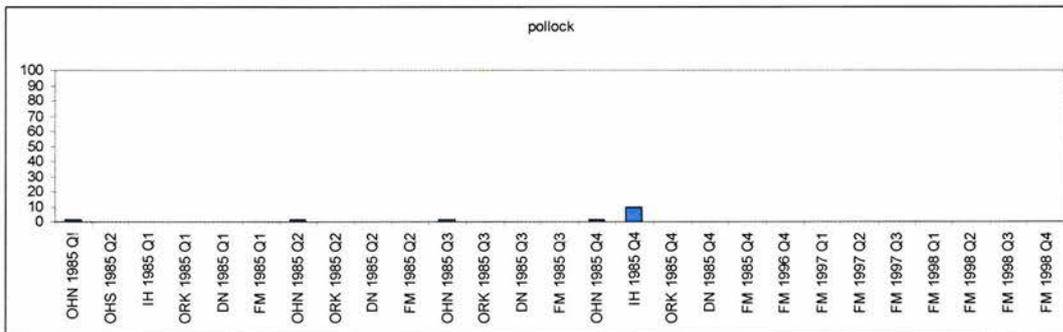
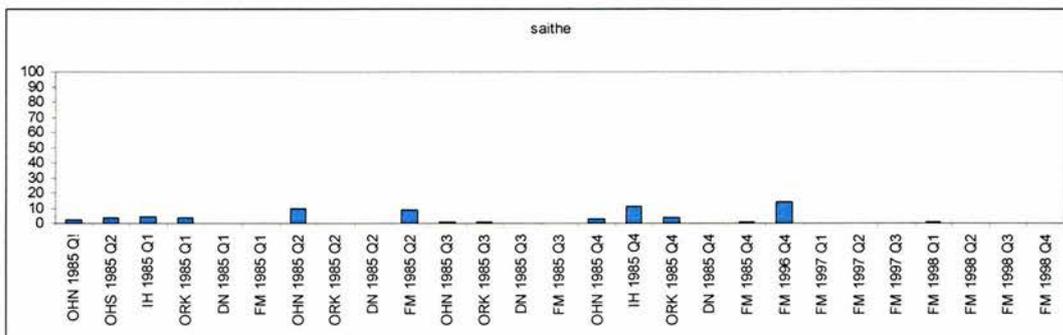
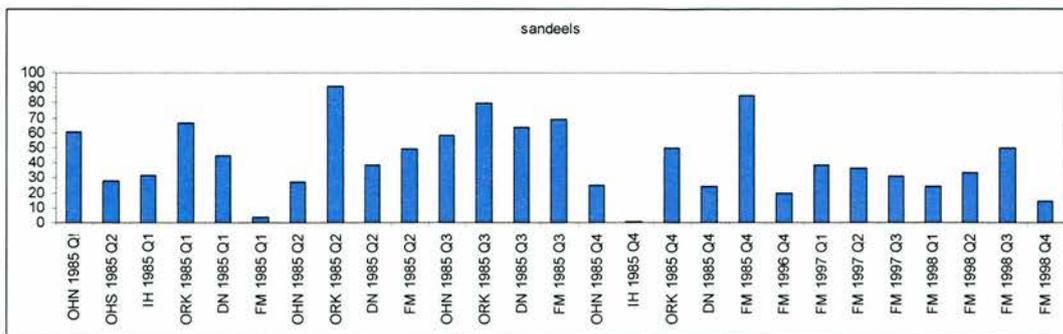


Figure 4.2 cntd.

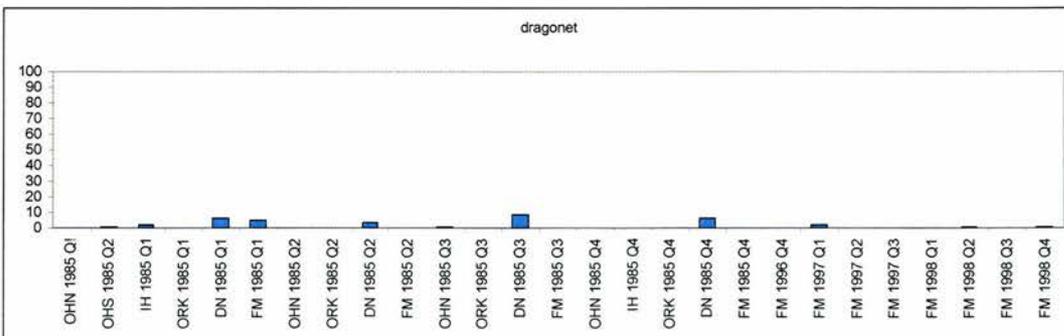
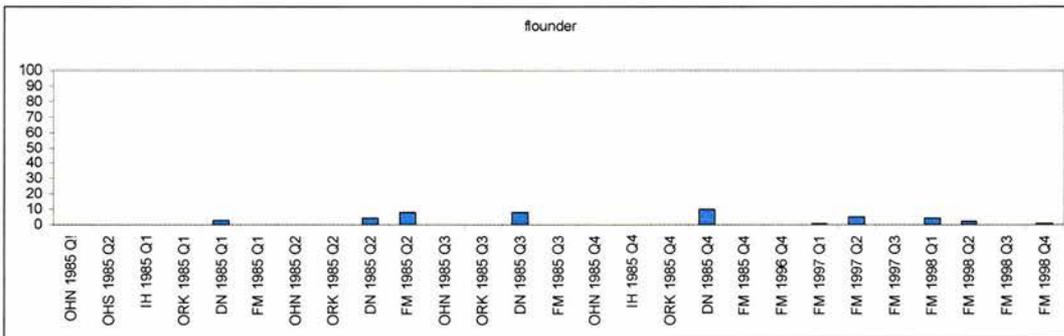
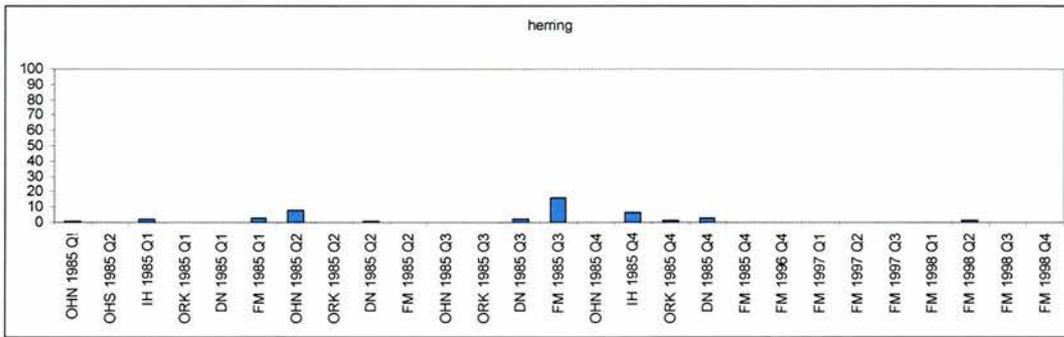
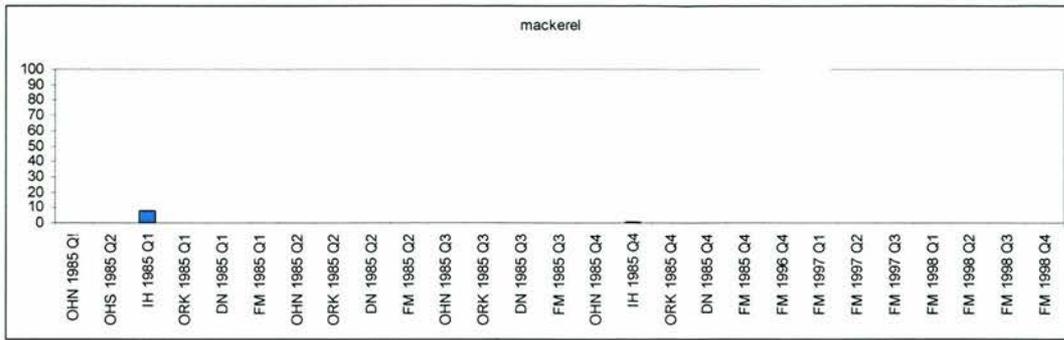


Figure 4.2 cntd.

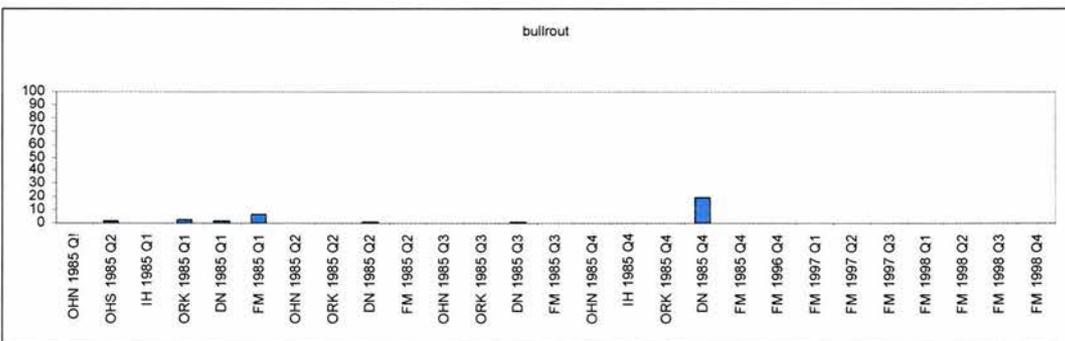
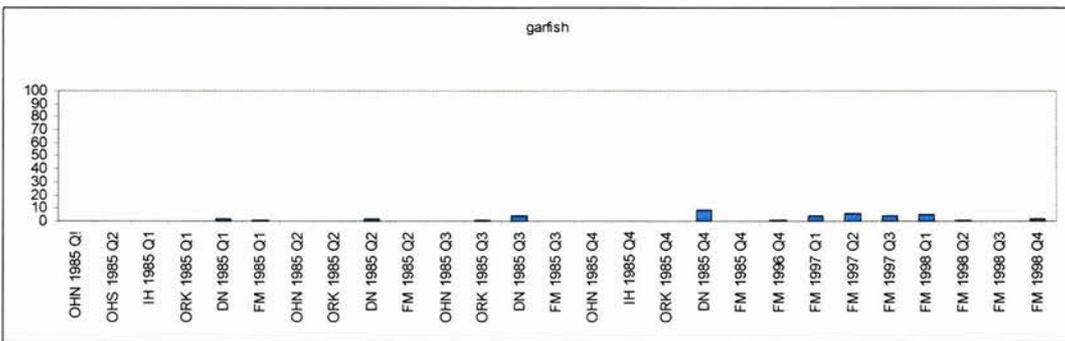
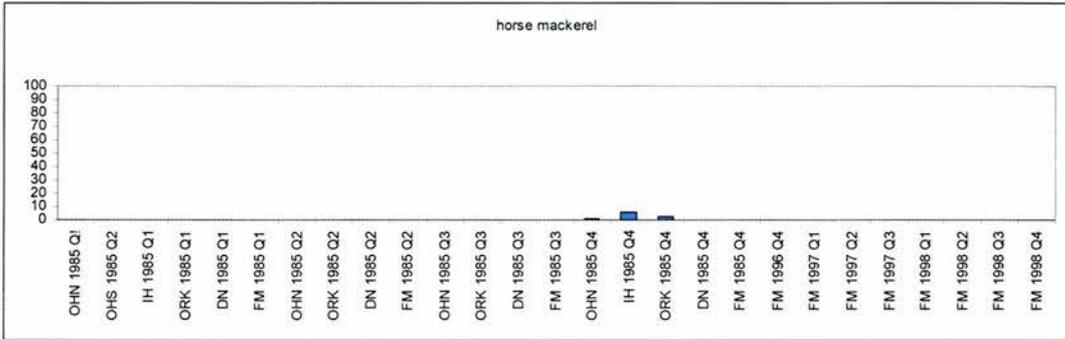
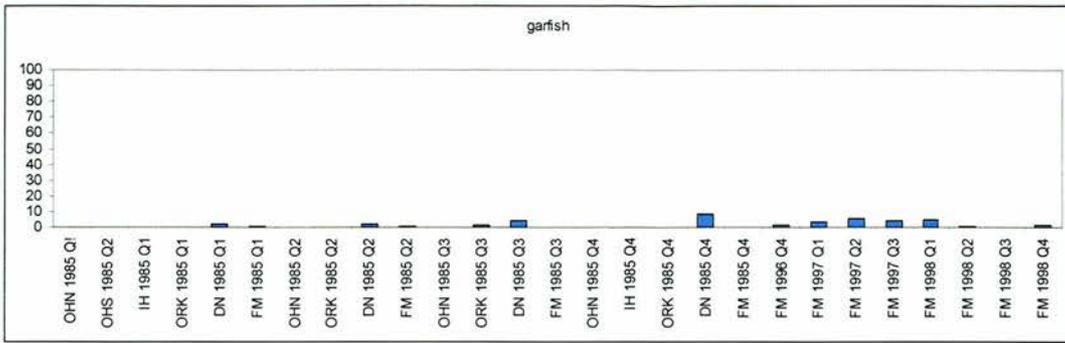
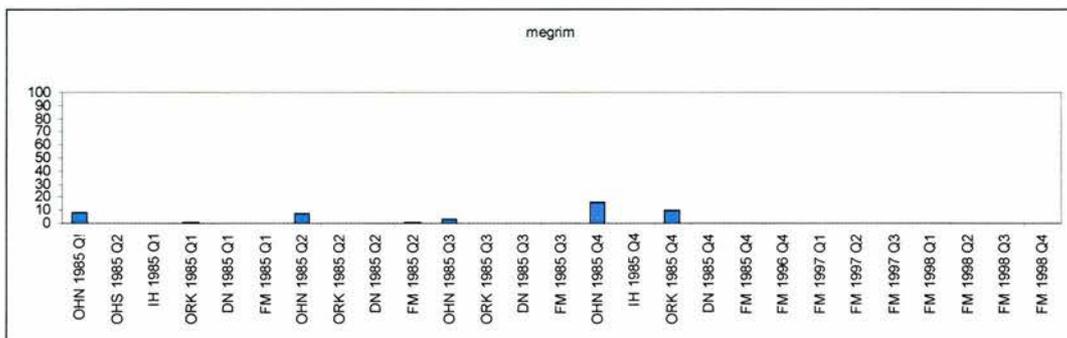
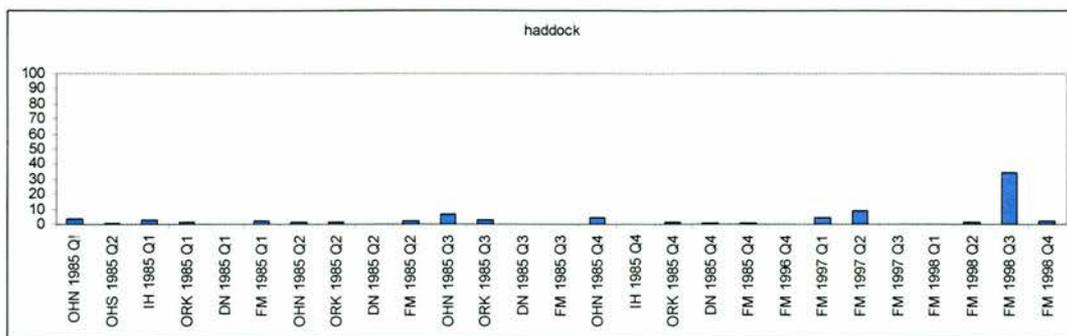


Figure 4.2 cntd.



**Table 4.2: total biomass of seven prey types represented in 21 sample collections**

At each site, all otoliths from each prey type were used to calculate the total biomass of that type that was represented in the scat samples. 'Total' is the sum of the biomass represented by all the otoliths that were identified. 'Other' is the biomass due to prey other than the 7 prey types included in the model.

site	year	quarter	cod0	cod1	whiting	plaice	saithe	ling	sandeels	other	total
ork	1985	1	51.37	35.60	28.87	134.90	63.78	79.74	1091.14	152.62	1638.02
fm	1985	1	17.34	5.72	9.10	1.85	0.00	4.00	2.15	17.13	57.30
dn	1985	1	37.04	12.49	19.68	23.41	0.00	0.00	174.87	123.21	390.70
ih	1985	1	3.82	0.00	11.76	0.00	4.21	31.25	31.38	18.99	101.41
ohn	1985	1	6.47	0.00	8.50	14.64	6.18	27.99	174.87	49.64	288.28
ohs	1985	1	4.21	4.85	0.54	2.69	0.99	2.74	8.27	4.91	29.20
ork	1985	3	8.67	4.33	3.21	22.18	3.13	31.85	406.20	29.38	508.95
fm	1985	3	1.13	0.00	1.55	0.00	0.00	0.00	12.38	2.87	17.93
dn	1985	3	7.08	2.46	12.95	22.61	0.00	0.00	321.15	140.04	506.29
ohn	1985	3	2.33	0.00	14.36	5.34	0.97	16.57	91.97	26.33	157.87
ork	1985	4	36.07	20.29	91.96	7.84	32.40	70.62	471.62	219.45	950.24
fm	1985	4	158.85	96.61	67.62	15.22	13.33	8.90	2318.11	45.90	2724.53
dn	1985	4	15.24	4.75	5.53	4.55	0.00	0.00	31.66	68.35	130.07
ih	1985	4	3.49	4.82	1.99	0.36	7.43	30.84	0.69	19.49	69.12
ohn	1985	4	18.71	0.00	4.47	3.06	3.49	21.00	34.08	49.91	134.73
fm	1996	4	22.44	2.40	2.24	0.00	6.43	0.00	8.87	2.26	44.63
fm	1997	1	23.68	0.00	8.26	0.27	0.00	0.00	24.89	8.09	65.19
fm	1997	3	0.00	0.00	0.00	11.46	0.00	0.00	5.50	0.78	17.74
fm	1998	1	44.33	10.41	16.46	10.06	1.78	6.17	41.55	27.05	157.81
fm	1998	3	0.06	0.00	0.28	0.66	0.00	0.00	3.31	2.26	6.57
fm	1998	4	55.49	5.85	20.06	0.70	0.00	2.07	15.90	9.96	110.02

prey in each of the 7 modelled prey classes, and the mass of 'other' prey, i.e. species that were not included in the model. Table 4.3 shows the estimated consumption of each prey class by mass, based on the constant energy assumption.

Table 4.4 shows the availability,  $N$ , corresponding to each scat collection documented in Table 4.1. Tables 4.5 and 4.6 given the shape and rate parameters for the gamma distribution associated with these availabilities.

Consumption and availability for each prey class are plotted in Figure 4.3. Positive correlations between consumption and availability were found for all prey classes, except plaice and mature cod. For plaice, a positive correlation was detectable if one data point was excluded from the analysis - the consumption estimate for this point was based on only nine samples. This point may be an outlier, but it was retained in the data set for the subsequent analysis because of the possibility that it was the result of a fluctuation in the availability of other species, and the full set of data at this point might then be useful in parameterising the model.

The correlations were not particularly strong for any prey class. This must be partly attributable to the uncertainties in the estimates of prey availability and also of consumption (Hammond and Rothery 1996). It is also likely that for a generalist predator, consumption of individual species is affected by the abundance of all other potential prey.

Table 4.3: estimated consumption for 21 sample collections

At each site, all otoliths from each prey type were used to calculate the total biomass of that type that was represented in the scat samples, giving the composition of the diet by mass. The energetic value of 1kg of this diet was calculated, and the mass required to meet seal energetic requirements was calculated. Consumption of each separate prey type, in kg, could then be calculated. These values are listed in the table below. 'Other' is the biomass due to prey other than the 7 prey types included in the model

site	year	quarter	immature cod	mature cod	whiting	plaice	saithe	ling	sandeels	other
ork	1985	1	0.14	0.10	0.08	0.38	0.18	0.22	3.07	0.43
fm	1985	1	2.00	0.66	0.82	0.21	0.00	0.46	0.25	1.98
dn	1985	1	0.48	0.16	0.25	0.30	0.00	0.00	2.24	1.58
ih	1985	1	0.20	0.00	0.51	0.00	0.22	1.61	1.62	0.98
ohn	1985	1	0.11	0.00	0.13	0.24	0.10	0.46	2.89	0.82
ohs	1985	1	0.82	0.94	0.11	0.52	0.19	0.53	1.61	0.95
ork	1985	3	0.07	0.04	0.03	0.19	0.03	0.27	3.50	0.25
fm	1985	3	0.26	0.00	0.36	0.00	0.00	0.00	2.89	0.67
dn	1985	3	0.06	0.02	0.12	0.20	0.00	0.00	2.91	1.27
ohn	1985	3	0.07	0.00	0.44	0.16	0.03	0.51	2.82	0.81
ork	1985	4	0.19	0.11	0.48	0.04	0.17	0.37	2.49	1.16
fm	1985	4	0.25	0.15	0.10	0.02	0.02	0.01	3.66	0.07
dn	1985	4	0.65	0.20	0.20	0.19	0.00	0.00	1.35	2.92
ih	1985	4	0.31	0.43	0.18	0.03	0.67	2.77	0.06	1.75
ohn	1985	4	0.80	0.00	0.19	0.13	0.15	0.89	1.45	2.13
fm	1996	4	3.11	0.33	0.31	0.00	0.89	0.00	1.23	0.31
fm	1997	1	2.04	0.00	0.63	0.02	0.00	0.00	2.14	0.70
fm	1997	3	0.00	0.00	0.00	3.35	0.00	0.00	1.61	0.23
fm	1998	1	1.66	0.39	0.59	0.38	0.07	0.23	1.56	1.01
fm	1998	3	0.05	0.00	0.22	0.52	0.00	0.00	2.58	1.76
fm	1998	4	3.27	0.34	1.18	0.04	0.00	0.12	0.94	0.59

Table 4.4: availability of seven prey types corresponding to 21 sample collections: mean N

At each site, availability was calculated from the overlap between the accessibility of space to seals, and the fish distribution prediction by a GAM

<i>location</i>	<i>year</i>	<i>quarter</i>	<i>immature cod</i>	<i>mature cod</i>	<i>whiting</i>	<i>allplaice</i>	<i>saithe</i>	<i>ling</i>	<i>sandeels</i>
ork	1985	1	3.92	2.31	10.60	5.89	1.3	1.32	1.00
fm	1985	1	7.90	2.58	14.80	6.5	0.8	0.49	0.73
dn	1985	1	7.32	2.92	14.40	10.3	0.2	0.42	0.33
ih	1985	1	2.26	4.13	10.30	8.73	2.4	1.09	0.61
ohn	1985	1	1.51	6.24	9.23	7.16	1.9	1.65	0.40
ohs	1985	1	1.55	4.37	9.96	9.7	1.4	0.98	0.56
ork	1985	3	3.65	2.26	9.75	5.58	1.8	1.25	1.14
fm	1985	3	7.50	2.52	13.80	6.14	1.3	0.45	0.83
dn	1985	3	6.94	2.85	13.40	9.81	0.4	0.39	0.41
ohn	1985	3	2.06	4.05	9.45	8.33	3.3	1.03	0.69
ork	1985	4	3.52	1.64	9.33	5.15	1.4	1.22	0.66
fm	1985	4	7.31	1.74	13.30	5.64	0.9	0.44	0.48
dn	1985	4	6.75	1.88	12.90	9.16	0.2	0.37	0.18
ih	1985	4	1.96	2.96	9.05	7.77	2.6	1.00	0.40
ohn	1985	4	1.26	4.67	8.05	6.28	2.1	1.54	0.22
fm	1996	4	6.91	1.03	15.90	3.48	0.3	0.32	0.51
fm	1997	1	7.49	1.61	17.80	3.82	0.2	0.32	0.76
fm	1997	3	7.10	1.57	16.60	3.55	0.4	0.29	0.88
fm	1998	1	7.50	1.61	17.90	3.51	0.2	0.29	0.72
fm	1998	3	7.12	1.57	16.70	3.26	0.3	0.27	0.83
fm	1998	4	6.93	1.01	16.20	2.92	0.2	0.26	0.47

**Table 4.5: availability of seven prey types corresponding to 21 sample collections: shape**

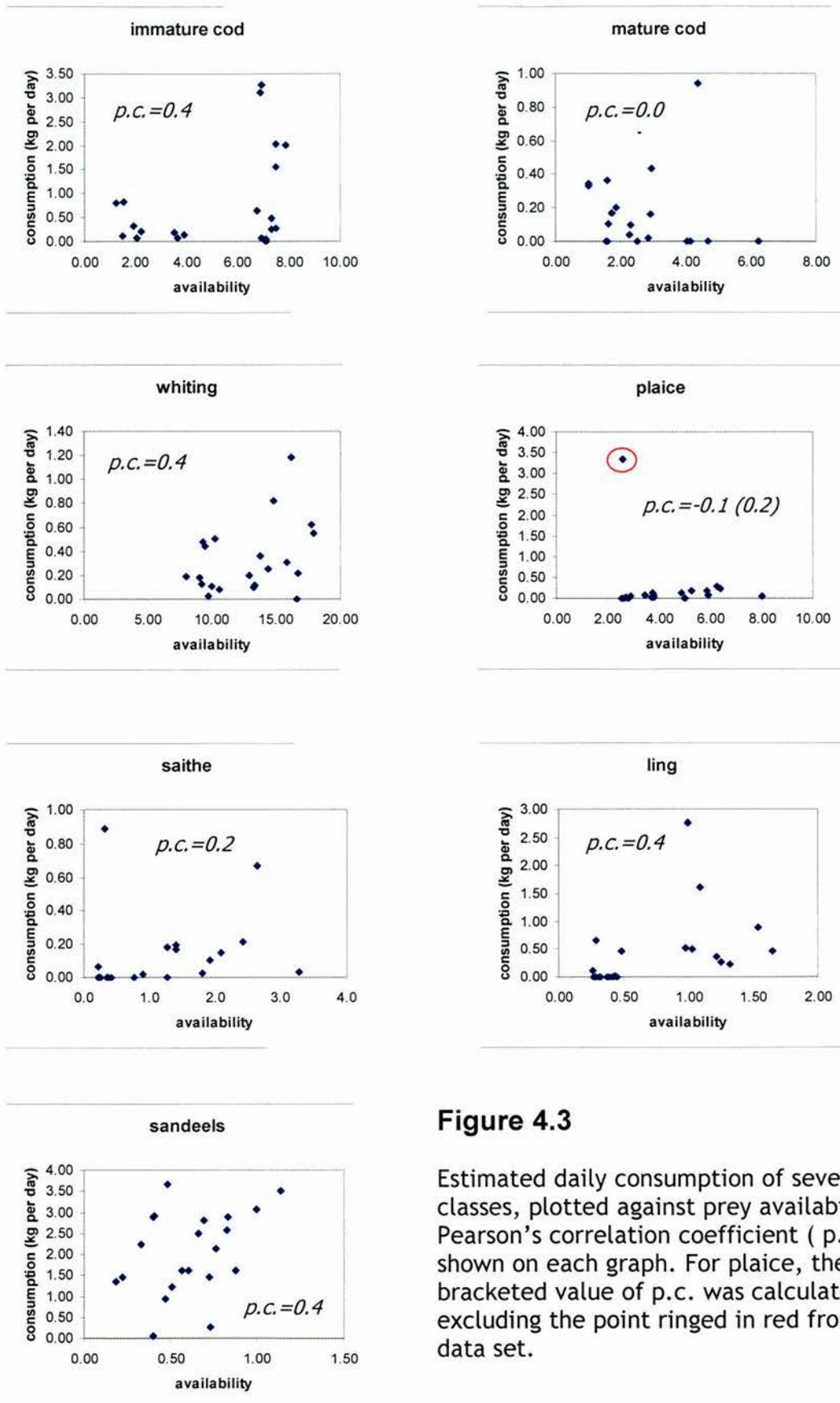
At each site, availability N was calculated from the overlap between the accessibility of space to seals, and the fish distribution predicted by a GAM. Shape and rate parameters were estimated from the mean and variance of N obtained from bootstrapping over fish abundance data used to fit the GAM

<i>location</i>	<i>year</i>	<i>quarter</i>	<i>immature cod</i>	<i>mature cod</i>	<i>whiting</i>	<i>plaice</i>	<i>saithe</i>	<i>ling</i>	<i>sandeels</i>
ork	1985	1	87.8	67.8	651.1	157.4	29.9	18.9	26.2
fm	1985	1	74.8	79.2	811.7	137.4	17.2	21.7	29.5
dn	1985	1	37.8	38.9	326.3	54.2	24.0	19.2	9.0
ih	1985	1	34.0	48.7	335.0	74.1	44.7	14.5	31.3
ohn	1985	1	28.4	25.3	326.6	97.0	29.6	21.3	20.1
ohs	1985	1	28.0	32.2	426.8	126.5	25.4	17.0	38.2
ork	1985	3	74.7	69.9	564.8	132.3	38.6	18.6	28.1
fm	1985	3	70.4	78.9	776.9	144.5	25.2	22.4	30.9
dn	1985	3	34.1	37.6	300.5	50.8	22.4	19.0	9.0
ohn	1985	3	28.8	46.8	294.4	67.6	57.7	14.0	24.2
ork	1985	4	66.3	47.1	486.3	110.6	27.9	18.4	19.5
fm	1985	4	66.6	43.4	707.2	130.8	15.1	22.0	33.0
dn	1985	4	32.1	25.1	277.9	45.4	17.5	18.3	9.2
ih	1985	4	25.7	33.7	266.7	59.1	41.1	13.6	21.5
ohn	1985	4	22.2	19.1	242.5	75.0	30.7	20.7	19.5
fm	1996	4	63.9	33.4	798.6	71.3	10.4	22.5	24.6
fm	1997	1	61.6	48.8	1071.6	70.7	14.3	19.9	18.5
fm	1997	3	60.4	55.0	954.7	71.5	14.0	20.8	18.3
fm	1998	1	54.8	43.6	854.7	60.4	18.9	19.5	17.1
fm	1998	3	53.9	48.6	846.5	60.3	12.8	20.4	16.9
fm	1998	4	52.3	29.1	765.7	51.5	12.1	20.5	23.9

Table 4.6: availability of seven prey types corresponding to 21 sample collections: rate

At each site, availability N was calculated from the overlap between the accessibility of space to seals, and the fish distribution predicted by a GAM. Shape and rate parameters were estimated from the mean and variance of N obtained from bootstrapping over fish abundance data used to fit the GAM

location	year	quarter	sites	immature cod	mature cod	whiting	plaice	saithe	ling	sandeels
ork	1985	1	5	22.4	29.4	61.4	26.39	24.74	14.3	26.2
fm	1985	1	12	9.5	30.7	54.8	21.31	23.25	44.4	40.5
dn	1985	1	13	5.2	13.3	22.7	5.02	116.40	46.2	27.5
ih	1985	1	24	15.1	11.8	32.5	9.06	18.10	13.3	51.7
ohn	1985	1	8	18.8	4.1	35.4	13.13	16.04	12.9	49.9
ohs	1985	1	23	18.1	7.4	42.9	13.62	17.94	17.3	67.8
ork	1985	3	5	20.5	30.9	57.9	24.20	21.59	14.9	24.6
fm	1985	3	12	9.4	31.3	56.3	24.59	19.61	49.3	37.2
dn	1985	3	13	4.9	13.2	22.4	5.06	60.59	49.0	22.3
ohn	1985	3	24	14.0	11.5	31.2	8.93	16.84	13.6	34.9
ork	1985	4	5	18.8	28.7	52.1	21.80	19.99	15.1	29.6
fm	1985	4	12	9.1	25.0	53.2	24.13	16.52	50.2	68.6
dn	1985	4	13	4.8	13.3	21.5	4.81	71.16	49.0	49.9
ih	1985	4	24	13.1	11.4	29.5	8.36	14.76	13.6	53.5
ohn	1985	4	8	17.6	4.1	30.1	11.88	14.64	13.4	88.1
fm	1996	4	12	9.2	32.4	50.2	21.08	30.79	69.6	48.4
fm	1997	1	12	8.2	30.3	60.2	18.10	60.46	62.8	24.3
fm	1997	3	12	8.5	35.0	57.5	20.58	32.04	71.0	20.9
fm	1998	1	12	7.3	27.1	47.7	16.63	86.66	66.7	23.7
fm	1998	3	12	7.6	30.9	50.7	18.71	35.35	75.4	20.4
fm	1998	4	12	7.6	28.8	47.3	17.72	48.36	78.7	51.2



**Figure 4.3**

Estimated daily consumption of seven prey classes, plotted against prey availability . Pearson's correlation coefficient ( p.c.) is shown on each graph. For plaice, the bracketed value of p.c. was calculated by excluding the point ringed in red from the data set.

Parameter values and standard deviations for the single species functional response that was fitted to the captive seal data are shown in Table 4.7, and the marginal posterior distributions are shown in Figure 4.4. The fit of the model to the data is illustrated in Figure 4.5. The form of the prior used for  $m$  in subsequent analysis is shown in Figure 4.6.

For both of the multi-species models, the MCMC algorithm ran in 5-15 minutes on a PC with an Intel Pentium M processor (1.7GHz). The MCMC converged successfully.

For Model 1, values of the attack rate parameter  $a$  for all prey classes were acutely sensitive to the choice of prior. Because there is no strong evidence available at present to suggest a form for these priors, it was decided to abandon the attempt to fit Model 1 and attention was focussed on the model of diet composition, Model 2.

Equation 6 was fitted to the prey availability distributions represented in Tables 4.4-4.6 and the raw estimates of total biomass for each prey class. This process automatically gave more weight to larger scat collections that represented a greater net mass of prey.

When the value of  $a$  for sandeels was fixed at 1, the posterior distributions of the other  $a$  parameters were well defined (Figure 4.7), and were insensitive

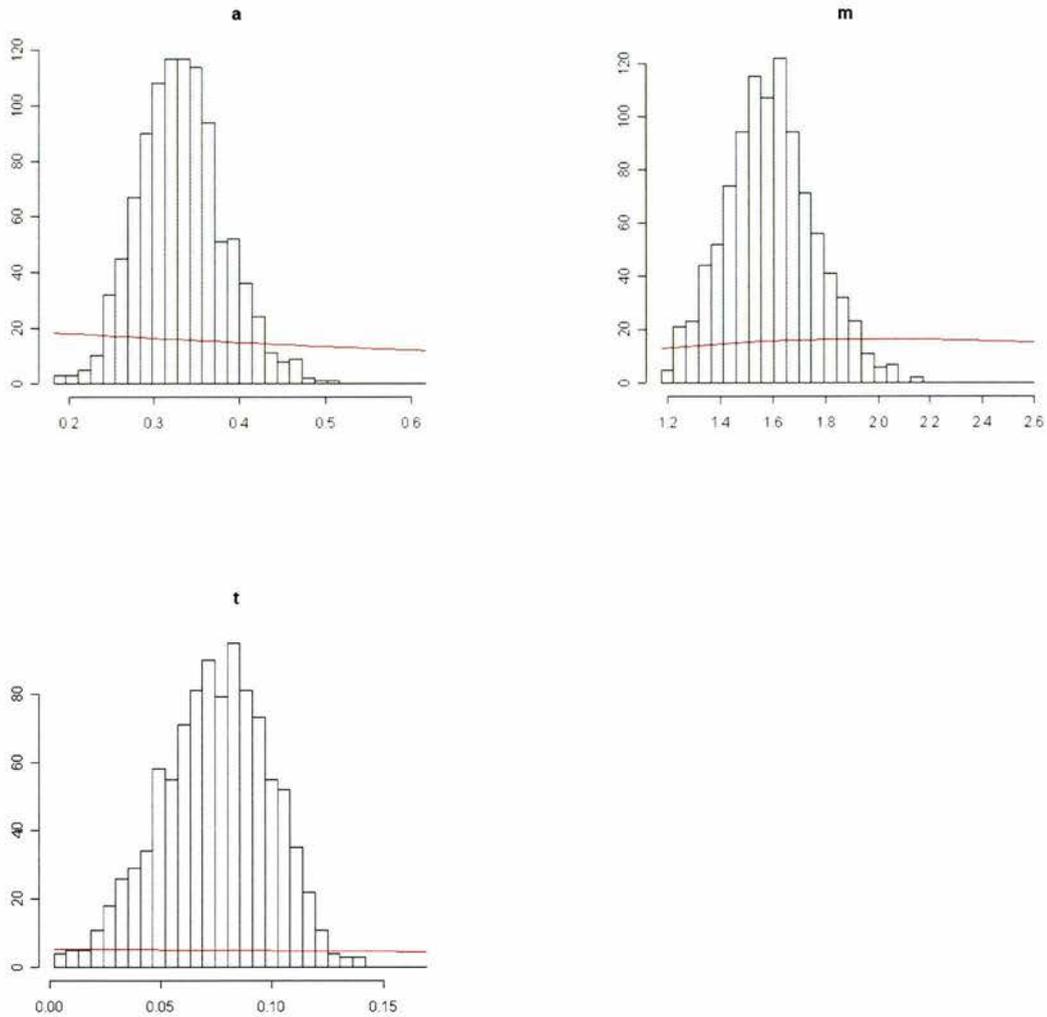
**Table 4.7: Parameters of the Single Species Functional Response**

Mean and standard deviation of parameters  $a$  and  $m$  based on 1000 samples from the Markov chain.

	mean	sd
<b>a</b>	0.331	0.0502
<b>m</b>	1.59	0.169
<b>t</b>	0.0745	0.0245

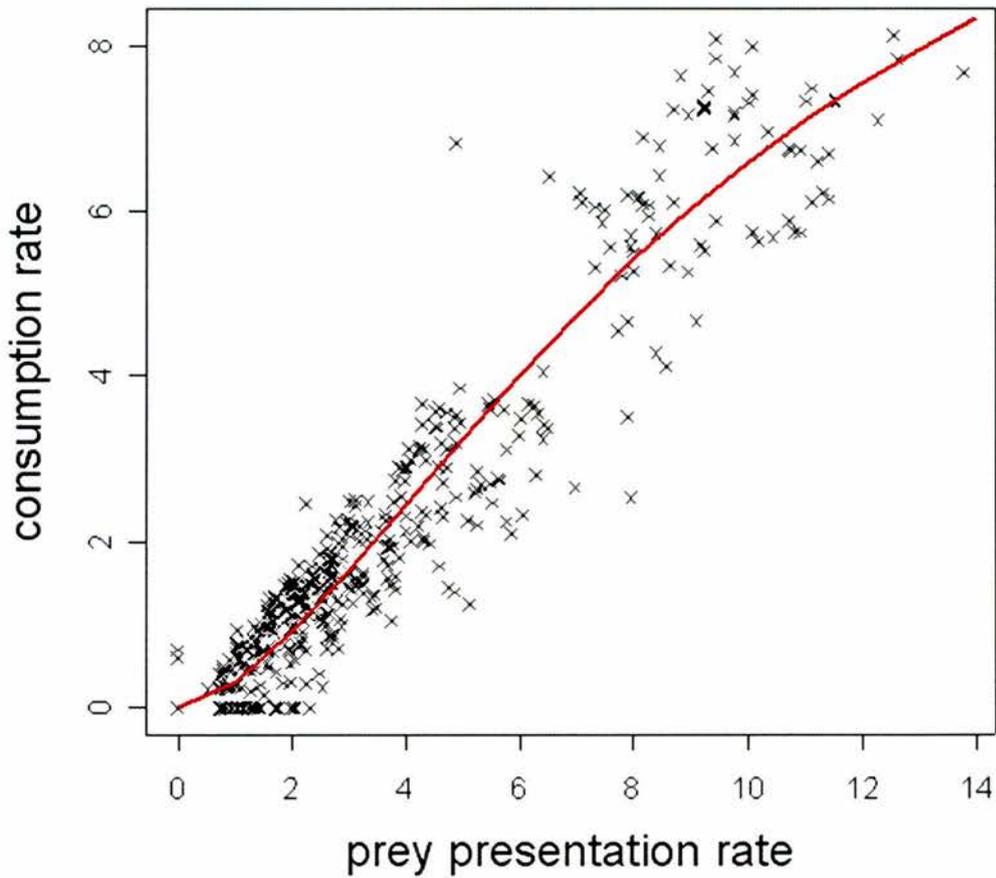
## Figure 4.4: Single Species Functional Response Parameters, Priors and Posteriors

Marginal distributions for the parameters  $a$ ,  $m$  and  $t$  for the single species functional response, fitted to experimental data from foraging studies on captive seals.



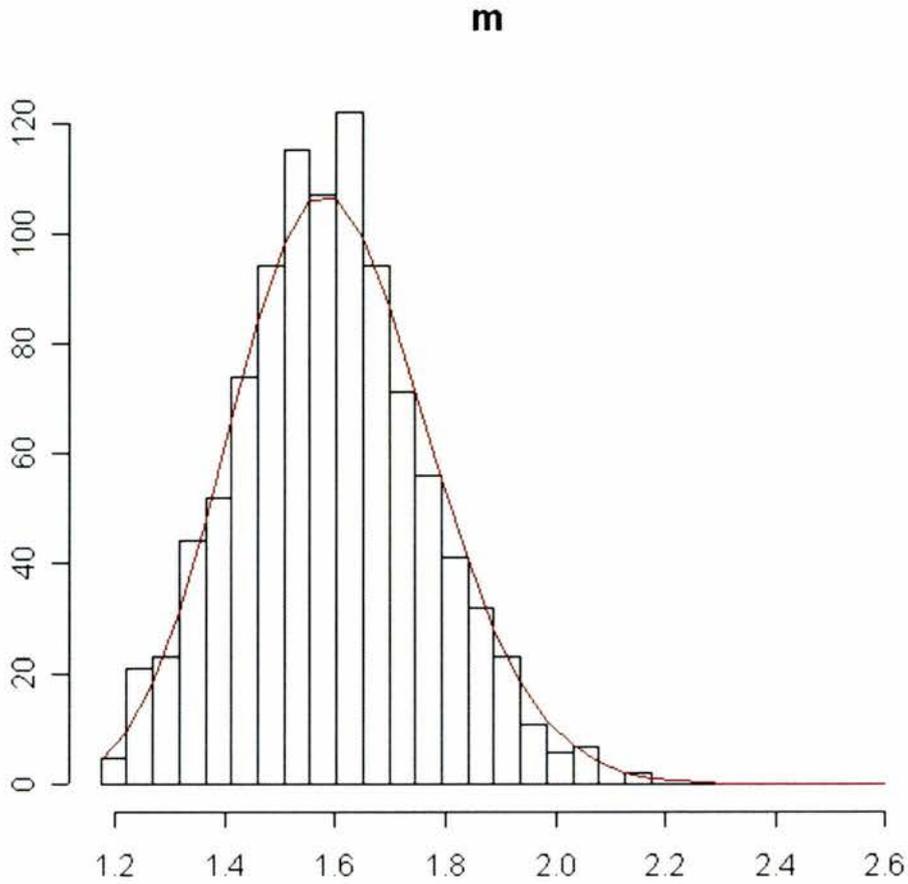
**Figure 4.5: Functional response of a captive grey seal to different rates of presentation of sandeels.**

The red curve was calculated using mean values of parameters from the posterior distribution. The black crosses are data points. The data was collected for seals diving to a range of different depths (40, 60, 80 and 130m) to forage on sandeels.



**Figure 4.6: prior for  $m$**

The prior for  $m$  which was used to fit the multi-species consumption model was derived from the posterior distribution for the fitted single species functional response. The posterior distribution of  $m$  is shown as a histogram, and the prior (a gamma distribution) that was inferred from it is shown in red.

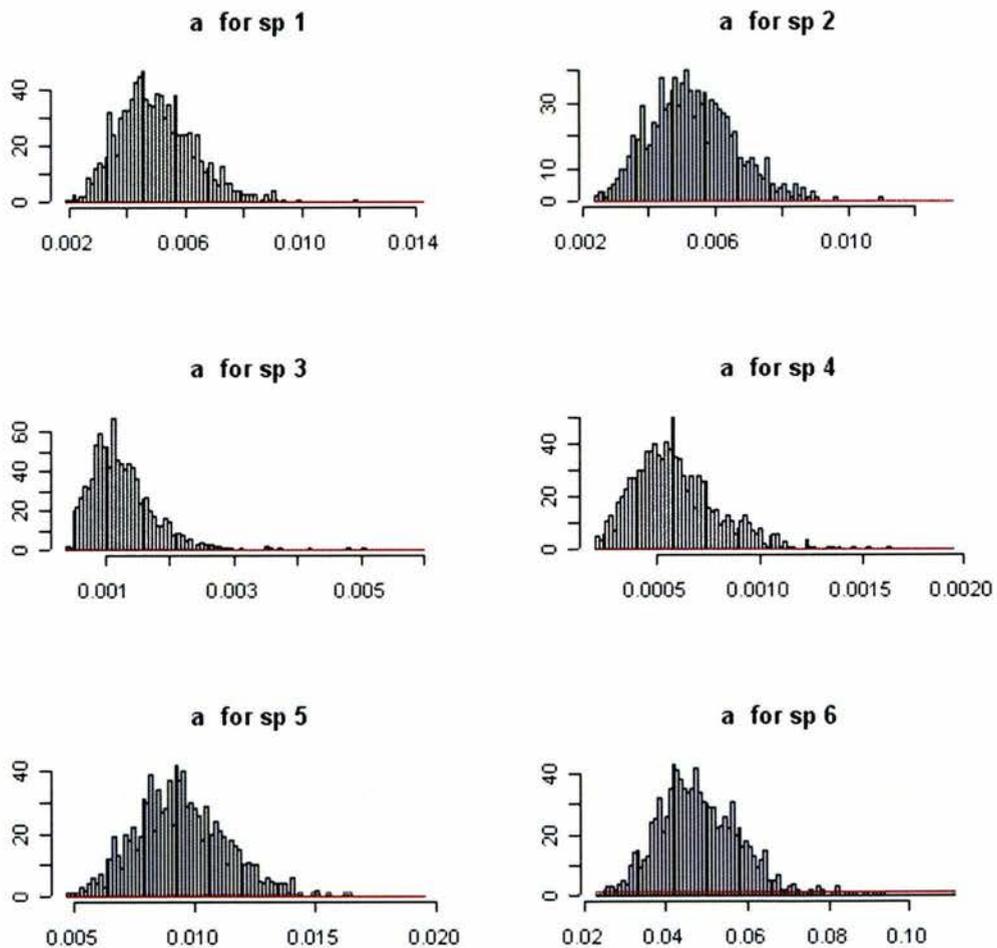


## Figure 4.7: Priors and posteriors for $a$

Marginal values of the posterior distribution for the  $a$  parameter, for each prey species in Model 2.

sp 1 = immature cod, sp 2 = mature cod, sp 3 = whiting, sp 4 = plaice, sp 5 = saithe  
sp 6 = ling.

(for species 7 (sandeels)  $a$  was set at 1)



to the limits used for the uniform priors, provided these were wide enough. The posterior distributions for  $m$  (Figure 4.8) were sensitive to the choice of priors.

A QQ plot, illustrating the fit of the data for Model 2, is shown in Figure 4.9. The points on a QQ plot should lie on the  $x=y$  line: the fit here appears moderately good.

Table 4.8 shows the mean and standard deviations of the marginal posterior values of the parameters for Model 2. The values of  $m$  are all slightly greater than 1, indicating a sigmoidal functional response to all prey species. Based on 1000 samples from the Markov chain, the probabilities that  $m < 1$  were between 0.986 and 1.0 for all prey classes. However, these results were strongly influenced by the form of the prior that was used for  $m$ .

Model 2 was used to predict diet composition at each haul-out location using the mean parameter values from the Markov chain. Figure 4.10 shows these values compared with those calculated directly from the scat data. In general, diet composition was predicted well but, for some scat collections, observed consumptions of particular prey classes were not well predicted. An example is at the Farnes/Isle of May in quarter 3 of 1997, where the estimated proportion of young plaice in the diet (based on scat analysis) was large, but this was not predicted by the model. This was a particularly small

## Figure 4.8: priors and posteriors for $m$

Marginal values of the posterior distribution for the  $m$  parameter, for each prey species in Model 2.

sp 1 = immature cod, sp 2 = mature cod, sp 3 = whiting, sp 4 = plaice, sp 5 = saithe  
sp 6 = ling, sp 7 = sandeels

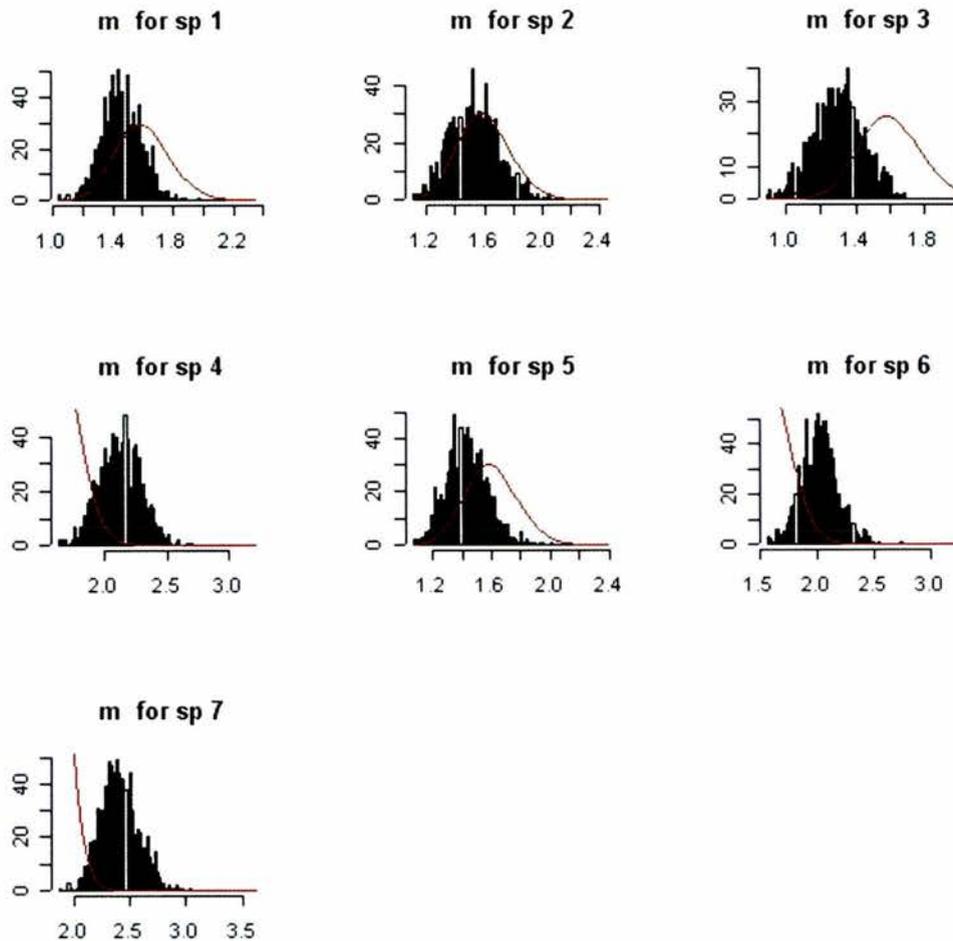
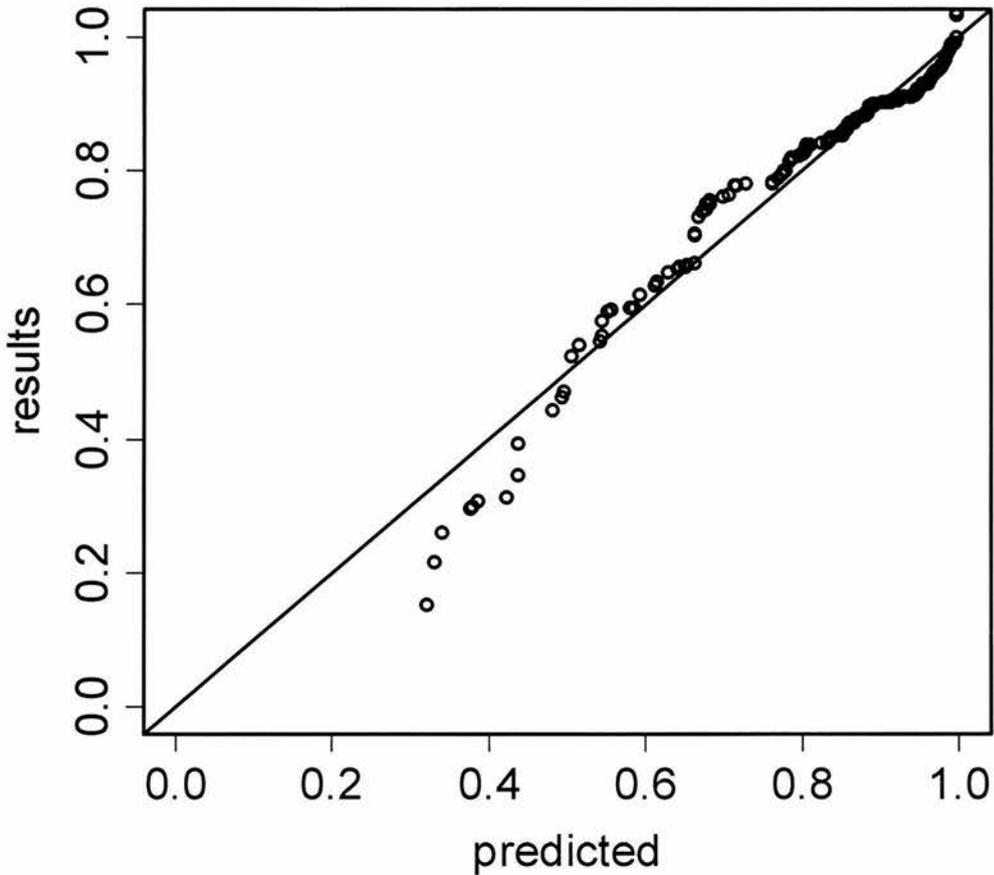


Figure 4.9: QQ plot for Model 2

For each data point, the probability that the estimated consumption or less would be observed, given the model prediction value was true, was calculated based on the continuous Poisson distribution. All p's were then ranked. The ranked p's were then compared with p's generated at random from Poisson distributions based around the prediction points. If the distribution has been modelled successfully, the points should be evenly scattered around the x=y line, with approximately as many points above as below the line.



**Table 4.8: Parameter estimates for model 2**

The mean and standard deviation of each parameter was calculated from 1000 draws from the Markov chain

Species codes: 1 = immature cod, 2 = mature cod, 3 = whiting, 4 = plaice, 5 = saithe, 6 = ling, 7 = sandeels

parameter	mean of marginal posterior distribution	SD of marginal posterior distribution
a[1]	0.005020	0.001320
a[2]	0.005290	0.001270
a[3]	0.001260	0.000523
a[4]	0.000596	0.000208
a[5]	0.009400	0.001860
a[6]	0.048200	0.010300
m[1]	1.45	0.129
m[2]	1.52	0.165
m[3]	1.30	0.141
m[4]	2.12	0.169
m[5]	1.43	0.142
m[6]	2.02	0.159
m[7]	2.40	0.170

**Figure 4.10: predictions of consumption model compared with consumption data**

Consumption of each species ( $\text{kg}\cdot\text{day}^{-1}$ ) is shown on the y-axis. On the x-axis, species are represented as follows: 1=immature cod; 2=mature cod; 3=whiting; 4=plaice; 5=saithe; 6=ling; 7=sandeels. Direct estimates of consumption from diet data are shown as solid blue circles, predictions are red open circles. 95% credibility intervals are shown with red bars. For site codes, see figure 4.1.

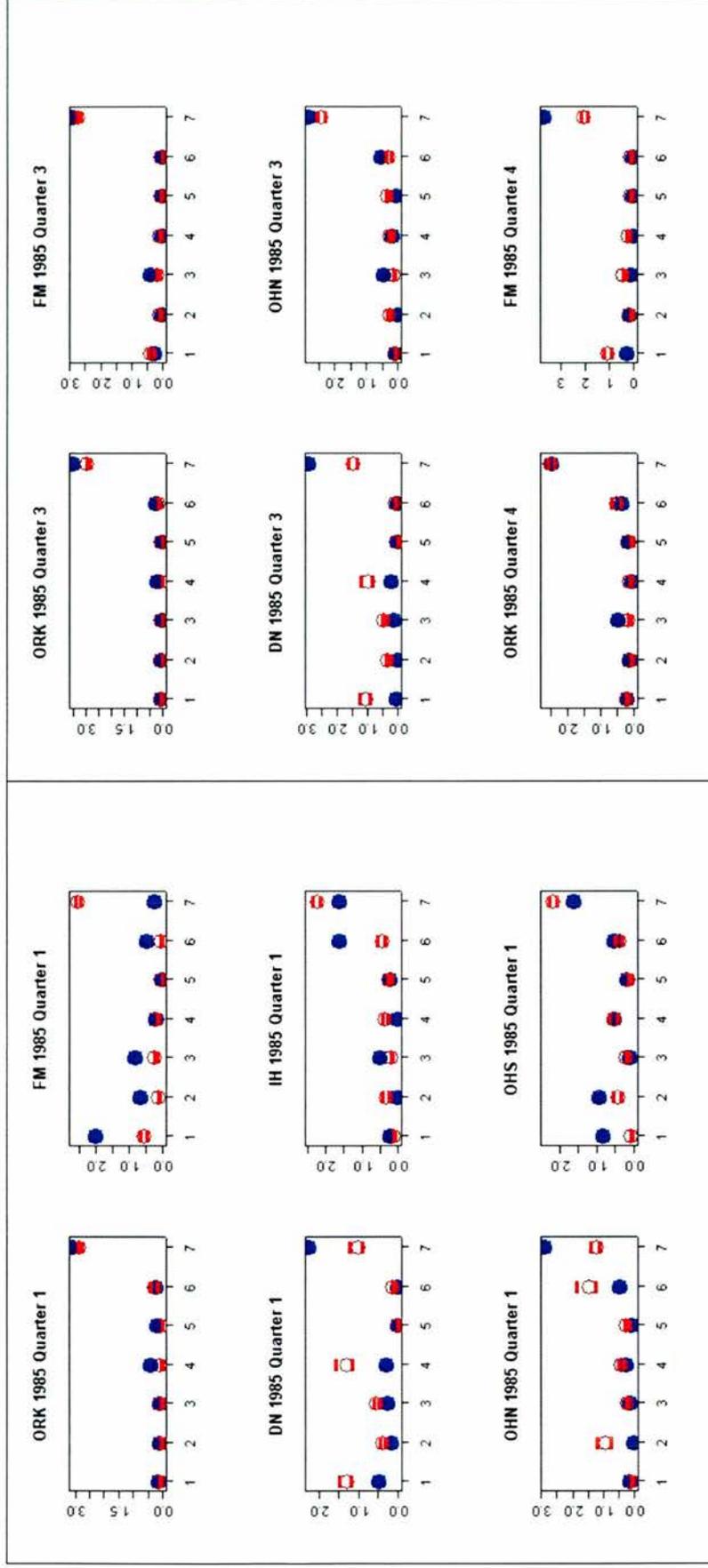
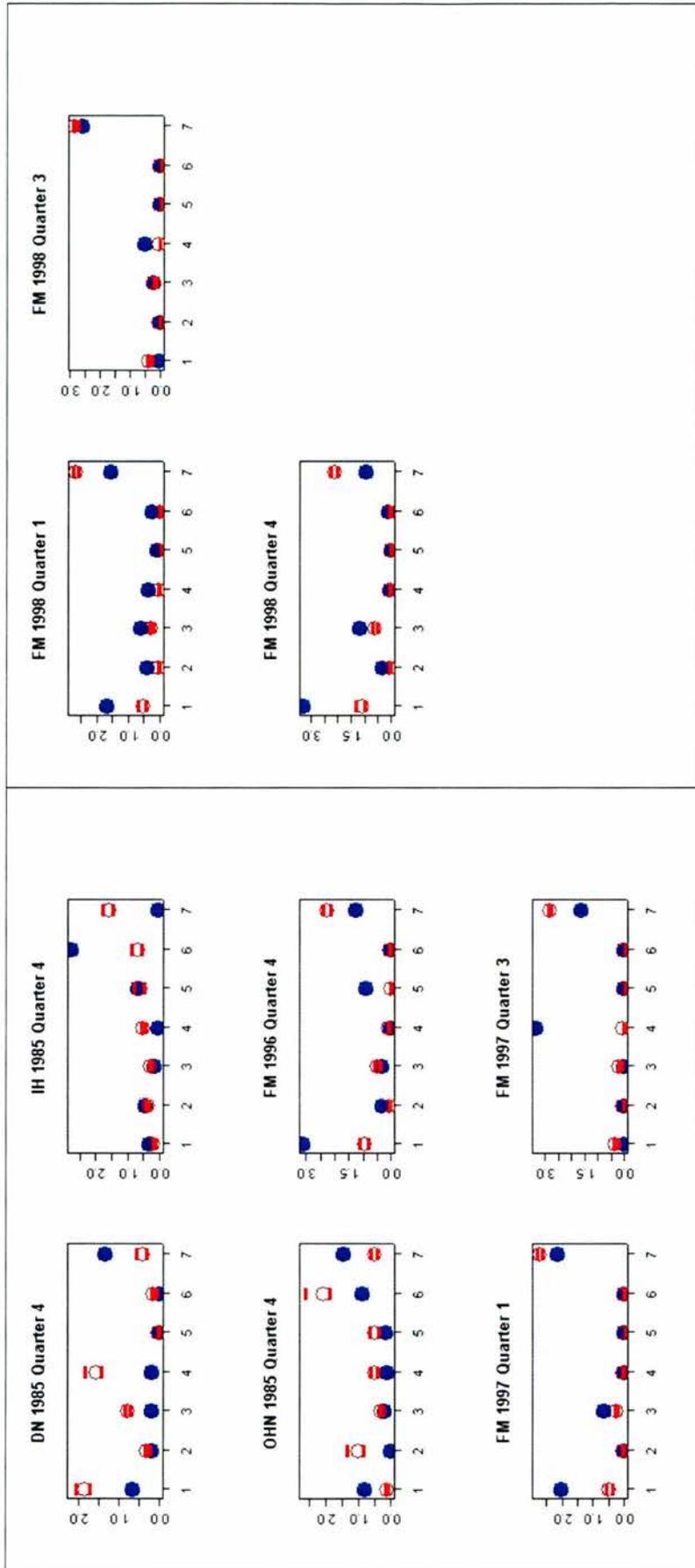


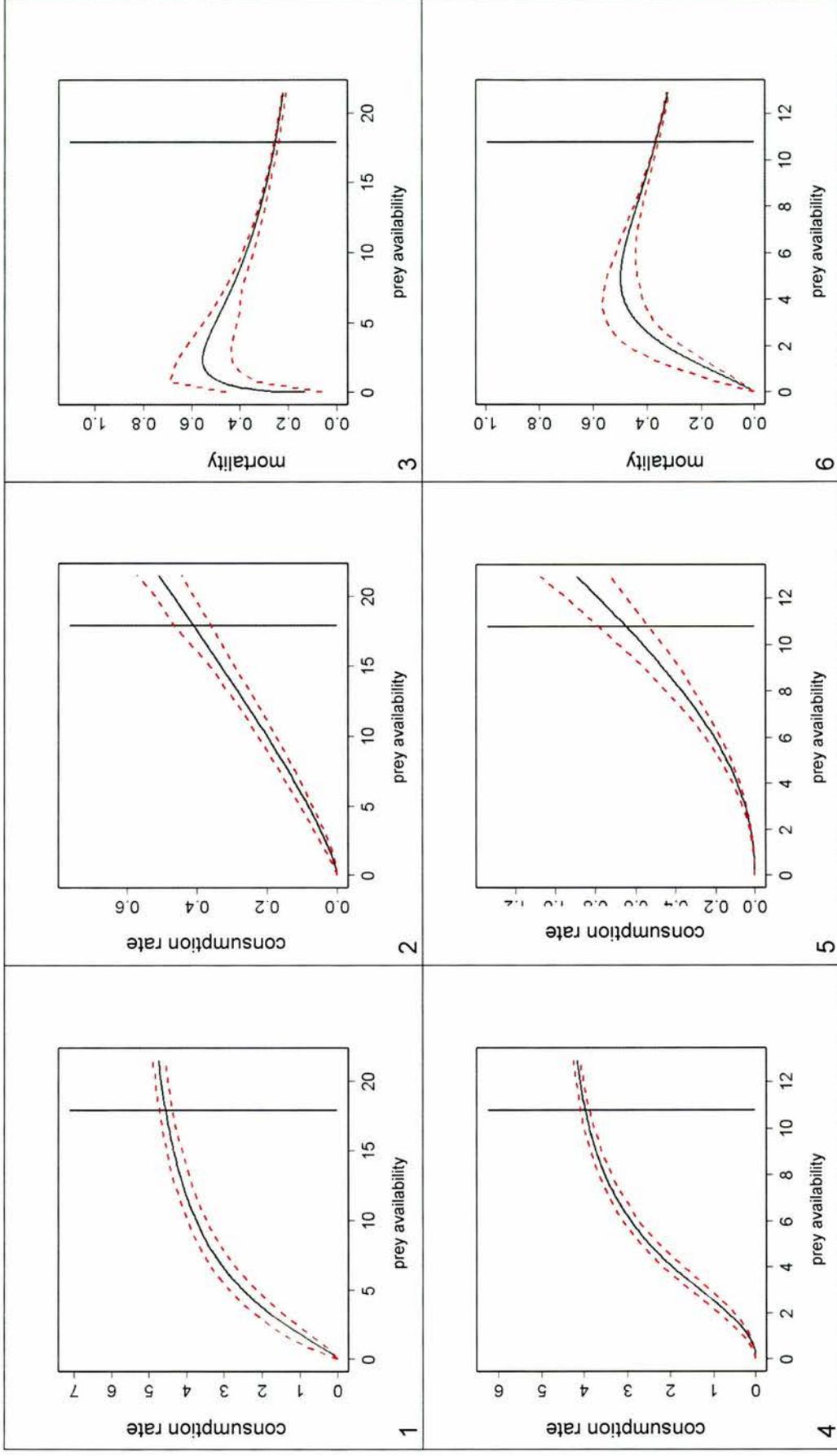
Figure 4.10 (continued)



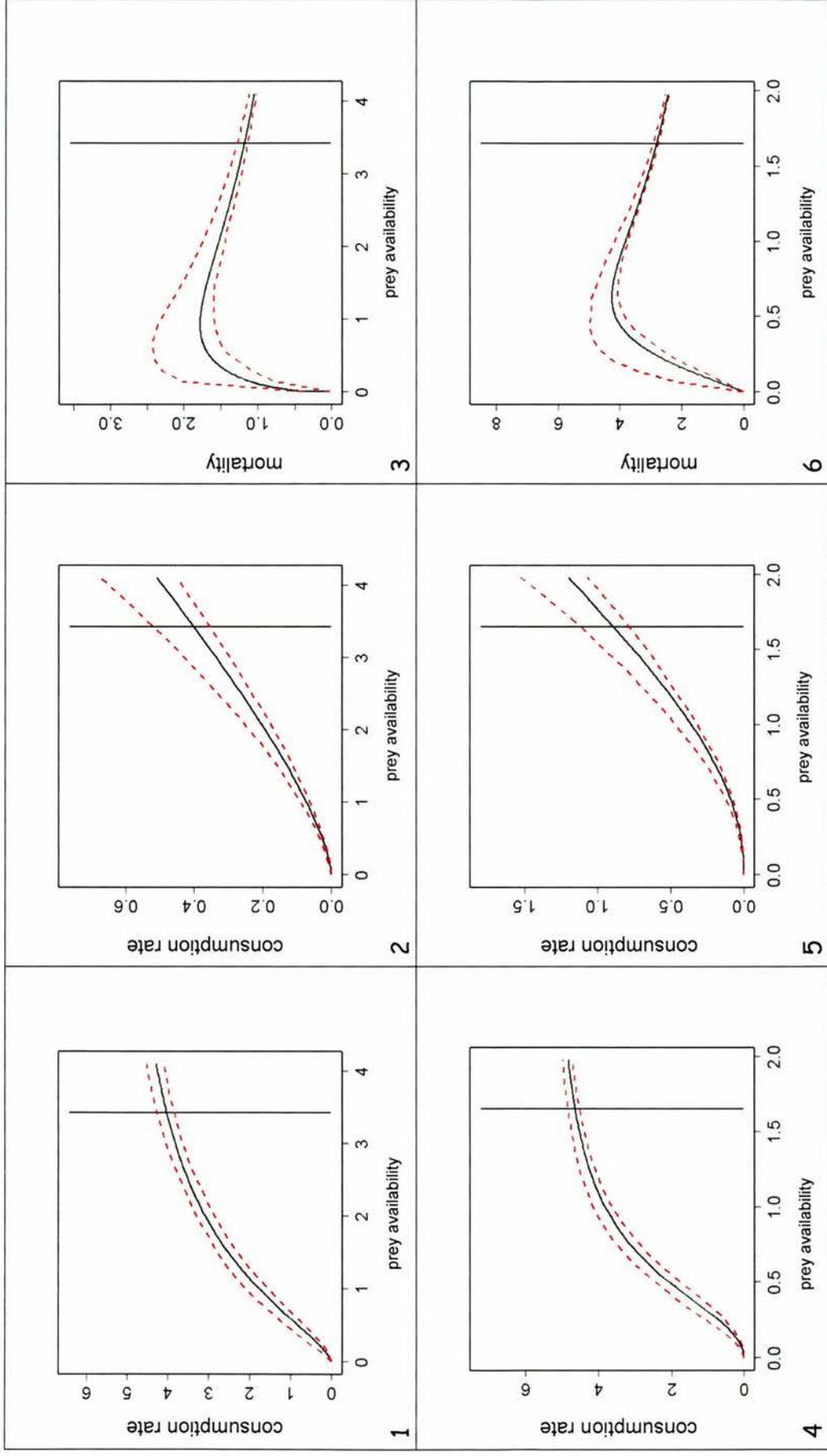
scat collection, however (9 scats) and there was considerable uncertainty in the diet estimates themselves.

The relationships between consumption and mortality, and prey availability, are illustrated in Figures 4.11-4.14 for all seven prey classes. The consumption rates shown in the second columns of these figures, in which 'other' prey was held at moderate abundance, are all lower than those in the first columns, in which 'other' prey was set at low abundance. The effect of 'other' prey was greater on the estimate of consumption for some prey classes than on others. This was a result of the estimated parameter values, and also of the ranges of prey availabilities that were used in the calculations (these were based on the range of prey availabilities represented within the data set). The effect of 'other' prey on the mortality curve for mature cod is illustrated in figure 4.15. The height and shape of the mortality curve are both sensitive to the presence of 'other' prey.

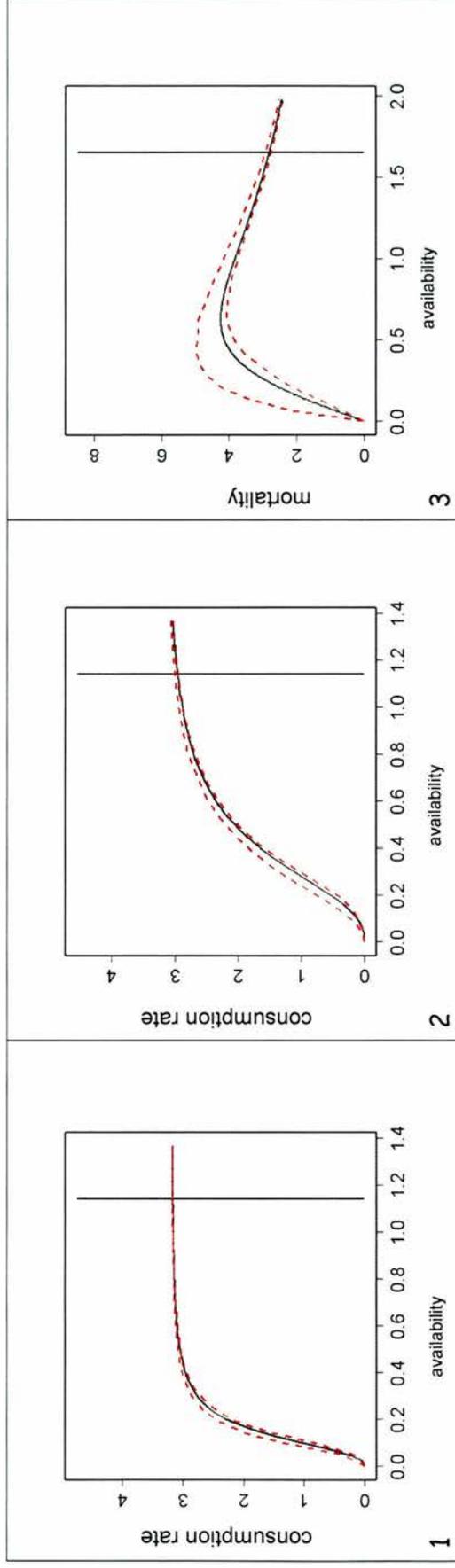
Sandeel availability had a strong effect on the consumption of other prey classes, due to the relative values of  $m$  and the high value of the attack rate parameter  $a$  for sandeels. This is illustrated in Figure 4.16, where the impact of sandeel abundance on the consumption of mature cod is shown in the first column. The consumption of mature cod was much more strongly influenced by fluctuations in the availability of sandeels, than it was by the availability of any other prey in the system: for example, the availability of immature cod had little effect on the consumption of mature cod (see the right panel of



**Figure 4.12:** Consumption of whiting when other prey are scarce (1); and when other prey are at moderate abundance (2). Mortality of whiting resulting from grey seal predation when other prey are scarce (3). Consumption of plaice when other prey are scarce (4); and when other prey are at moderate abundance (5). Mortality of plaice resulting from grey seal predation, when other prey are scarce (6). Consumption rates are in  $\text{kg}\cdot\text{hr}^{-1}$ ; prey availability is based on predator-prey overlap.



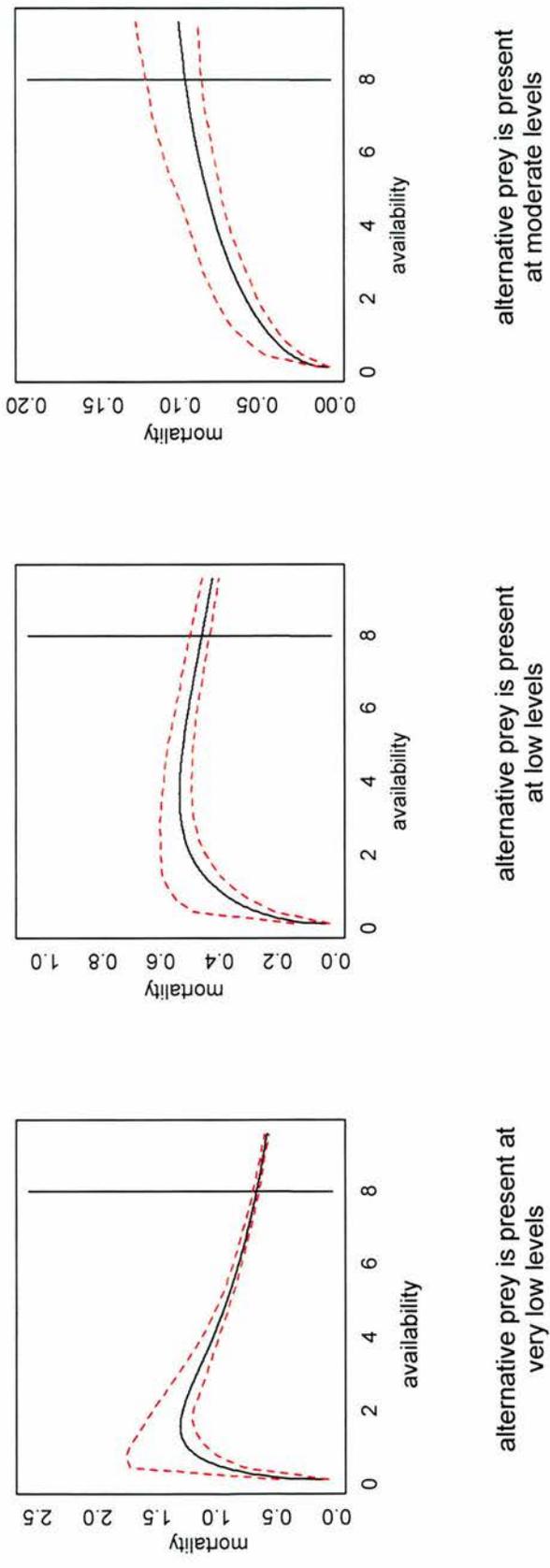
**Figure 4.13:** Consumption of saithe when other prey are scarce (1); and when other prey are at moderate abundance (2). Mortality of saithe resulting from grey seal predation when other prey are scarce (3). Consumption of ling when other prey are scarce (4); and when other prey are at moderate abundance (5). Mortality of ling resulting from grey seal predation, when other prey are scarce (6). Consumption rates are in  $\text{kg}\cdot\text{hr}^{-1}$ ; prey availability is based on predator-prey overlap.



**Figure 4.14:** Consumption of sandeels when other prey are scarce (1); and when other prey are at moderate abundance (2). Mortality of sandeels resulting from grey seal predation when other prey are scarce (3). Consumption rates are in  $\text{kg}\cdot\text{hr}^{-1}$ ; prey availability is based on predator-prey overlap.

**Figure 4.15: Predation mortality for mature cod, and the effect of alternative prey**

An index of instantaneous mortality as predicted by Model 2 is plotted on the y-axis, and the availability of cod is shown on the x-axis. The availability of alternative prey (whiting, immature cod, plaice, saithe, ling and sandeels) varies. 95% credibility intervals are shown with red dashed curves.



**Figure 4.16: The effect of alternative prey on the consumption of mature cod**

Panel 1 shows the effect of sandeel availability (x axis) on the rate of consumption of mature cod by seals (y axis, the units of consumption rate are  $\text{kg}\cdot\text{day}^{-1}$ ). Panel 2 illustrates the effect of immature cod availability (x axis) on mature cod consumption.

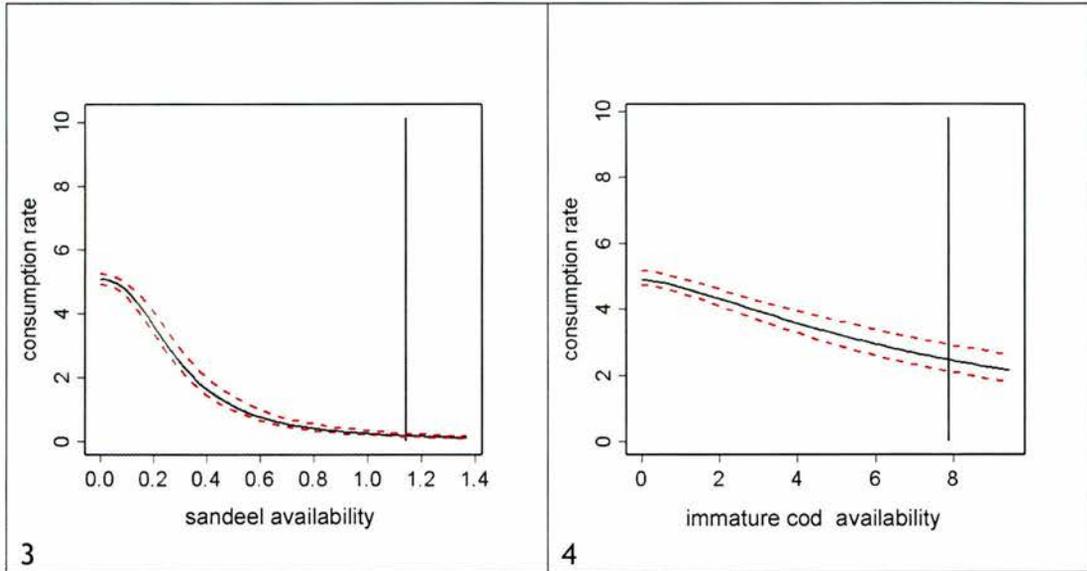


Figure 4.16). This points to the potential importance of variations in sandeel abundance, even where sandeels are themselves not the subject of a major fishery, in influencing potential competition between seals and fisheries on other species.

Figure 4.17 compares the predicted annual consumption of all seven prey classes in the North Sea in 1985 with direct estimates of consumption from the scat samples. Estimated prey consumptions lie within the 95% confidence intervals of the predictions for all prey classes except plaice.

Figure 4.18 compares the predicted consumption by an individual seal of each of the prey classes at the three North Sea sites in 1985 and 2002. Sandeel consumption in 2002 was substantially lower than in 1985, but consumption of immature cod was higher - not because there were more cod available but due to the shortage of alternative prey.

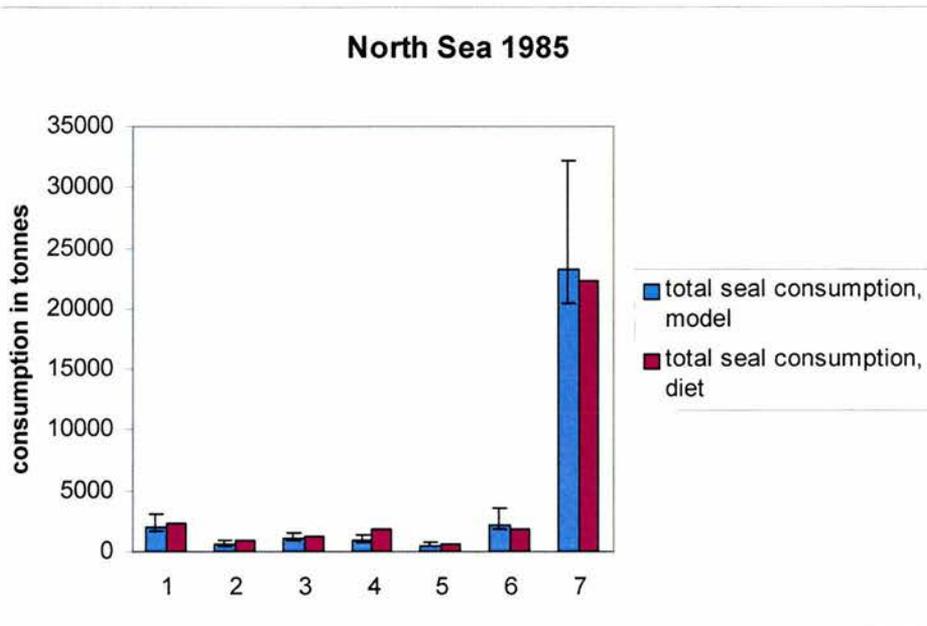
Figure 4.19 and Table 4.9 compare the predicted total annual consumption of cod and sandeels by seals in the North Sea with ICES working group estimates of stock size and annual catch for 1985. Figure 20 and Table 4.10 show the same comparison for 2002.

It appears that seal predation was a larger component of overall mortality for sandeels and cod in 2002 than 1985. For example, seals removed 0.5% of the

**Figure 4.17: Total consumption by North Sea seals estimated from the predictions of Model 2, compared with estimates based directly on scat analysis, in 1985.**

Red bars are consumption estimated directly from diet data, blue bars indicate estimates from Model 2. (The fish species are: 1 = immature cod; 2 = mature cod; 3 = whiting; 4 = plaice; 5 = saithe; 6 = ling; 7 = sandeels).

The error bars represent 95% confidence intervals for the predictions of Model 2. Consumption estimates were recalculated 1000 times based on random draws of parameters from the Markov chain, and confidence intervals were based on the distribution of these estimates.



**Figure 4.18: The Predicted Diet of North Sea seals in 1985 and 2002**

Predicted consumption ( $\text{kg}\cdot\text{day}^{-1}$ ) of seven different prey classes (1 = immature cod, 2 = mature cod, 3 = whiting, 4 = plaice, 5 = saithe, 6 = ling, 7 = sandeels) by individual grey seals foraging from haul-outs in Orkney (ORK), the Farnes and Isle of May (FM) and Donna Nook (DN) during 1985 and 2002

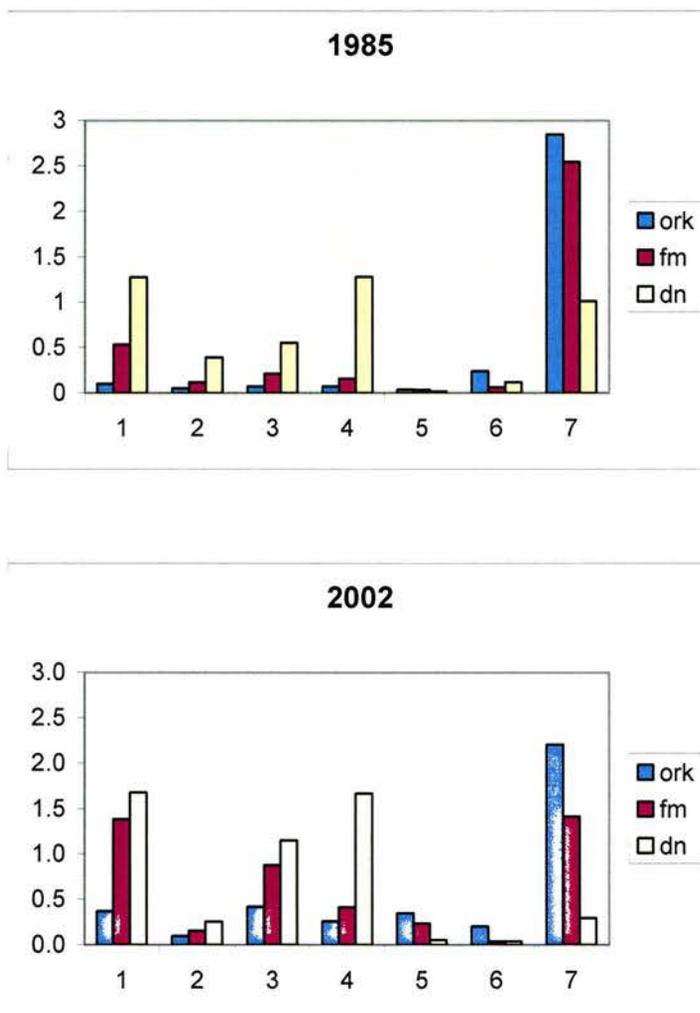
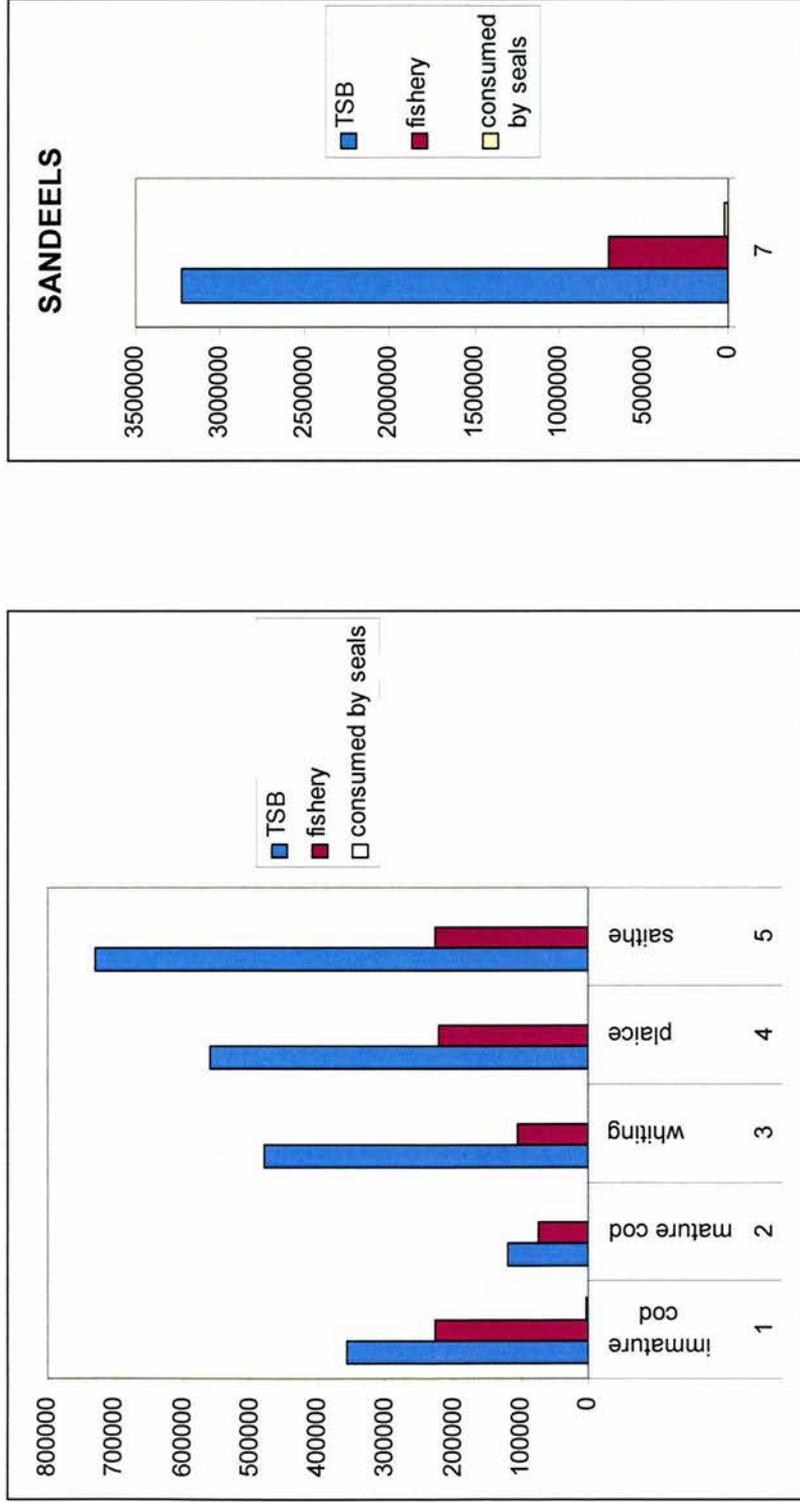


Figure 4.19: Consumption of seven different prey classes by grey seals in the North Sea in 1985 as predicted by a functional response. Total stock biomass (TSB) and commercial landings (“fishery”) are also shown.

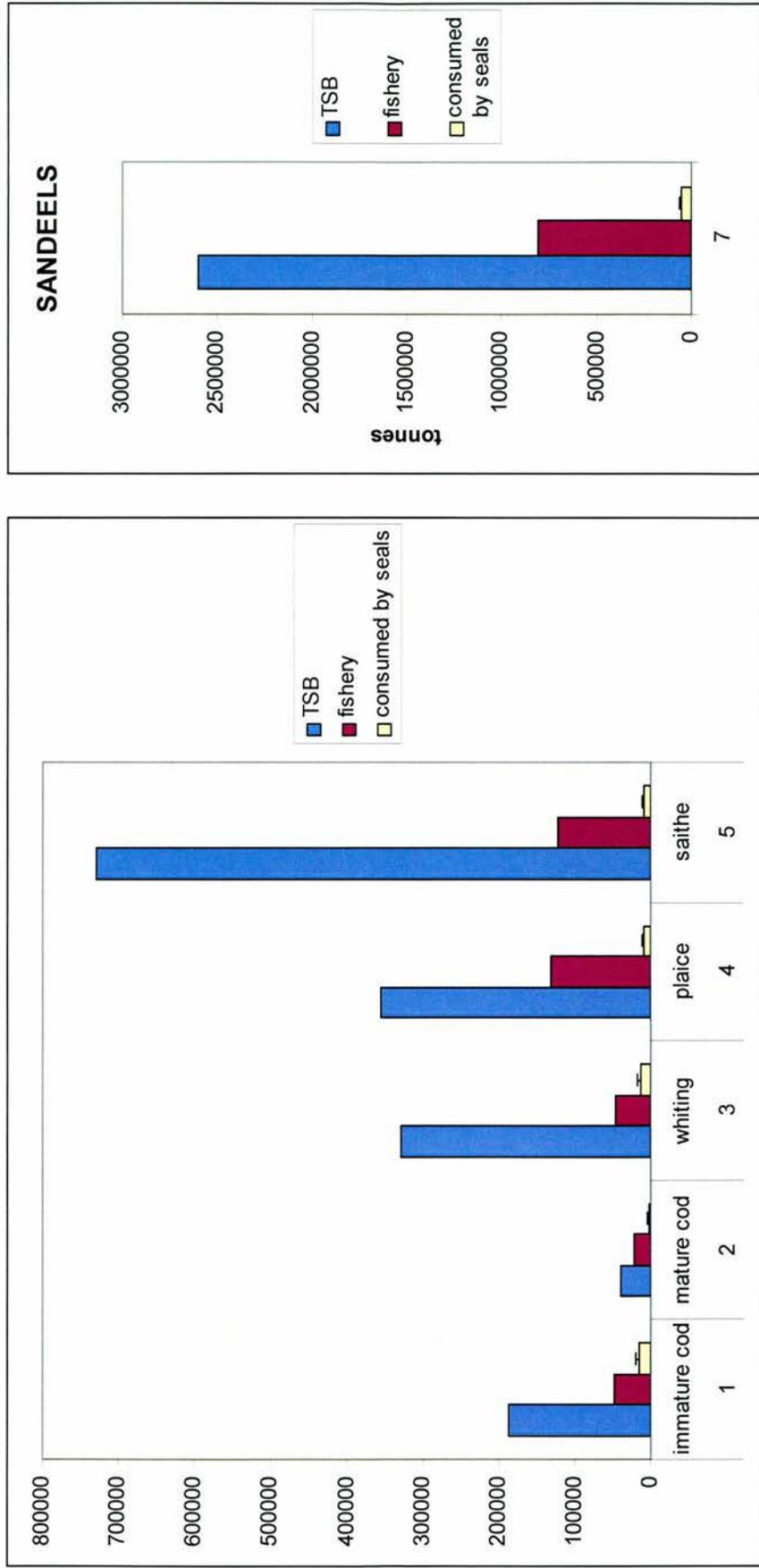


**Table 4.9: Model 2 predictions for 1985**

The annual consumption of fish in the North Sea by all UK seals was estimated based on individual consumptions predicted by model 2, and the population models of Thomas and Harwood (2005).

	fish data from ICES		model predictions	
	TSB	FISHERY	total consumption by North Sea seals (tonnes)	% SEALS/TSB
1	immature cod	356790	225534	0.6
2	mature cod	117996	73266	0.5
3	whiting	479956	106363	0.2
4	plaice	560000	220700	0.2
5	saithe	712000	226129	0.1
7	sandeels	3223488	707105	0.7

Figure 4.20: Consumption of seven different prey classes by grey seals in the North Sea in 2002 as predicted by a functional response. Total stock biomass (TSB) and commercial landings (“fishery”) are also shown.



**Table 4.10: Model 2 predictions for 2002**

The annual consumption of fish in the North Sea by all UK seals was estimated based on individual consumptions predicted by model 2, and the population models of Thomas and Harwood (2005).

	fish data from ICES		model predictions		
	TSB	FISHERY	total consumption by North Sea seals (tonnes)	% SEALS/TSB	
1	immature cod	185381	49414	12853	6.9
2	mature cod	39153	23235	2537	6.5
3	whiting	327488	46552	11787	3.6
4	plaice	355000	130700	7424	2.1
5	saithe	729772	121974	7501	1.1
7	sandeels	2598612	806921	47753	1.8

immature cod biomass in 1985 (equivalent to 7% of the commercial catch), compared with 7% of the biomass (32% of the commercial catch) in 2002.

#### 4.4 Discussion

Using Bayesian methods, consumption data and prey availability data were successfully used to fit a model of diet composition for grey seals, taking account of the uncertainty in prey availability. Estimates of consumption and the uncertainty in consumption were calculated from the posterior distribution of model parameters, on the assumption that the seals' energetic requirements were always met and that the energetic contribution of 'other' prey (i.e. prey not included in the model) was constant.

The consumption model necessarily excluded many important biological details, such as seasonality in energy requirements (Sparling, 2003), differences in diet between males, females and juveniles (Beck *et al.* 2003), and habitat preference (Aarts *in prep.*). Some of this simplification was a consequence of the nature of the data available: a scat sample, for example, cannot be easily assigned to an individual animal with known characteristics such as age. Moreover, the limited quantity of data (21 separate sets of availability and consumption estimates) does not realistically allow for a large number of extra parameters to be fitted. However, one important aim of the exercise was to make inferences about the interactions between the entire seal population and fish stocks, and for this purpose it may be adequate to

model consumption for a 'typical' seal, on a spatial scale that can be reconciled with existing marine ecosystem models.

#### **4.4.1 The choice of prey classes to include in the consumption model**

This choice was based on a simple criterion: only those prey classes that formed more than 10% of the diet in two or more scat collections. This method was based on the suggestion of Yodzis (1998), that it may be acceptable to disregard the weakest trophic links in a food-web, when exploring the outcomes of trophic interactions in a complex community. However, such reasoning could have been applied differently. For example, those prey classes that were most abundant in the diet averaged over all sample sites could have been chosen. Alternatively, all species which formed more than 10% of the diet at one or more scat locations could have been included - this would have resulted in 16 prey classes being included in the model.

An alternative method for tackling this problem is to group prey into sets according to predator preference using cluster analysis (Matthiopoulos, 2000). Such a method is potentially more objective, and allows for the inclusion of prey groupings that include more than one prey species and size class which might represent sets of prey that share niches and are likely to be encountered by seals as an ensemble. However, for this reason, its application resulted in prey groupings that did not correspond to the species categories used in existing multi-species models of the North Sea and because

of potential difficulties incorporating the results of the present modelling work into such models, the approach was not pursued here.

Another approach would be to use reversible-jump MCMC (Green 1995) to explore a range of different consumption models, each containing a different selection of prey classes. RJMCMC should then indicate which model, or set of models, is most plausible. However, this would require substantially larger data sets than were available to this study.

#### **4.4.2 Appropriateness of prey availability data**

The spatial resolution of the prey availability data was generally poor compared with the resolution of the telemetry data that was used to model the way in which seals used the available space (Matthiopoulos *et al.* 2004). For example, the nearest research trawl to a particular scat sample might be as distant as 55km away, and might have been collected 3 months earlier or later in time. In addition, there is known to be high temporal variability in research trawl catches at the same location (Nicholson and Jennings 2004). Fish aggregations can be highly mobile, so that the location of concentrations of fish in any given area may vary rapidly (Harbitz and Lindstrom 2001).

This problem was addressed, at least in part, by using GAMs to interpolate in space and time between the available trawl samples. However, interpolation cannot compensate for missing information. The lack of correspondence in space and time between the diet and prey availability data may account for

the wide confidence intervals on the estimates of consumption for some species, and a noticeably poor fit to the data from some sites, such as Farnes/May in quarter 3 of 1997. In the latter case, a large amount of plaice was consumed although there is no indication that plaice was particularly abundant in the area at the time.

Despite these limitations, correlations were detected between estimated consumption and availability for individual prey species, and a multi-species consumption model was successfully fitted to the data set. The fish survey data that were used to estimate prey availability are still being collected, as are additional data on grey seal diet, thus allowing the model to be updated from time to time.

#### **4.4.3 Estimation of consumption from a functional response model**

Model 1 relied upon the assumption that all seals whose scats were sampled were able to obtain their minimum daily energy requirements. The British grey seal population has been increasing for decades, and is still increasing (SCOS 2005). It therefore seems reasonable to assume that grey seals were able to satisfy their energy requirements in the period covered by this study.

It would have been interesting to use Model 1 to predict how the consumption of grey seals might vary when prey was scarce. However, it was impossible to estimate the parameters of this model with any reliability: the posterior distributions for the attack rate parameter were entirely dependent on the

prior distributions that were used. This difficulty may have arisen because of the strong nature of the assumptions that were made in order to calculate the daily consumption rate of prey.

If the energetic content of the seal's daily food ration is given by  $E_{tot}$ , then the daily energy intake is given by the combined energy obtained from all food items.

$$E_{tot} = \sum_i e_i c_i = \frac{\sum_i e_i a_i N_i^{m_i}}{1 + \sum_j a_j t_j N_j^{m_j}} = \frac{\sum_i e_i a_i N_i^{m_i}}{1 + \sum_j a_j \frac{e_j}{E_{tot}} N_j^{m_j}} \quad (9)$$

where  $e_j$  is the specific calorific content of prey class  $i$

rearranging:

$$E_{tot} \left( 1 + \sum_j a_j \frac{e_j}{E_{tot}} N_j^{m_j} \right) = \sum_i e_i a_i N_i^{m_i} \quad (10)$$

or

$$E_{tot} + \sum_j e_j a_j N_j^{m_j} = \sum_i e_i a_i N_i^{m_i} \quad (11)$$

This will be true only if one or more of the prey items is very abundant, such that

$$E_{tot} \ll \sum_i e_i a_i N_i^{m_i} \quad (12)$$

or

$$1 \ll \sum_i \frac{e_i}{E_{tot}} a_i N_i^{m_i} \quad (13)$$

consumption of an individual prey class  $i$  then becomes

$$c_i \approx \frac{a_i N_i^{m_i}}{\sum_{j=1, \dots, n} a_j \frac{e_j}{E_{tot}} N_j^{m_j}} = E_{tot} \frac{a_i N_i^{m_i}}{\sum_{j=1, \dots, n} a_j e_j N_j^{m_j}} \quad (14)$$

if the values of  $e_j$  are similar, then this becomes

$$c_i \approx \frac{E_{tot}}{e} \frac{a_i N_i^{m_i}}{\sum_{j=1, \dots, n} a_j N_j^{m_j}} \quad (15)$$

i.e. the functional response model approximates to a model based on diet composition and a set total daily consumption ( $E_{tot}/e$ ), in which consumption is determined by the relative rather than the absolute values of  $a_j$  (compare with equation 2).

The values of  $e$  for the seven prey classes included in the consumption models were similar. These values were:

(739, 739, 772, 937, 794, 822 and 1367) Kcal.kg<sup>-1</sup>

This may be why it was difficult to obtain absolute values for the  $a_j$  parameters, while a model of diet composition could be fitted to the data. It

is possible that these parameters could be estimated if more diet data become available.

Model 2, based on diet composition, can be used to model the relative consumption of any subset of prey, because equation (2) will hold true, whatever value of  $n$  (the number of prey classes) is chosen. However, an additional assumption is needed in order to predict absolute consumptions: some value for the total biomass or energy of the modelled prey classes must be set. This can then be apportioned using Model 2. If sufficient prey were included, the total daily energy requirement could be partitioned in this way. However, only seven prey classes were included in the present model, so consumption of 'other' prey was held fixed. The mean mass of 'other prey' from the estimates of diet composition based on the scat samples was 1.28kg, standard deviation 0.763kg. It should be noted that this is a very strong assumption, and is unlikely to hold true particularly if the prey regime around the UK undergoes substantial changes, because seals are versatile generalists.

'Other' prey could be modelled as a separate prey species with assumed constant availability. Exploratory studies of this approach indicated that it did not produce a better fit to the data, because the assumption of constant availability of 'other' results in this prey 'class' having no effect on the consumption of other classes. This difficulty would become less important if more prey classes could be explicitly incorporated into the model.

#### 4.4.4. The importance of priors

It would almost certainly have been possible to fit a full multi-species functional response if more informative priors had been available for even one value of  $a_j$ , because it was reasonably easy to estimate the relative values of the  $a$ 's. Direct observations of seal foraging (e.g. from cameras attached to their heads - see Hooker *et al.* 2002) at different sites and/or in different years might provide sufficient information to set a joint prior on  $m$  and  $a$ , as was done by Asseburg *et al.* (2006).

For Model 2, only relative values of  $a$  were required and these were estimated by fixing  $a$  for sandeels at 1, under the assumption that sandeels were likely to show the highest values of  $a$ . The fitted values for all other prey classes were indeed considerably less than 1, supporting this assumption.

A reasonably informative prior was used for  $m$ , because this was based on experimental data. The MCMC routine did not converge successfully when broader priors were used. It is not entirely clear, however, whether information collected from captive animals is appropriate for use in a model of foraging in the wild. However, the mean and variance of  $m$  obtained from the pool data appear entirely reasonable, both in terms of the underlying model described by the functional response equation (Real 1979) and with regard to the implications for predator/prey dynamics. Planned future work on captive seals which will measure consumption rates over daily timescales

rather than from individual dives and with a wider range of prey species should provide more realistic priors for this parameter.

#### **4.4.5 What the consumption model implies**

##### **4.4.5.1. Seals, fish stocks, and the fishery: point estimates compared with observations**

The diet composition model (Model 2) produced reasonable estimates of North Sea-wide fish consumption by seals (Figure 4.17) and was able to reproduce patterns of consumption estimated directly from the diet data in 1985 and 2002 (Hammond and Grellier *in prep*).

Grey seal predation did not appear to be a major component of the total mortality of immature or mature cod in the North Sea in 1985: seal predation removed far less cod than the cod fishery. However, seal predation was predicted to remove a far greater fraction of stock biomass in 2002, both for cod and sandeels. Cod consumption by individual seals was enhanced in 2002, even though cod availability was significantly reduced, because sandeel availability was also reduced. This is consistent with the properties of the multi-species consumption model illustrated in Figure 4.14.

The proportion of the sandeel stock consumed by seals also increased between 1985 and 2002, even though the consumption of sandeels by individual seals was reduced, because of the increased size of the North Sea seal population.

Model 2 predicts that consumption of any given prey is likely to be strongly influenced by the availability of other prey classes (this point is illustrated in Figures 4.11-4.14 and also Figures 4.15 and 4.16), and sandeel abundance appears to have a particularly strong influence on the consumption of the other prey species in the model (Figure 4.16). Given the poor state of the North Sea sandeel stocks at present, it might be expected that there will be indirect impacts on other prey via seal predation, and probably also as a result of other predators such as seabirds which are likely to change their diet in response to sandeel shortages (Wanless *et al.* 2004, Frederiksen *et al.* 2005).

Figure 4.18 and 4.19 compare model predictions of seal consumption, total stock biomass, and fishery catches for 1985 and 2002. They suggest that, under the present regime of low cod and sandeel availability, there may be some competition between seals and the cod fishery in the North Sea. The biomass of cod removed by seal predation represents about 7% of the stock. Hammond and Grellier (*in prep.*) calculated that grey seals consumed 8.4% of cod biomass in the North Sea in 2002, based on diet samples collected in that year. This suggests that the model may have considerable predictive power and supports the approach used to scale the 1985 local prey availabilities according to stock trends.

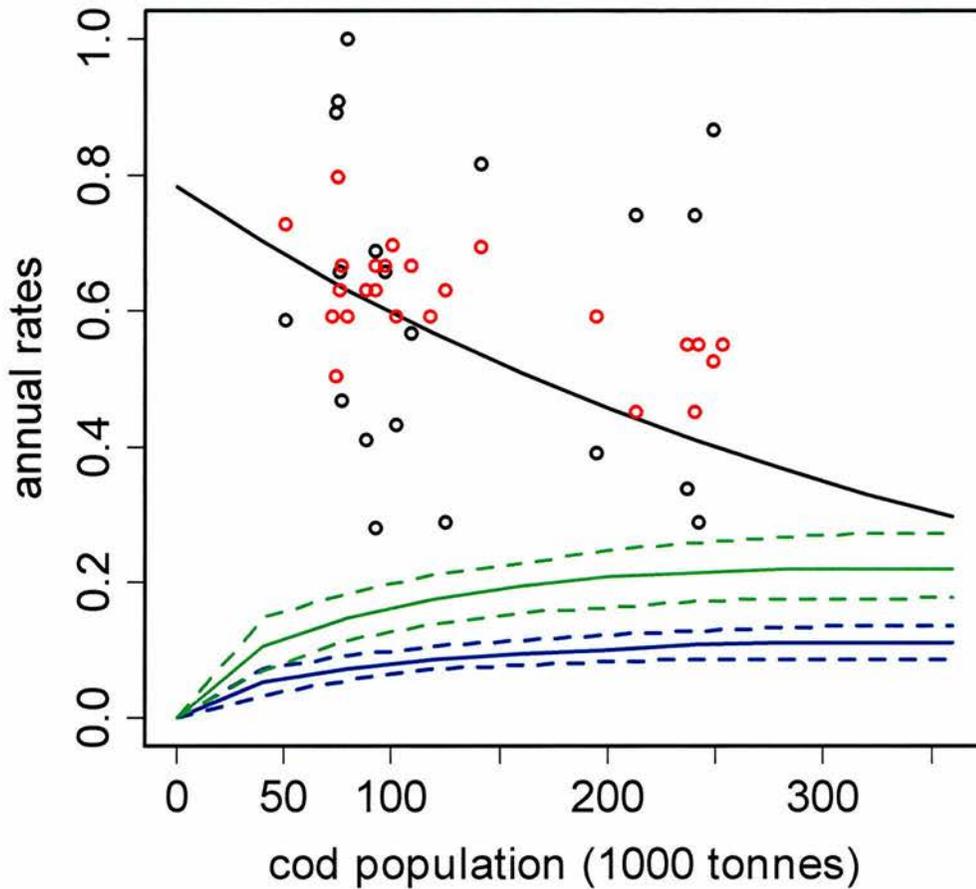
#### 4.4.5.2 Implications for dynamics

All of the fitted values of the shape parameter  $m$  were greater than 1, suggesting that seals show a sigmoidal functional response to all seven modelled prey classes. A sigmoidal functional response implies that prey mortality will increase with prey abundance, when prey abundance is low (Case 1999). In these circumstances, it is possible for the predator and its prey to coexist, although the existence of any equilibria depends also on other factors including the form of density-dependence in the prey population (Sinclair *et al.* 1997). The predicted functional responses are therefore consistent with the observed persistence of seals and their prey in the North Sea ecosystem.

Because of the complexity of the food-web of which seals and fish are part, it is difficult to make strong predictions about the long-term interactions between seals and any one type of prey by examining the consumption model alone. The shape of the mortality curve for any given prey class depends on the availability of other prey, and therefore the abundance of other prey can also be expected to play a part in determining the position and nature of any equilibria - and, this abundance is likely to vary along with the abundance of the focal prey. However, it may be possible to explore the consequences of seal predation for one prey class in a speculative way, by comparing known patterns of recruitment and predicted predation mortality for different stock sizes of cod, while the availability of other prey is held at a fixed level.

In 2002, in general, the stocks of 'other' fish that are important in seal diets were low, including whiting. The seal population was also high, compared to previous decades. Given these conditions, the impact of predation by seals on cod might be expected to be high. Figure 21 was constructed to illustrate the potential impact of seal predation on adult cod (aged 3 years or more) if 'other' prey remained fixed at their 2002 levels. The figure shows that even under these conditions, the impact of seal predation on mature cod is estimated by Model 2 to be less than that of the fishery (assuming that the fishery is expected to react as it has done historically, to changing levels of cod abundance). And, importantly, the level of seal predation appeared to be less than the recruitment of fish into the adult stock, when recruitment was predicted either by the model of Brander and Mohn (2004) or from the VPA. Because Figure 21 was constructed with 'other prey' kept fixed, none of the indirect interactions between seals and their fish prey are represented. For example the figure cannot capture the potentially important effect that seal predation on immature cod might be higher when adult cod are scarce, as a result of seals changing their diet in response to the relative abundance of these two prey items. This diet shift might result in reduced recruitment of juvenile fish into the adult stock, when adults are scarce. To some extent this effect should be represented within the historical data used to calculate the point estimates of recruitment, but recruitment at very low cod stock sizes may not be fully represented in the data as yet, because cod stocks are currently at a historic low.

Figure 4.21: Recruitment and Predation Mortality for Mature Cod



The predation mortality for mature cod was predicted from Model 2 for North Sea seals, with the density of 'other' prey set at 2002 levels. Values for the total population size of the seals were set at the mean values from the models of Thomas and Harwood 2005 (with density dependence operating through pup survival in one model (blue curves), and through fecundity in the other (green curves)). The dotted curves represent the uncertainty (95% confidence intervals) resulting from parameter uncertainty in Model 2.

A model of the stock-recruitment relationship fitted by Brander and Mohn (2004) was used to produce a curve (black) representing recruitment into the adult stock. Recruitment into the year-3 cohort was calculated by re-scaling recruitment into the year-1 age cohort by a factor calculated from the average mass at year 3 produced by one kilogram of year 1 recruits.

Separate estimates of annual recruitment into the age-3 stock were also calculated directly from the ICES VPAs over the period for which VPA estimates are available (1963-2003). These are shown as points in the figure.

Red points represent VPA estimates of fishing mortality from 1980 onwards.

To properly explore the consequences of seal predation for fish stocks, a consumption model would need to be incorporated into a multi-species dynamic model (ICES 2005, Vinther *et al.* 2004) in order to capture all the important direct and indirect interactions between seals and their prey.

#### **4.4.6. Spatial issues**

##### **4.4.6.1: Prey availability, and prey abundance**

One objective of the current study was to produce models of seal consumption that might inform multi-species models for the whole North Sea. Current multi-species models for the North Sea are not spatially explicit. In order to incorporate predation by predators, such as seals, some form of relationship between fish distributions and fish abundance would have to be assumed - for example, that the general distribution of prey is constant and does not change over time, so that abundance in a given area can be calculated simply by scaling the entire distribution surface. (This was the assumption made in order to calculate the estimates of seal consumption in 2002).

GAMs for fish distributions which take account of time predict that redistribution of fish is a significant effect for some of the 7 prey species, and the work of other authors also supports the idea that re-distribution of prey is likely to occur (Blanchard *et al.* 2005). However, given the success of using a time-independent spatial-distribution to estimate prey availability for 2002 in

the example above, the use of a generalised spatial distribution for prey species may be a useful approach and one that could potentially be adopted within a multi-species model for the North Sea.

#### **4.4.6.2. Aggregative responses**

If a predator moves in order to find prey, and is more likely to be found in areas where prey is abundant, then the predator shows an aggregative response, (Turchin, 2000). This can result in a local change in predator numbers over a short time scale, and is distinct from numerical responses which arise from reproduction by the predator. An aggregative response may, like a functional response, be the result of interactions with more than one prey species (Asseburg 2005).

Aggregative behaviour by predators can modify the way in which local prey mortality is related to a predator's functional response, (Gascoigne and Lipcius 2004), and may therefore have an important effect on predator prey dynamics (Graham 2005, Matthiopoulos *et al.* 2006). Seals, like fish, are mobile, and it is possible that seals re-locate between haul-outs in response to changes in prey availability. Even if the overall distributions of individual fish stocks do not change significantly with time, relative changes in fish abundance could trigger the relocation of seals, if the seals show an aggregative response to more than one prey species or a threshold response to one prey. Movement of seals might cause individual consumptions to change, as seals are exposed to a new regime of prey availability in their new

location. If significant numbers of seals move, there may be impacts on the whole-sea scale for consumption of different prey species.

#### 4.5 Conclusions

Two questions provided the motivation for the present study.

1. Given the current poor status of fish stocks, particularly sandeels, is it likely that the survival or fecundity of seals will be reduced in future?
2. Is it likely the seals could prevent the recovery of fish stocks from their present low levels?

It was not possible to fit a full multi-species functional response with the current data, so the energy intake of seals under different regimes of prey availability could not be predicted reliably, and at present no inferences can be made concerning the implications of food availability for UK seal populations. To make such predictions, a full functional response model and further information about the impact of food intake on the life history of seals would be needed

It was possible, however, to predict the potential impact of seals on prey populations subject to the strong assumption that seals are always able to meet their daily energetic requirements. Predictions of the consumption of

cod and sandeels in the North Sea in 2002 appear to be consistent with the preliminary results of a 2002 diet survey.

In order to provide a predictive relationship between seal consumption and fish abundance, local predation by seals which have a limited foraging range around particular haul-outs (Matthiopoulos 2003) must be linked to the overall abundance of fish stocks which mix and migrate on a larger spatial scales. A clear priority is therefore to model the relationship between prey distribution and prey abundance, and to investigate the aggregative responses of grey seals.

## Chapter 5: Modelling prey consumption by minke whales foraging in the Barents Sea - a localised study

### Summary

Minke whales are important generalist predators in the Barents Sea, whose diet includes krill and commercial fish species, such as herring. Folkow *et al.* (2000) estimate that the minke whale population may consume in excess of 200,000 tonnes of fish each year. In order to understand the role of these important predators in the ecosystem and their impact on fish stocks, it is important to model how their consumption varies in response to the availability of prey: that is, their multi-species functional response (MSFR).

During a study off the north Norwegian coast, consumption by minke whales was estimated from the stomach contents of captured whales (Lindstrom and Haug 2001). Prey abundance was determined from acoustic surveys conducted in a localised area around the point of capture. Although only stomach contents less than 2 hours old were used to estimate the whales' diets, the precise foraging locations of the whales prior to capture were unknown. Therefore, a spatial sampling approach was developed to estimate the density of prey experienced by the whales during the feeding period represented by the stomach contents data, and the uncertainty in this value. An MSFR was fitted to the prey-abundance estimates and the consumption-rate data using Bayesian methods. The parameter estimates for this function depended on what assumptions were made about whale movement, suggesting that further data on whale speed and typical foraging movements are required if consumption by minke whales is to be estimated

reliably. On the localised scale of this study, minke whales show a sigmoidal functional response to herring, capelin and krill.

A model that takes account of all important trophic interactions is required if the commercial and conservation impacts of fishing and whaling on the Barents Sea ecosystem are to be predicted reliably. MSFRs, such as the one derived here for minke whales, should be a fundamental part of such a model. The parameter values estimated here for the minke whale MSFR could either be included directly in such a model or they could be used to provide informative prior distributions to assist in fitting the entire model using Bayesian techniques. In either case, predator-prey overlap must be modelled on an appropriate spatial scale.

## 5.1. Introduction

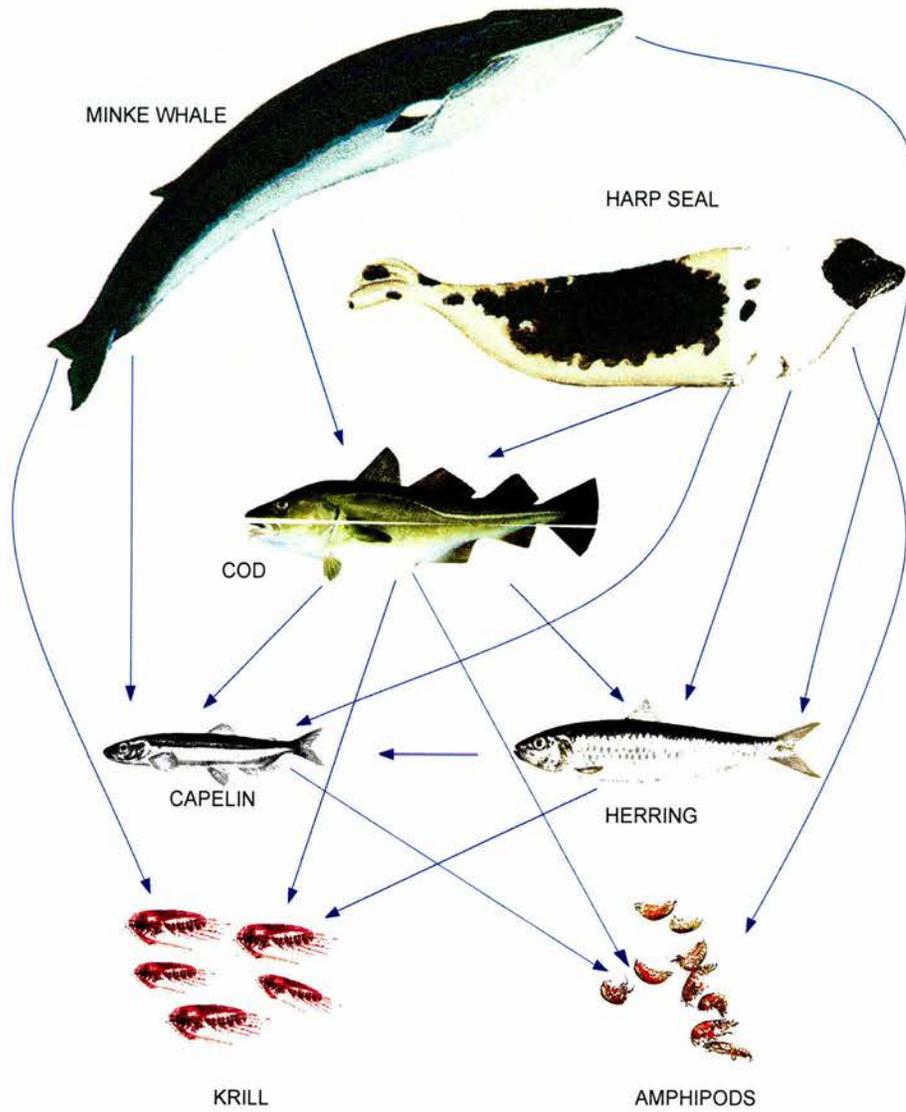
### 5.1.1 The Barents Sea ecosystem

The Barents Sea is a large, productive, shallow shelf sea with a relatively simple trophic structure (Figure 5.1). Bogstad *et al.* (1997) took advantage of this simple structure to develop a mathematical model of the Barents Sea ecosystem that could be used to provide advice on the management of its commercial fish stocks. Two of the most important commercial species (capelin and herring) underwent extreme fluctuations in the 1980s and 1990s (Hjermann *et al.* 2004).

The world's largest capelin stock is found in the Barents Sea (Hjermann *et al.* 2004), where they are an important prey for higher predators, such as harp seals, minke whales and cod. Off the Norwegian coast, capelin spawn just once, at between 2 and 5 years of age, in April. During summer, capelin move northwards to feed, and during winter, their distribution is more southerly.

The size of the Barents Sea capelin stock has fluctuated considerably during recent decades (Figure 5.2). Major stock collapses occurred in the 1980s and 1990s, reducing the total capelin biomass by more than 95%. The exact cause of these fluctuations is still a matter of controversy but it is likely that overexploitation during the 1970s was a major factor in the first of these population declines, whereas predation by an unusually large year-

MULTISPECIES INTERACTIONS  
IN THE NORWEGIAN SEA - BARENTS SEA ECOSYSTEM



**Figure 5.1: the Barents Sea Foodweb**

(picture supplied by Bjarte Bogstad)

## Capelin and Herring

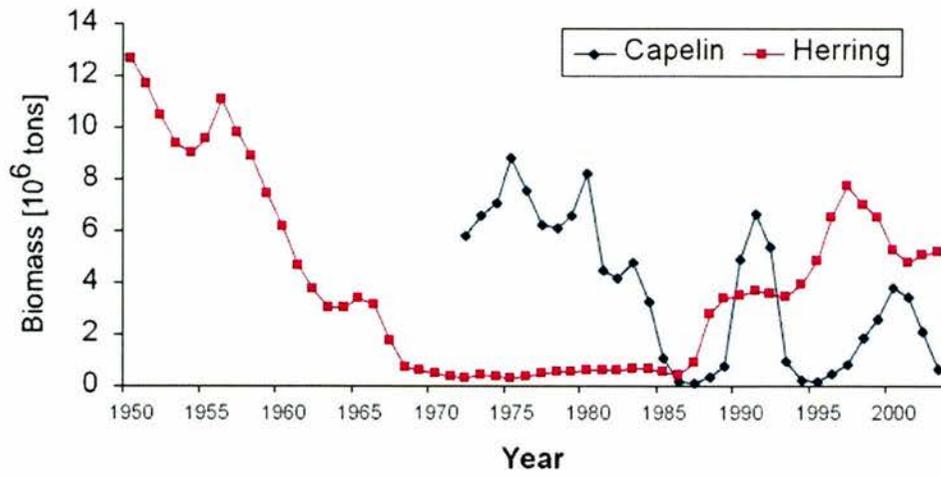


Figure 5.2: fish stocks in the Barents Sea

class of young herring may have been a more significant factor in the 1990s collapse, (Hjermann *et al.* 2005).

The biomass of the Norwegian spring-spawning herring stock, for which there is a substantial fishery, can be very large, sometimes exceeding 10 million tonnes. Adult herring over winter inshore off northern Norway and in the fjords around the Barents Sea. They move south to spawn off the north-west coast of Norway in April, and spend the summer feeding in the North Sea. Their larvae drift north into the Barents Sea, where immature herring remain until they are 2-4 years old.

Environmental factors are important in determining recruitment to the herring stock, and exploitation has a significant top-down effect (Hjermann *et al.* 2005). A combination of over-fishing and poor recruitment caused a significant population decline during the 1960s, with low stock sizes persisting until the 1980s (Figure 5.2). Stock size then increased, as a result of several years of strong recruitment, to the present level of about 5 million tonnes (Tjelmeland and Lindstrom 2005).

The biomass of krill and other zooplankton in the Barents Sea peaks in summer, in response to a predictable phytoplankton bloom that results from changes in temperature, flows of water into the Barents Sea from outside and the melting of sea-ice. There is substantial among-year variation in zooplankton biomass which appears to be due, at least in part, to fluctuations in these abiotic factors. There is some evidence for top-down

control by capelin (Dalpadado and Skjoldal 1996, Gjosaeter *et al.* 2002). Accumulations of zooplankton at ocean fronts may be responsible for the observed aggregations of fish and marine mammals in particular regions of the Barents Sea (Joiris 2000).

The Northeast Atlantic stock of minke whales appears to be a genetically distinct population (Anderson *et al.* 2003), numbering about 107,000 individuals at present (Skaug *et al.* 2004) - see Figure 5.3. Of these, about 40,000 are resident in the Barents Sea between May and August. They gain weight during this time, especially during the later part of the summer (Haug *et al.* 2002). Their distribution during winter, when calves are born, is not well known, but minke whales have been observed as far south as Mexico and Bermuda at this time of year.

During the summer, the distribution of whales appears to vary in response to shifts in prey aggregations, which themselves are probably driven by regular seasonal changes in temperature and ocean circulation (Joiris 2000).

However, data from whaling logbooks and dedicated surveys (Skaug *et al.* 2004) suggest that this distribution may shift from year to year. Their most important prey, at this time, are krill (*Thysanoessa* sp. and *Meganyctophanes novogica*), capelin (*Mallotus villosus*), herring (*Clupea harengus*), and gadoids. Capelin are a particularly important prey item for adult female minke whales.

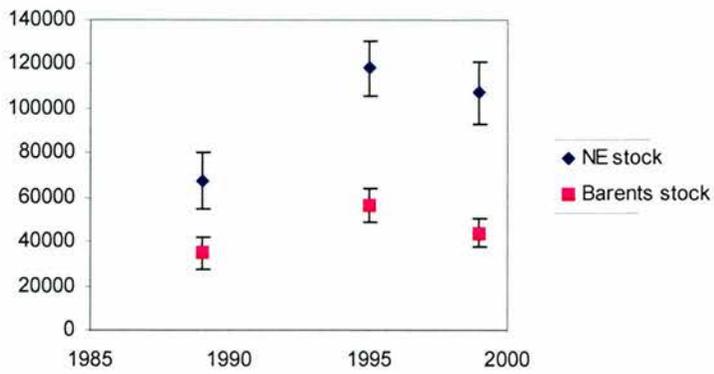


Figure 5.3: whale abundance in the North-East Atlantic and in the Barents Sea, estimated from boat-based surveys (Skaug et al 2004).

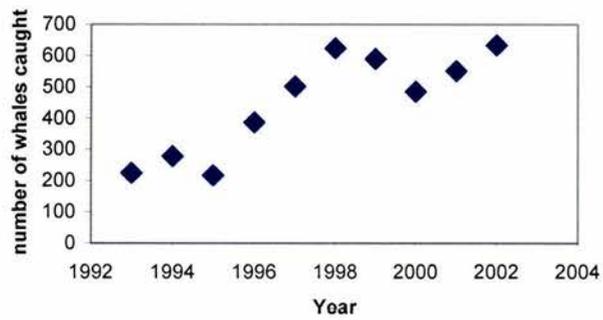


Figure 5.4: Annual Norwegian catch of minke whales in the Barents Sea

Within the Barents Sea, and elsewhere, minke whales appear to adapt their diet according to prey availability: substantial changes in the diet of whales have been observed, from year to year, with consequent changes in body condition (Haug *et al.* 2002, Haug *et al.* 1995, Kasamatsu and Tanaka 1992). Prey preferences also appear to vary both locally, and between different regions of the Barents Sea. One way to model these variations is through a multi-species functional response (MSFR) that predicts how consumption is expected to vary in response to changes in the abundance of all prey species. An MSFR also summarises the available information on predator preference and consumption rates, provides predictions of the nutritional consequences for whales of changes in prey availability and, when applied at the correct spatial scale, can be used to investigate the potential impact of predation on prey dynamics.

### 5.1.2 Of whales and men

Commercial whaling in the Barents Sea is carried out under catch quotas set by the Norwegian government using the catch limit algorithm (CLA) which forms part of the revised management procedure (RMP) of the International Whaling Commission (IWC 2004). The CLA is designed to minimize the risk of extinction for cetacean populations. Factors included in the analysis are uncertainties in stock assessments, carrying capacity, stock structure and catch. Yearly Norwegian catches are shown in Figure 5.4.

Folkow *et al.* (2000) calculated that an individual minke whale can consume approximately 90kg of fish per day in the summer months, and that the

Barents Sea minke whale population may take 200,000 tonnes during one season. This figure can be compared with, for example, the  $3 \times 10^6$  tonnes of fish taken annually by the capelin fishery during the 1970s. Such a high level of predation may have a significant impact on fish stocks. For example, Tjelmeland and Lindstrom (2004) calculated that minke whales might be responsible for approximately 50% of the natural mortality of adult herring, and 10% of the mortality for immature herring in the Barents Sea. Folkow *et al.* (2000) argue that minke whales may have a significant economic impact on commercial fisheries in the Barents Sea. This raises two questions about the multispecies management of fisheries in the Barents Sea.

- a) How can the harvesting of whales and commercial fish stocks be managed, in order to maximize profits for the interested parties?
- b) How should whales and fish be harvested, in order to conserve stocks of both fish and marine mammals?

Developing an understanding of the MSFR of minke whales is an important step towards answering these questions, because this MSFR can be used to predict consumption by minke whales under different regimes of prey availability. This consumption can then be used to estimate the consequences of changes in prey availability for whale life history and prey mortality.

### 5.1.3 The minke whale functional response, and multi-species models of the Barents Sea

If prey distributions are uniform, predator numbers are constant or predictable, and the functional response of a predator is known, then it may be possible to draw some general conclusions about predator-prey dynamics. For example, it may be possible to identify whether minke whales can maintain one or more prey species at a stable low-density equilibrium (Holling 1965, Hilborn and Walters 1992). However, even in this simplified situation, the form of the functional response is not sufficient, on its own, to predict whether or not such a low-density equilibrium will actually occur (Sinclair and Krebs 2002).

Simplified dynamic models that explore the interaction between one predator and one prey, with 'other prey' kept at fixed values, may be useful if it can be assumed that the predator shows no numerical or large-scale aggregative response to prey. Simple models may have the advantage that relatively few assumptions are made about the biological interactions in the system and the number of parameters that have to be fitted to data is more manageable (Tjelmeland and Lindstrom 2004). However, if predator and prey populations are to be modelled realistically, over longer time scales, it is more appropriate to employ multi-species models with all the implied demands for data. One way to assemble such models is to parameterise individual sub-models with independent data sets.

Multi-species models of systems such as the Barents Sea ecosystem sometimes point to unexpected consequences of multi-species trophic interactions. Bogstad *et al.* (1997) used such a model to investigate the effects of predation by minke whales and harp seals on the dynamics of fish stocks in the Barents Sea. The Barents Sea was divided into discrete areas, with migration of predators and prey between these areas modelled using movement matrices based on observed historical distributions of whales and fish. Trophic interactions of the whales were described by a multi-species consumption model similar to the one parameterised for grey seals in chapter 4, in which the whales always satisfied their daily energetic requirements, and the composition of the diet was determined by the relative abundance of prey - a form of hyperbolic or type 2 MSFR, with parameter values that were either assumed or derived from first principles. This model predicted that complete removal of minke whales from the system would result in the herring population increasing. However, as a consequence, capelin decreased due to increased predation on capelin eggs by juvenile herring. Cod numbers were predicted to remain unchanged, due to the contradictory effects of reduced predation by marine mammals and decreased capelin availability. The results were more sensitive to changes in cod food preferences, defined as parameters of the cod MSFR, than changes in the abundance or food preferences of marine mammals. These results indicate not only that the impact of minke whales on commercial fish stocks may be less than is generally supposed, (Yodzis 2000), but also that the parameter values of an MSFR have important consequences for the performance of multi-species models. MSFR parameters should therefore be

determined in the most objective way possible. In addition, uncertainties associated with these parameter estimates need to be accounted for, because they may significantly effect model predictions and management recommendations.

Schweder *et al.* (2000) developed a multi-species model of the entire Barents Sea in which they represented consumption by a modified logistic function, which took into account the fact that the distributions of capelin and cod tend to be spatially correlated. This consumption sub-model was parameterised using a maximum likelihood fit to data on the diet composition of minke whales and harp seals, and prey availability. In contrast to Bogstad *et al.* (1997), they predicted that minke predation has a negative impact on catches of both herring and cod. They point to two key differences that may account for the different predictions of the two models: their model incorporates a response in fishing effort to the availability of commercial fish, and uses a different form for the minke whale consumption function. This again demonstrates the central importance of MSFR modelling and parameterisation for the outcome of multi-species models.

Tjelmeland and Lindstrom (2005) used an MSFR based on the work of Real (1977) to incorporate predation by minke whales on herring and other prey (capelin and krill) into a herring stock assessment model. Maximum consumption rate by minke whales was determined using a size-based model of their energetic requirements. The availability of minke whales and their

other prey was set to fixed values using historical data. The model did not, therefore, allow for any numerical response by the whales, and their other prey was not depleted. The fit to whole Barents Sea herring abundance was used to determine the MSFR parameters, and a sigmoidal FR was predicted for all three prey species.

An MSFR fitted to independent data on prey availability and consumption can be used as a sub-model in a multi-species ecosystem model.

Alternatively, the parameter distributions found by fitting the MSFR to independent data could be used to provide informative prior distributions to assist in fitting a Bayesian ecosystem model to abundance data, (Harwood and McLaren 2004). Given that fitting an MSFR may therefore be a valuable exercise, what data are available concerning minke whale diets and consumption rates, which might allow for parameterisation of an MSFR?

#### **5.1.4 The diet of whales**

Minke whales have a global distribution, and over this range, they forage on a wide variety of prey. Different subpopulations appear to have different diets. For example, minke whales in the Antarctic forage almost exclusively on krill (Kasamatsu and Tanaka 1992) while, within the North Sea, minke whales consume large quantities of sandeels (Pierce *et al.* 2004). In the Barents Sea, minke whales feed on herring, capelin, krill, and gadoids. The diet of minke whales within the Barents Sea also varies by season, and from place to place, presumably as a result of the changing availability of prey (Haug *et al.* 2002).

Between-year variations in diet at the scale of the entire Barents Sea appear to be correlated with changes in the size of the herring stock (Haug *et al.* 2002). However the correlation between minke whale diet and the abundance of other prey species, such as capelin and cod, is less strong (Haug *et al.* 2002). This may well be a consequence of the non-uniform spatial distribution of prey and the aggregative response of minke whales to prey concentrations within the Barents Sea. Such spatial effects will result in a complex relationship between regional stock sizes and local prey availability. It may therefore be difficult to model the functional response of minke whales successfully on a whole-ocean scale.

Lindstrom and Haug (2001) investigated prey choice by minke whales in a more localised study, based in the southern area of the Barents Sea. They compared prey consumption and availability in four areas, each approximately 100n.mile square, and showed that whales are selective in their choice of prey using Chesson's preference index (Chesson 1978). This could be the result of a preference for food containing particular nutrients or with a high energetic value, the ease or efficiency with which whales can capture the preferred prey, or the ease with which certain prey species can be detected. Minke whales appear to feed mostly in the upper layers of the ocean, and this may result in a preference for those prey species (krill, capelin, and herring) that occur in this stratum over benthic species, such as gadoids. Prey preference also varied among foraging areas. These changes

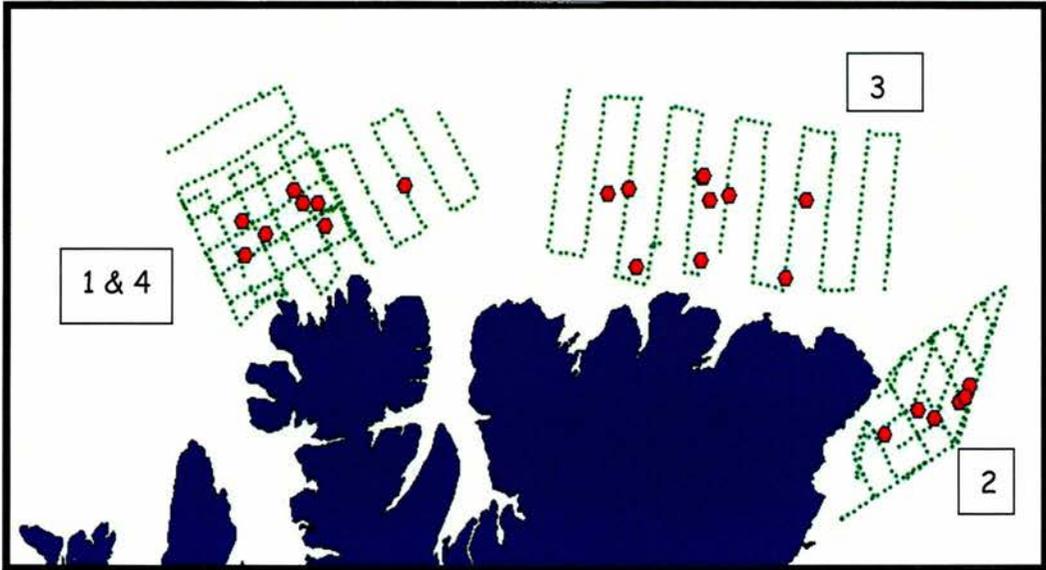
could be the result of optimal foraging behaviour or a sigmoidal MSFR, of the form found by Tjelmeland and Lindstrom (2005).

Lindstrom and Haug's (2001) data set was collected to investigate changes in preference, but it can also be used to estimate the parameters of an MSFR (Asseburg *et al.* 2006). The prey abundance data were closely matched in time and space with predator foraging, and were collected on a sufficiently local spatial scale that some of the properties of the foraging behaviour of whales may be discernible in the relationship between consumption and prey availability. This chapter describes the results of fitting an MSFR to these data.

## **5.2. Methods**

### **5.2.1 Data collection**

Lindstrom and Haug (2001) analysed the stomach contents of minke whales captured by the commercial whaling fleet off the north Norwegian coast during May-June 1998. Prey abundance was then determined from five acoustic surveys conducted within 24 hours of capture in a localised area around each point where a whale was captured (Harbitz and Lindstrom 2001). Abundance measurements were averaged over each n.mile of transect (Lindstrom and Haug 2001). The locations of whale captures and prey-survey transects are shown in Figure 5.5.



**Figure 5.5: Prey surveys and whale captures**

Locations of whale captures are shown in red. Positions of point averages, at 1 n.mile spacing, from the acoustic prey abundance surveys are shown in green. Areas 1-4 are labelled: areas 1 and 4 overlap, but area 1 was surveyed earlier than area 4.

Consumption rates were estimated based on the contents of the fore-stomachs. Food remains were extracted, sieved, identified, weighed, and classified according to digestion state. More details of the procedures used are given in Haug *et al.* (1995). Only fresh stomach contents were used in the analysis, otoliths and other partly-digested remains were not included in order to avoid biases due to differential passage rates of these items (Lindstrom *et al.* 1997). Fresh stomach contents were assumed to represent food consumed within the past 2 hours, based on *in vitro* digestion studies (Nordoy *et al.* 1993). After an initial examination of the stomach data, I decided to focus on the consumption of three prey species: capelin, herring and krill. Gadoids sometimes occur in minke stomachs in large quantities but only one stomach in this study contained significant quantities of fresh gadoids. The biomass of the three prey types found in the stomachs is shown in Appendix 2. Prey were classified on the basis of species only and not sorted into size classes, following the findings of a previous study by Lindstrom and Haug (2001), which indicated that whales do not select prey according to size.

### **5.2.2 The availability of prey to the whales:**

#### **Modelling whale movement as a random walk**

The precise foraging locations of the whales prior to capture were unknown. Potentially a whale can travel more than 5 n.miles during a 2 hour period and the availability of prey, as measured by the acoustic surveys, varied

substantially on this scale, resulting in considerable uncertainty as to what prey densities any given whale may have experienced. I therefore modelled whale foraging movements to provide a more appropriate measure of prey availability. The following assumptions were made:

- The direction of movement of a foraging whale is random, so its movements can be approximated by a random walk and the distribution of whale locations prior to capture can be estimated using a diffusion model with a Gaussian kernel centred on the point of capture (Turchin 1998).
- Fresh food in the whale stomachs was derived from one discrete foraging episode during the 2 hours prior to capture (Nordoy 1993).

The available data on minke whale movement patterns has mainly been collected by observers based on boats. It is known, for example, that minke whales in Canada return repeatedly to favoured foraging areas and may remain in such areas for some time (Piatt and Methven 1992). However, details of movement within the foraging area, such as average speed and range, are not well known. Minke whales have been observed to travel at high speeds of up to 20 n. miles.  $\text{hr}^{-1}$  for short periods (Lindstrom, pers. com.), but it is unlikely that they sustain such speeds while foraging. Two movement kernels were used

1. The first kernel was based on telemetry data collected by Nordoy *et al.* (2003) from three minke whales tagged in the Barents Sea. Only one animal was tracked successfully over a 31 day period, giving 1.58 uplinks

per day on average. Data from those parts of the tracks that, according to the authors, represented foraging periods, were used to estimate the area that would correspond to a 2-hour period of foraging. Assuming that the foraging movements could be approximated as a random walk, the extent of the re-scaled area was calculated as follows:

The diffusion equation can be written

$$\sigma^2 = Dt \quad (5.1)$$

Where  $\sigma$  represents the width (standard deviation) of the gaussian kernel,  $D$  is the diffusion coefficient, and  $t$  is time.

The diameter of the foraging region of the tagged minke whale was estimated to be 80 n.miles. Assuming that 95% of the foraging took place within this region, then

$$80 \text{ n.miles} = 4\sigma$$

And the corresponding diameter over a 2 hour period would be 7.3 n.miles, giving

$$\sigma = 1.83 \text{ n.miles}$$

2. A widely-used estimate of 'average' whale speed is  $5 \text{ km.hr}^{-1}$ , (Lindstrom, pers com). This was used as the basis for a second kernel, where 95% of whale movements would have occurred within 5km of the point of capture, with  $\sigma = 2.5 \text{ n.miles}$ .

### Spatial models of prey abundance

In order to generate estimates of the abundance of prey available to whales based on the two kernels, it was necessary to model prey distributions over a continuous surface in the areas surrounding whale captures.

Interpolation was carried out using Generalised Additive Models (GAMs), which were fitted to the point estimates of abundance using the statistical package R (R Development Core Team 2005). This method of spatial smoothing was chosen because, unlike some other standard smoothing techniques such as kriging, (Rivoirard and Simonds 2000), a suitable choice of statistical distributions for comparing model predictions and biological survey data is readily available using the mgcv package (Wood and Augustin 2002, Venables and Dichmont 2004). Cartesian co-ordinates, rather than latitude and longitude, were used as covariates (Augustin *et al.* 1998). A square-root link function and over-dispersed Poisson error distribution were chosen (Venables and Ripley 1999). A separate GAM was fitted for each survey area, and for each prey species. Although the GAMs could be used to predict prey abundance at any given point, each GAM was only applied within the area defined by the distribution of prey data (i.e. the convex hull of the survey data), henceforth referred to as the 'prediction area'. Prey density outside the prediction area was set to the mean prey density within the area.

### Modelling encounters with prey

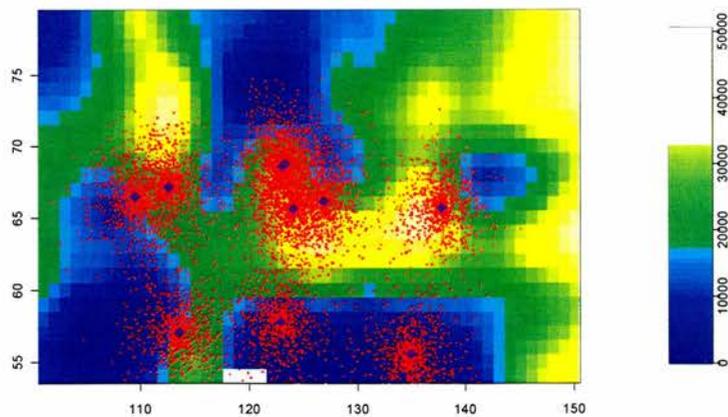
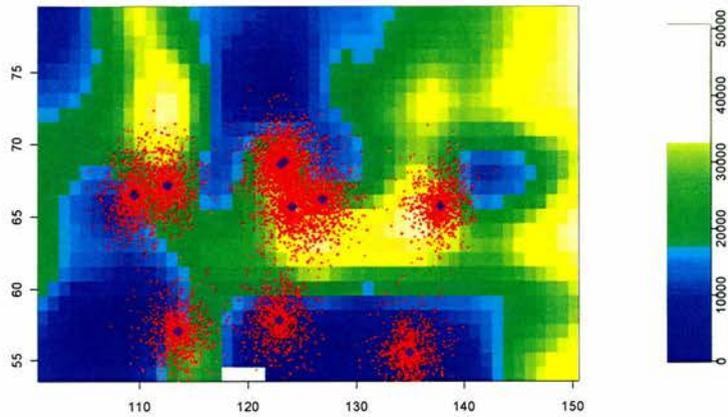
The abundance of each prey type in the area likely to be visited by each of the whales prior to capture was then sampled from the smoothed prey abundance surfaces, using the following algorithm (see also Figure 5.6):

1. Set the point of capture as the centre of the movement kernel;
2. Draw a distance value at random from the Gaussian kernel;
3. Chose a random direction for the whale to move;
4. Calculate the abundance of each prey species from the relevant GAM at the unique point defined by 1, 2 and 3;
5. Repeat this process 1000 times to provide a statistical distribution of prey abundance for each prey type and for each whale.

This process produced two sets of sampled prey abundances for each whale, one for each kernel. Only a small proportion (<1% for kernel 1; <2% for kernel 2) of the sampling points fell outside the boundaries of the prediction area.

## Figure 5.6: Spatial sampling of prey distributions.

The map shows the abundance of krill in area 3, plotted over a grid of 1 n.mile squares. Positions of whale captures are shown in purple, and randomly sampled points in red. Upper figure: Model 1, kernel width=1.8n.miles. Lower figure: Model 2, kernel width=2.5n.miles.



### 5.2.3 The MSFR model

The chosen MSFR model was based on the multi-species version of the function proposed by Real (1977):

$$C_i = \frac{\alpha_i N_i^{m_i}}{1 + \sum_{j=1}^s \alpha_j t_j N_j^{m_j}} \quad (5.2)$$

Where

$C_i$  represents consumption rate of prey type  $i$

$N_i$  represent the abundance of prey type  $i$

$t_j$  is the handling time for prey  $i$

$\alpha_i$  represents an 'attack rate parameter' that relates the attack rate to the density of prey

$m_i$  is a 'shape' parameter which determines the form of the single-species conditional form of the functional response.  $m=1$  gives a hyperbolic functional response, and  $m>1$  gives a sigmoidal functional response.

This equation was re-parameterised using the following relationships:

As  $N_i$  tends to infinity, the value of  $C_i$  tends towards  $1/t_j$ . This is easiest to see for the single species case, but it is also true for the multi-species case.

This asymptotic value is the parameter  $cmax_i$ ; the maximum consumption rate for prey  $i$ .

In the single species case, it can be shown that the consumption rate for prey  $i$  will be half its maximum value, ( $c_{max_i}/2$ ), when

$$N_i = N_{half_i} = m_i \sqrt{\frac{1}{t_i \alpha_i}} \quad (5.3)$$

$N_{half_i}$  is then the 'half-saturation' prey density, for the single species case

Using these relationships, equation 5.2 becomes :

$$c_i = \frac{c_{max_i} \left( \frac{N_i}{N_{half_i}} \right)^{m_i}}{1 + \sum_j \left( \frac{N_j}{N_{half_j}} \right)^{m_j}} \quad (5.4)$$

Where

$c_i$  represents the consumption rate for prey species  $i$ , in kg per hour

$N_i$  represents the availability of species  $i$  to the whale, in tonnes per km<sup>2</sup>

$m_i$  is a shape parameter which sets the shape of the functional response.

$N_{half_i}$  is the half-saturation value for prey availability (tonnes per km<sup>2</sup>)

$c_{max_i}$  is the maximum consumption rate in kg per hour

This re-parameterisation was convenient for comparing the fitted parameters with those used in the fisheries literature, and had some numerical advantages for the fitting procedure because all the parameters were expected to have reasonably-sized values, and did not tend towards zero.

For simplicity, all whales were assumed to have identical MSFRs, and were not divided into age or sex classes (Haug *et al.* 1995).

#### 5.2.4 Fitting the model

The model was fitted using a Monte Carlo Markov Chain (MCMC) algorithm, implemented in WinBugs (Gelman 1995). Prior distributions were chosen as follows.

##### ***c<sub>max</sub>***

Based on measurements of the undigested food in 400 minke whale stomachs, the mean and coefficient of variation of *c<sub>max</sub>* was estimated for the three prey species using bootstrap re-sampling (Lindstrom, pers com).

Assuming that food remained in the stomach for 2 hours only, *c<sub>max</sub>*, (maximum consumption rate), was then calculated as

$$c_{max} = \frac{\text{maximum stomach content}}{2}$$

Gamma priors were used for the values of *cmax*, with the shape and rate parameters adjusted so that the distribution had the appropriate mean and cv, i.e.

$$\text{rate} = \frac{1}{\text{cv}}$$

$$\text{shape} = \text{mean} \times \text{rate}$$

Table 5.1 shows the resulting values.

### ***Nhalf***

No data were available to inform priors in *Nhalf*, so broad priors that included the full range of prey abundances derived from the spatial sampling were used. Table 5.2 shows the values used.

### ***m***

Priors for *m* were based on the results of Tjelmeland and Lindstrom (2005). The full parameter distributions that resulted from their analysis were not available, so gamma priors, which had the same mean and cv, were used, (see Table 5.3).

### ***Prob.eat***

There were a large number of observations of zero consumption, i.e. empty stomachs indicating that animals had not recently fed. This was modelled by calculating predicted consumption based on MSFR, and then multiplying this

**Table 5.1: Priors for  $C_{max}$** 

The mean and variance of maximum stomach content were obtained by bootstrapping over the stomach data set. These were used to set the shape and rate parameters for gamma priors, for each prey species in the model.

	Mean of maximum stomach content (kg)	cv	Gamma shape	Gamma rate
Capelin	105	3.3	31	0.30
Herring	44	2.9	15	0.34
Krill	52.5	1.7	30	0.59

**Table 5.2: Priors for  $N_{half}$** 

	Mean $N_{half}$	cv	Gamma shape	Gamma rate
Capelin	30000	10000	3	0.0001
Herring	30000	10000	3	0.0001
Krill	60000	20000	3	0.00005

**Table 5.3: Priors for  $m$** 

	Mean $m$	cv	Gamma shape	Gamma rate
Capelin	3.79	0.05	75.80	20.00
herring	1.94	0.10	19.40	10.00
krill	3.15	0.09	35.00	11.11

value by 1 or 0, based on a random draw with probability *prob.eat*, which was then treated as a parameter to be estimated by the MCMC.

An uninformative prior was set on the quantity *prob.eat*

$$0 \leq \text{prob.eat} \leq 1$$

Figure 5.7 shows the prior distributions for *cmax*, *Nhalf* and *m* for each species.

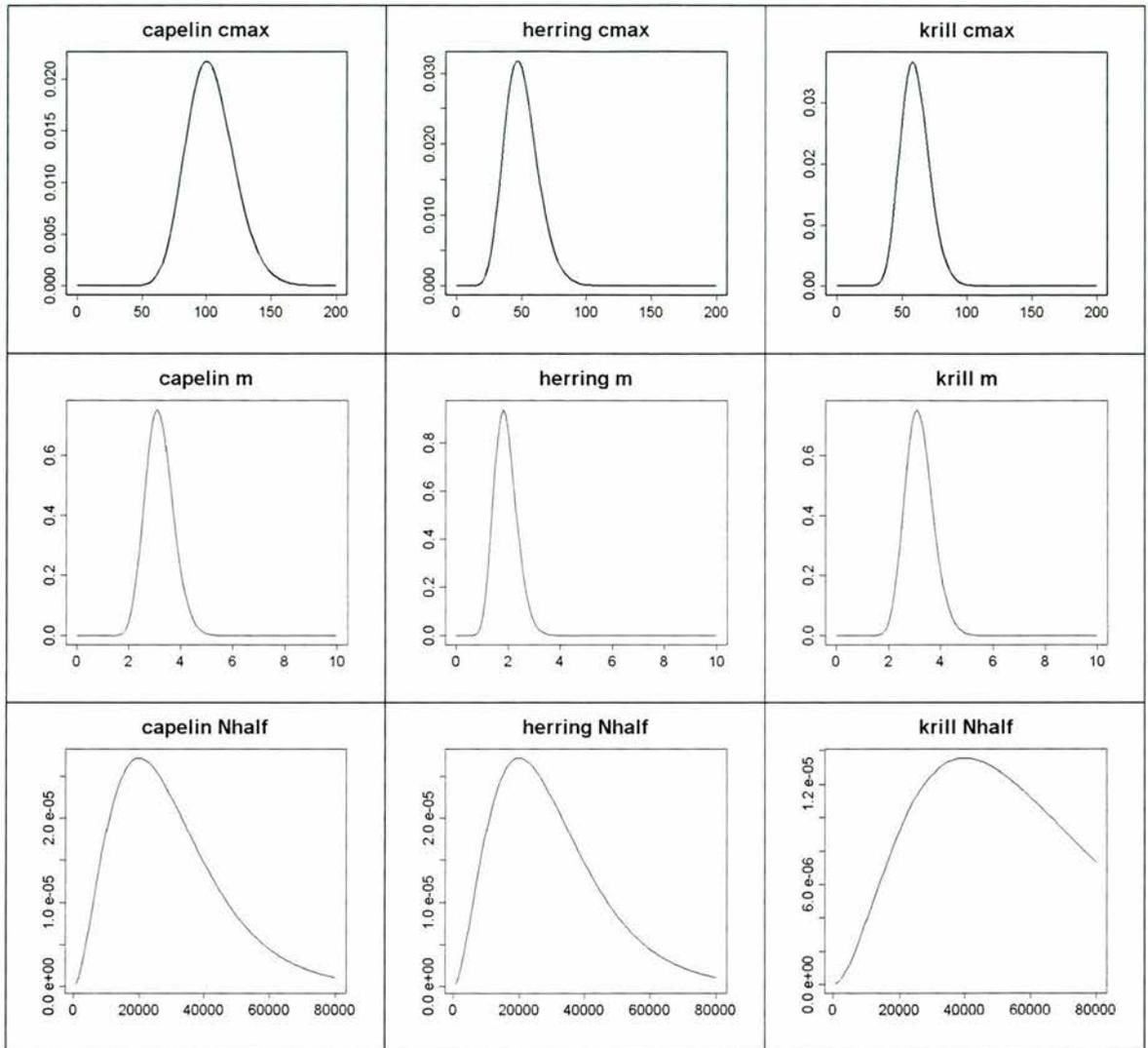
### The MCMC

The observations of fresh biomass from stomach samples represented 2-hourly consumption rates. The 1000 replicate samples of prey availability for each stomach sample were matched to the corresponding consumption rate for each whale.

A ‘continuous Poisson’ error model, (Venables and Ripley 1999), was chosen for consumption because this was the only distribution available in WinBugs that could successfully model the possibility of zero consumptions, where non-zero consumptions are predicted, and zero predictions.

The WinBugs code is given in Appendix 1 and implemented using the slice sampling algorithm due to Neal (1997). Two parallel chains were run to check for convergence.

Figure 5.7: prior distributions for the parameters  $c_{max}$ ,  $m$  and  $N_{half}$  for all prey types



Three separate models were fitted. The term 'model' is used here to include both the MSFR model itself, and the model of spatial usage that was used to calculate availabilities.

1. full MSFR model, prey abundances estimated using kernel 1
2. full MSFR model, prey abundances estimated using kernel 2
3.  $m$  in the MSFR set to 1 for all prey species, prey abundances estimated using kernel 1.

## 5.3 Results

### 5.3.1 Prey availability

The GAM fitting was straightforward for all prey species. To give an indication of goodness of fit, the deviance explained by each GAM, for each area and species, is shown in table 5.4. No model was fitted for herring in Area 3, because no herring were recorded during the survey.

The predicted surface for krill abundance in Area 3 on a 1 n.mile grid is shown as an example in Figure 5.8.

The procedure for sampling prey availability over such a surface is illustrated in Figure 5.6. The mean and standard deviation of prey availability that resulted from the spatial sampling of prey distributions around the site of each whale capture is shown in Appendix 2. The statistical distributions of prey availability obtained from spatial sampling were skewed to the right in some cases. This shape depended on the spatial distribution of prey relative to the whale (Figure 5.9). If the prey was tightly clustered, the variance of the availability distribution was likely to be large, while if the spatial distribution was more uniform the variance would be expected to be small.

### 5.3.2 MCMC

The results of the Bayesian analysis were fairly robust to small changes in the prior distributions for the parameters  $m$  and  $N_{half}$ , for all prey species.

**Table 5.4: GAMs - Deviance Explained**

The %deviance explained is shown for each GAM (one model, for each prey species, for each area). There is no GAM for herring in area 3 because no herring were found during the Area 3 survey.

	Area 1	Area 2	Area 3	Area 4
Capelin	65	57	57	60
Herring	73	73	**	62
Krill	64	40	60	97

**Table 5.5: Parameter values for MSFR (Model 1)**

The mean and standard deviation for each parameter were found from 1000 samples from the Markov chain. In Model 1, the whale movement kernel was fixed at 1.8 n.miles. Species 1 = capelin, species 2 = herring, species 3=krill.

	<i>mean</i>	<i>sd</i>
<i>nhalf[1]</i>	7130	1490
<i>nhalf[2]</i>	27900	12200
<i>nhalf[3]</i>	7430	711
<i>cmax[1]</i>	125	19.5
<i>cmax[2]</i>	52	12.7
<i>cmax[3]</i>	10	0.617
<i>m[1]</i>	1.69	0.156
<i>m[2]</i>	1.60	0.361
<i>m[3]</i>	3.98	0.356

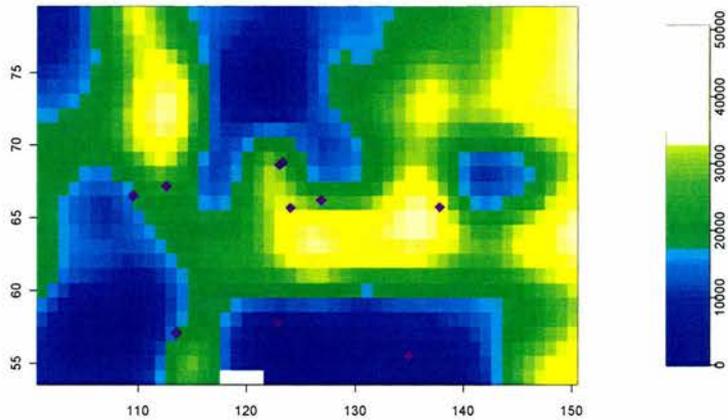
**Table 5.6: Parameter values for MSFR (Model 3)**

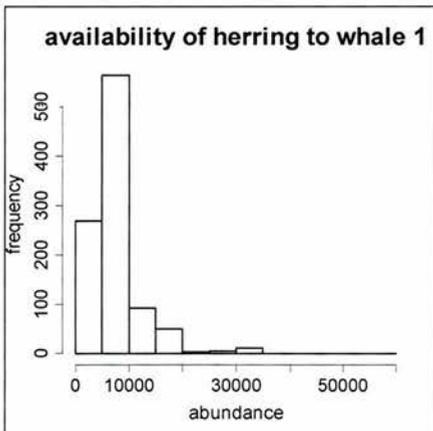
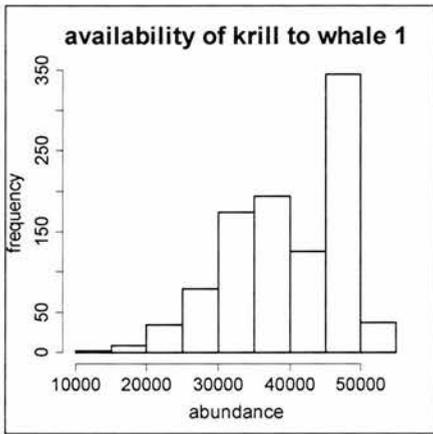
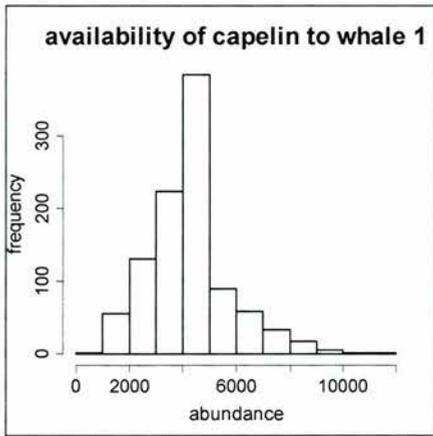
MSFR parameters, mean and standard deviations based on 1000 draws from the Markov chain. In Model 3, the kernel SD was 1.8 n.miles, and *m* was fixed at 1 for all prey species. Species 1 = capelin, species 2 = herring, species 3=krill.

	<i>mean</i>	<i>sd</i>
<i>nhalf[1]</i>	24100	8060
<i>nhalf[2]</i>	51900	20700
<i>nhalf[3]</i>	5420	2330
<i>cmax[1]</i>	111.0	18.4
<i>cmax[2]</i>	46.9	12.2
<i>cmax[3]</i>	12.2	1.35

### Figure 5.8: An example of a prey abundance surface - krill in Area 3

The GAM for krill in Area 3 was used to predict an abundance surface over a grid of 1 n.mile squares. The scale indicates predicted values of abundance, in units of  $\text{kg n.mile}^{-1}$





**Figure 5.9: Statistical distribution of prey availability for whale 1**

However, there was considerable sensitivity to changes in the priors for *cmax*. Significant shifts in the posterior distribution occurred, for example, when *cmax* priors were based on the estimated daily calorific requirements of minke whales, rather than observations of consumption. All results presented below were based on *cmax* priors derived from stomach content data.

The MCMC converged satisfactorily after 100,000 iterations (approximately 12 hours run time) for all three models. MCMC chains were examined by eye to check that good mixing had taken place (Gilks *et al.* 1996).

The deviance information criterion (DIC) gives a measure of fit that is a Bayesian analogue to the more conventional Akaike Information Criterion, with a likelihood term that is penalised for the effective number of parameters in the model: smaller values of the DIC indicate a better fit than larger ones, (Speigelhalter 2002). For Model 1 the DIC was 495; for Model 2 it was 615; and for Model 3 it was 505.

The posterior parameter distributions for Models 1 and 3, and their respective priors are shown in Figures 5.10 and 5.11. The means and standard deviations of the marginal posterior distributions for the individual parameters are summarised in Tables 5.5 and 5.6.

The choice of movement kernel had a significant effect on the posterior distributions. The DIC for Model 2, with  $\sigma=2.5$  n.miles, was significantly

Figure 5.10: posterior distributions for MSFR, Model 1

Red curves represent prior distributions, histograms are the marginal posterior distributions. Species 1 = capelin, species 2 = herring, species 3 = krill.

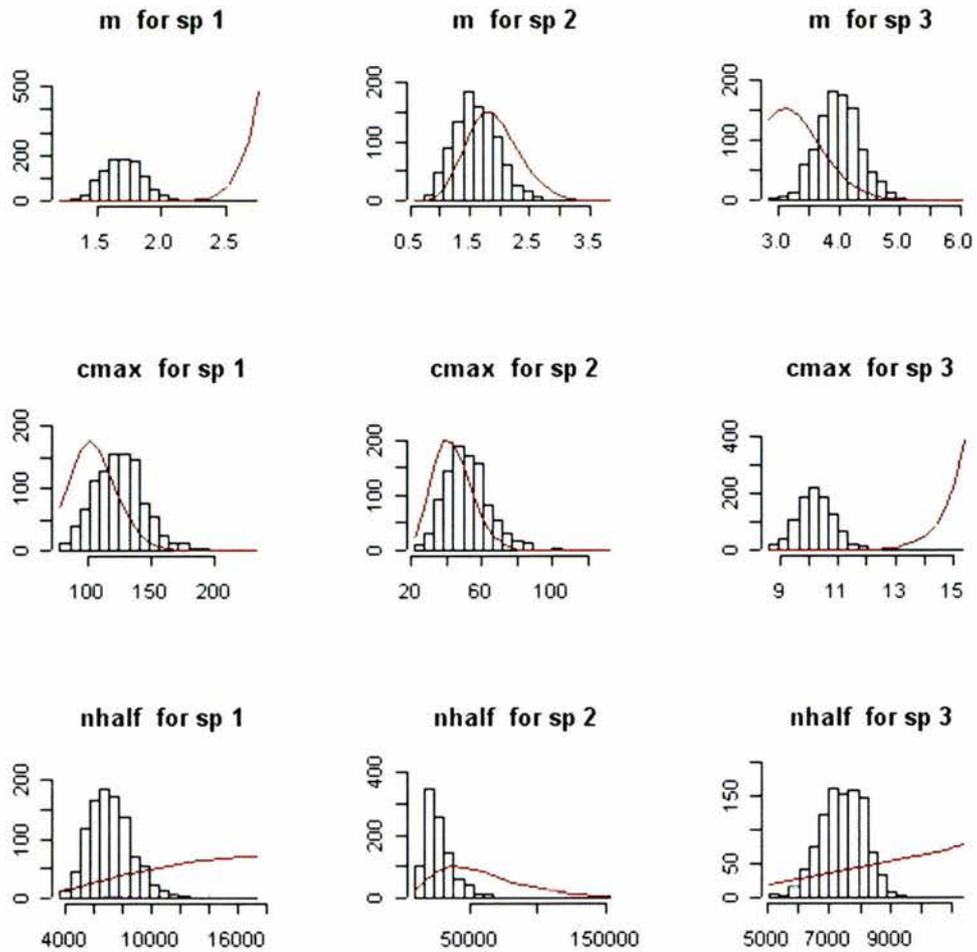
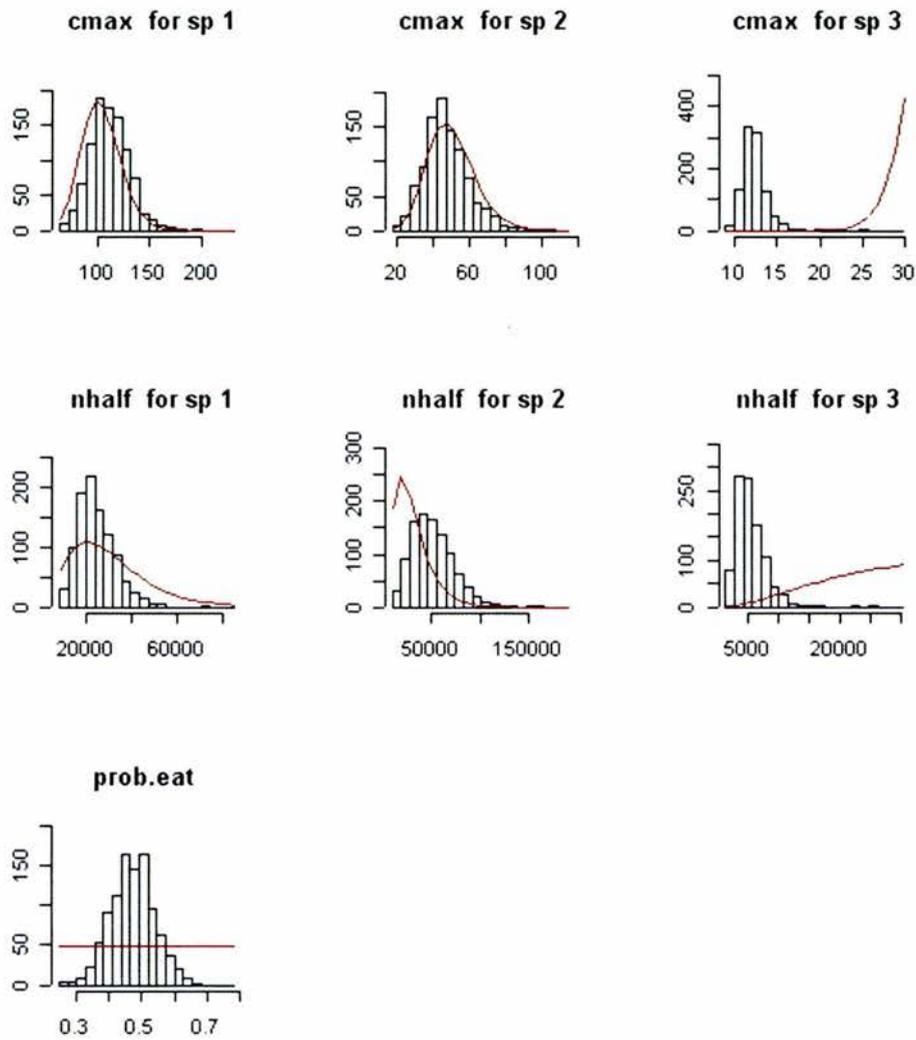


Figure 5.11: posterior distributions for MSFR, Model 3

Red curves represent prior distributions, histograms are the marginal posterior distributions. Species 1 = capelin, species 2 = herring, species 3 = krill.



higher than the DIC for Model 1, suggesting that prey abundance was best estimated on the more localised scale suggested by the telemetry data, with a kernel of width 1.8 n.miles.

Figures 5.12 and 5.13 show boxplots of observed consumption and consumption estimated from models 1 and 3 as follows:

- ❖ for each whale, predicted consumptions of capelin, herring and krill were calculated based on a set of MSFR parameters drawn at random from the Markov chain, together with a set of prey abundances drawn from the 1000 prey availability estimates for that whale;
- ❖ this process was repeated to produce 1000 predictions of consumption for each prey
- ❖ The effect of the ‘zero-consumption’ term was not included, so the boxes on the plot represent predictions for non-zero data, and no attempt was made to reproduce the effect of measurement error.

Model 1 is substantially better at predicting the contrasts observed in capelin and herring consumption than model 3. Both models reproduce the consumption of capelin and herring better than the consumption of krill.

Predicted consumptions of each prey species for different levels of prey abundance based on model 1 are shown in Figure 5.14, those based on model 3 are shown in Figure 5.15. These Figures show conditional forms of the MSFR in which consumptions is calculated for the focal species while the

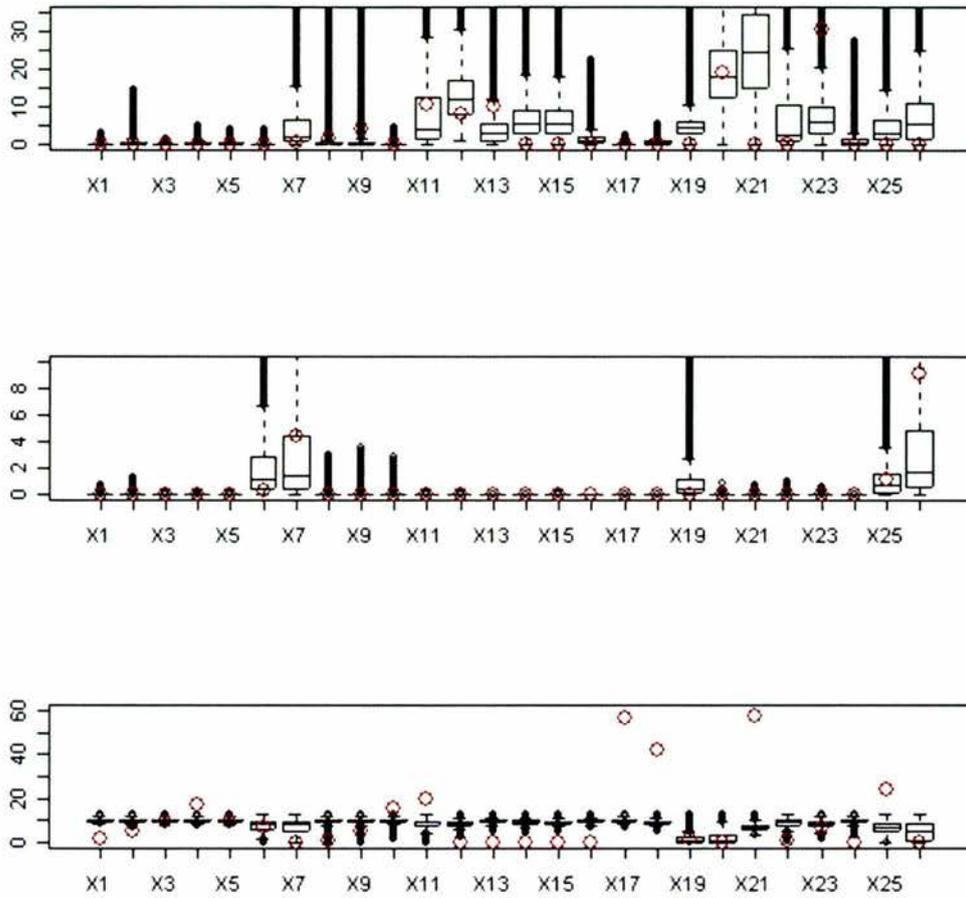


Figure 5.12: Data and predictions for MSFR, Model 1

Predictions are calculated based on the mean value of prey availability at the site of each whale capture, with 200 draws of parameter sets from the Markov chain used to create boxplots representing the uncertainty that results from the distribution of model parameters. Observed consumption is shown in red.

Upper panel = Capelin, middle panel = herring, lower panel = krill

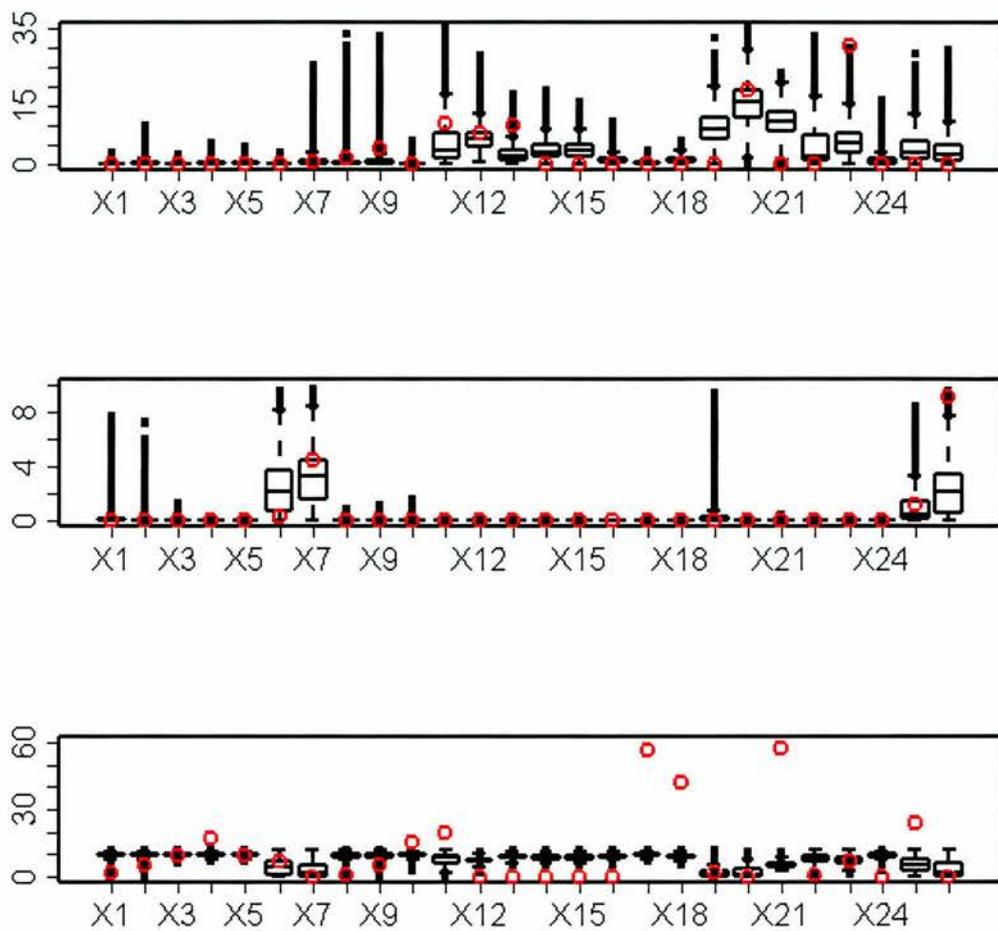
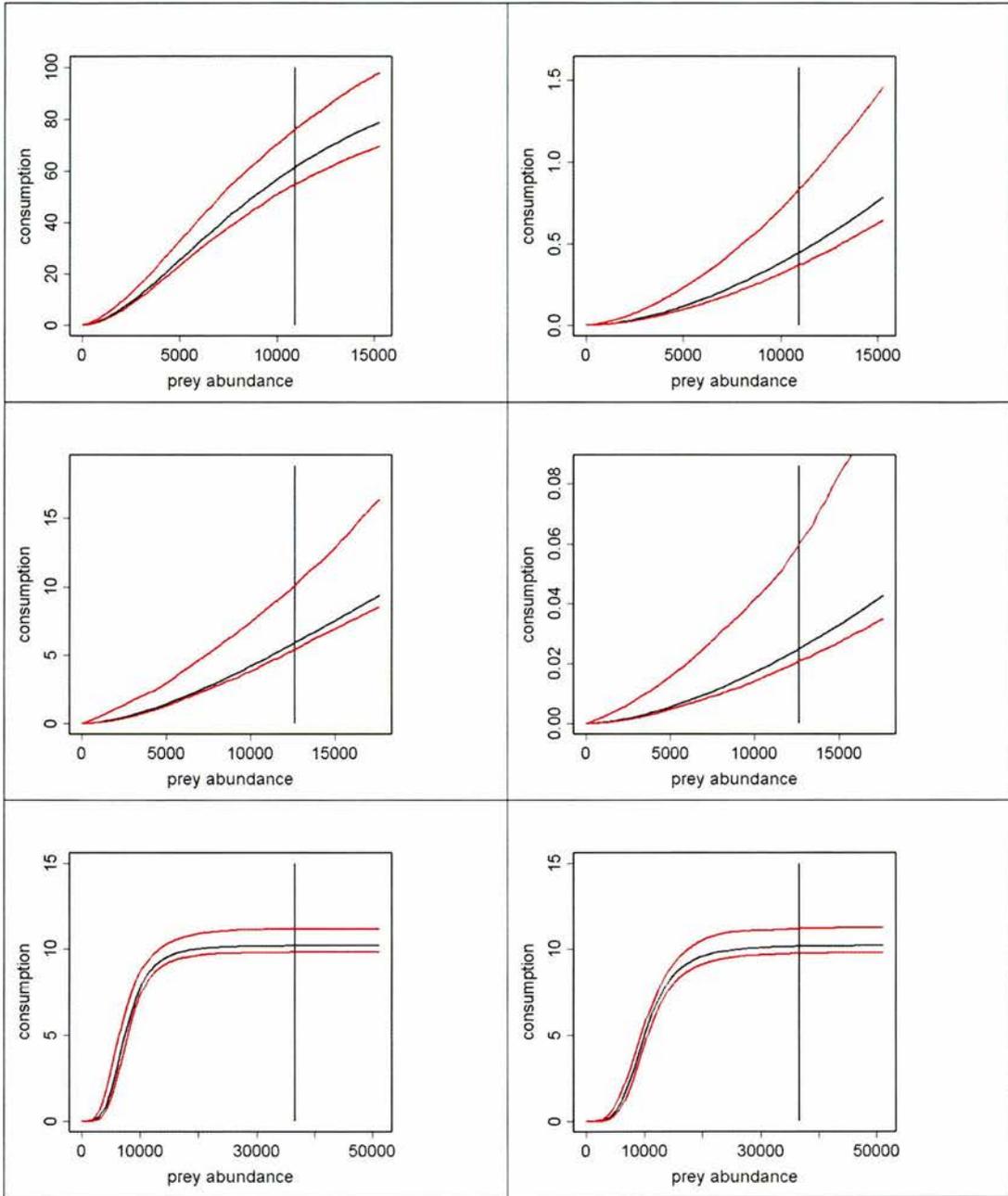


Figure 5.13: Data and predictions for MSFR (Model 3)

Predictions are calculated based on the mean value of prey availability at the site of each whale capture, with 200 draws of parameter sets from the Markov chain used to create boxplots representing the uncertainty that results from the distribution of model parameters.

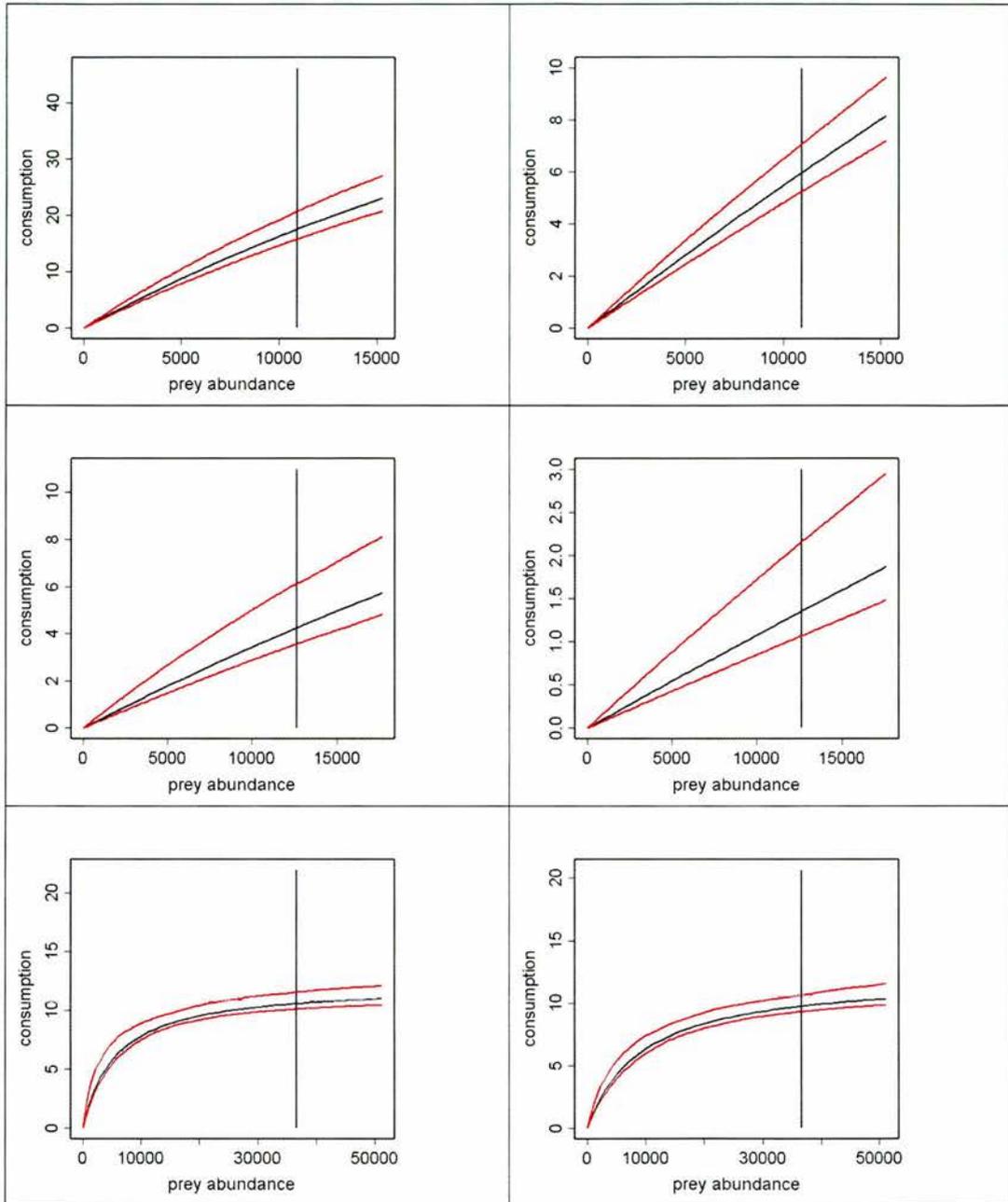
Upper panel = Capelin, middle panel = herring, lower panel = krill

**Figure 5.14: Model 1, predicted consumption of three prey types in response to changes in prey density**



Consumption rate in  $\text{kgHr}^{-1}$  is plotted on the y-axis. Prey abundance is in units of  $\text{kg n.mile}^{-2}$ . The top row represents the consumption of capelin, the middle row represents herring consumption, and the bottom row krill consumption. Vertical black lines mark the upper bound of prey abundance that is represented within the original data set - above this, the model is being used to extrapolate. In column 1, alternative prey is absent. In column 2, alternative prey is abundant (values of abundance are the highest from the data set).

**Figure 5.15: Model 3, predicted consumption of three prey types in response to changes in prey density**



Consumption rate in  $\text{kgHr}^{-1}$  is plotted on the y-axis. Prey abundance is in units of  $\text{kg n.mile}^{-2}$ . The top row represents the consumption of capelin, the middle row represents herring consumption, and the bottom row krill consumption.

In column 1, alternative prey is absent. In column 2, alternative prey is abundant (values of abundance are the highest from the data set)

abundance of all 'other' prey is held fixed at either zero abundance or at an arbitrarily high value. In this case, the high values were based on the maximum abundances observed in the data set (see Appendix 2).

The plots of predicted consumption were constructed on the assumption that I had perfect knowledge of the abundance of all prey. If the MSFR was to be used to predict consumption from a set of measured values, it would be necessary to take account of the uncertainty in the prey abundance estimates.

## **5.4 Discussion**

### **5.4.1 Spatial sampling**

The prey data were collected over a short time-period, with good spatial resolution and at most the same time as the whale captures, so that the predicted prey distributions should have been representative of those encountered by the whales while foraging (Harbitz and Lindstrom 2001). This is therefore an exceptionally good data set for studying the relationship between prey abundance and consumption by a marine predator.

Fitting spatial models to the prey abundance data from the acoustic surveys proved straightforward. The GAMs converged easily and fitted the data well, indicating that the spatial distribution of the prey could be modelled successfully at the scale (1n.mile) of data collection. However, there were almost certainly some fine-scale details of the prey distribution which were

not captured by the acoustic surveys, as indicated by trawl data collected synoptically with the acoustic surveys (Lindstrom *et al.* 2005). Fine-scale variation was particularly noticeable in the krill distributions. This may have been responsible for the apparent over-dispersion in the consumption data if foraging whales respond to prey aggregations that were not detected by the spatial models. It may also explain why the predictions of krill consumption are substantially worse than those for herring and capelin (Figure 5.12).

The method used to estimate the availability of prey to each whale was based on two assumptions: that foraging occurs in discrete bouts, and that foraging movements can be represented as a random walk.

The first assumption may not be strictly correct because some stomachs contained more than one prey item even though prey aggregations tend to be distinct (Harbitz and Lindstrom 2001). This suggests that, from time to time, several foraging episodes may be represented in one stomach.

Behavioural studies of individual minke whales have also shown that minke whales may visit different shoals of fish while foraging, sometimes within a short period of time (Hoelzel 1989). However, in the present analysis, the assumption that foraging occurred in only one location may be justifiable. The prey distributions are smoothed, so that individual point estimates of prey density represent a local average that will be representative of an area rather than a true geometric point. Provided that actively foraging whales do not move significant distances between feeding bouts, the assumption of a single foraging event may be relaxed a little to include localised episodes

of foraging. This type of behaviour has been observed in boat-based studies of minke whales (Simard *et al.* 2002).

The assumption that foraging can be approximated by a random walk described by a Gaussian kernel has been used in other studies of marine mammal movement (e.g. Austin *et al.* 2004, Matthiopoulos 2003). However, the technique described here can easily be adapted to use any other probabilistic 2-dimensional representation.

Figure 5.9 shows the marginal distributions of each prey species that are derived from a joint distribution for all three prey species. A strength of this approach is that these correlations in prey abundance were accounted for in the calculation of prey availabilities, which were subsequently used to fit the functional response.

#### 5.4.2 Bayesian analysis

##### Sensitivity to prior distributions

The computational demands for fitting the three different MSFR models were considerable, because 1000 different prey abundance values were compared with a single consumption datum for each whale, for each step of the Markov chain. Nevertheless, all models converged satisfactorily, and the marginal posterior distributions indicate that the priors for all parameters except *c<sub>max</sub>* were significantly improved by the data (Gelman 1995).

The results of a Bayesian analysis may be sensitive to the form of the prior distributions, and this sensitivity is likely to be most important in studies, such as this one, where data are relatively sparse (O'Hagan 1998). Trial runs of the MCMC showed that the form of the priors on *cmax* had a strong influence on the results.

*cmax*, which is equivalent to the reciprocal of handling time in the Holling's parameterisation of the functional response, is likely to be troublesome parameter when a functional response is fitted to field data from a generalist because maximum consumption of a given prey is only likely to be observed in the field if this prey is abundant and other prey are either absent or scarce. This combination of prey abundances may not be represented in the data set.

If the outcome of a Bayesian analysis is strongly dependent on choice of prior distributions, it is particularly important that these prior distributions are appropriate and informative (O'Hagan 1998, Lambert *et al.* 2005). Stomach contents represent sporadic episodes of foraging. As a result, estimates of consumption rate based on stomach contents analysis are expected to be highly variable, and dependent on the foraging period they represent. Maximum rates are likely to be significantly higher than the equivalent rates would be if these were measured over a longer time period, (Armstrong *et al.* 1998). The priors chosen for *cmax* in this study were therefore based on stomach content data, and should be

representative of the distribution of maximum stomach capacities that results from individual variation within the whale population.

#### **5.4.2 Empty stomachs**

The contents of each whale's stomach represented the results of a few hours foraging. However, feeding and stomach-emptying are both sporadic processes and the amount of a given prey in the stomach of an individual may vary from zero to some large value, regardless of its long term feeding rate (Beyer 1998). Measured consumption rates may thus be over-dispersed when stomachs are collected by killing animals at random. In this study, a Bernoulli model was used to represent the loss of prey from stomachs due to stomach-emptying, and a continuous-Poisson model was used to compare the predicted and observed consumption of prey when sufficiently recent feeding had taken place for there to be fresh prey in the stomach at the time of capture. The mean posterior value of the Bernoulli probability, was 0.6, suggesting that the probability that a stomach would contain prey when a whale was captured was 60%.

#### **5.4.3 Scale-dependence**

The scale over which prey abundance was estimated made a significant difference to the outcome of the model fitting process. If the quality of the fit was correctly indicated by the DIC, then a better fit to the data was obtained when sampling was carried out on the smaller of the two scales that were simulated. It may be that stomach data of the kind used in this study represent the outcome of localized foraging, and that the best fitting

spatial scale is the most appropriate for estimating prey availability.

However, some caution is needed in interpreting the results in this way. The distributions of prey were assumed to be spatially auto-correlated, and the GAMs were smoothed. Therefore, the variance of the statistical distribution of prey availability for each whale was likely to increase as the scale of the sampling area was increased, making it more difficult to fit the MSFR model

#### **5.4.4 The importance of other prey in predictions of the consumption of individual prey species**

MSFR model 1 predicts that the consumption of either capelin or herring by minke whales will be strongly influenced by the presence of other prey in the system. Where alternative prey are abundant, the consumption of herring or capelin is likely to be considerably reduced. These effects are illustrated by the marginal functional responses of minke whales to capelin and herring (Figure 5.14) at different levels of alternative prey. The consumption of krill, by contrast, saturates at relatively low krill density and is almost unaffected by the presence of alternative prey items when krill densities are above this level.

The predicted maximum consumption rate for krill was  $10\text{kg}\cdot\text{hr}^{-1}$ . Lindstrom (pers com) predicted that the intake of krill for an average minke whale should then be  $5\text{kg}\cdot\text{hr}^{-1}$ , based on its energy requirements and the energy content of krill. Given that whales forage less actively at night, the MSFR prediction of the daytime foraging is quite consistent with Lindstrom's calculation. In contrast, the fitted maximum consumption rates of capelin

and herring (125kg/hr and 52kg/hr respectively) are very much higher than those predicted from energetic considerations, (5kg/hr and 3.6kg/hr respectively). However, such high rates of consumption for the fish prey are only likely to occur when foraging whales encounter dense aggregations of fish. It is interesting to note that, while Antarctic minke whales may consume krill almost exclusively (Armstrong and Siegfried 1991), North East Atlantic minke whales may not be so dependent on krill: they are less abundant in the Barents Sea in years when their fish prey is scarce, and their body condition is adversely affected in these years (Haug *et al.* 2002).

If the interactions between whales and fish stocks are to be modelled realistically, it is essential that all major prey species are included in an MSFR or some equivalent transfer function (Yodzis 2000). The modelling work in this chapter has indicated the consumption of specific prey species may be strongly influenced by the abundance of other prey in the system. Schweder *et al.* (2000) did not include krill in their minke whale model, although krill are an important part of the whales' diets in years when herring and capelin abundance are low (Haug *et al.* 2002). It may be justifiable to ignore a prey species in the modelling process if its abundance can be considered constant, or insignificant, or if consumption rates of the prey are never high. However, none of these is true for minke whales preying on krill in the Barents Sea: krill is not generally scarce here, nor is its abundance uniform in time or space (Delpadado and Skjoldal 1996); and whales consume substantial quantities of krill (Folkow *et al.* 2000). However, the MSFR fitted here suggests that krill consumption is almost

constant across a wide ranges of krill densities. If this is true throughout the Barents Sea, this might justify regarding krill as a constant 'background' component in the diet of minke whales and modelling the consumption of krill as a 'constant ration'. However, krill are also important prey for some fish species in the Barents Sea, and their abundance varies considerably within and between years. So they need to be modelled explicitly if an ecosystem model is to be realistic (Dalpadado *et al.* 2001, Bogstad *et al.* 1997).

This analysis was restricted to the prey species found in the whale stomachs used in this study. However, other prey species have been observed in significant quantities in whale stomachs collected elsewhere in the Barents Sea (Schweder *et al.* 2000). Thus, the MSFR fitted here may not be applicable throughout the entire summer and over their whole range within the Barents Sea. Data from other areas of the Barents Sea and from different months would be required in order to fully parameterise the MSFR (Haug *et al.* 2002).

#### **5.4.5 Can the diet of all minke whales be described by a single MSFR?**

In this analysis, I assumed that one MSFR model could adequately represent the behaviour of the entire minke whale population throughout the foraging season. If there was variation in the functional response of minke whales, then it was assumed that this was relatively slight and that the whales used in the study were a random unbiased sample of the whole population. The effects of individual variation would then appear as over-dispersion in the

consumption data, and thus increase the uncertainty associated with any resulting inference. The 'true' behaviour of the population should be represented within the confidence bounds of these inferences, provided no extrapolation was made outside the range of prey availabilities observed in the study.

It is a frequent observation that individual predators adapt their behaviour to specialize on certain prey (Rayor and Munson 2002, Bolnick *et al.* 2003); minke whales caught in close proximity to one another often have entirely different prey items in their stomachs (Lindstrom and Haug 2001). One explanation of these observations is that individual whales are specialists. However, it could be that whales, which are caught close together, may not have fed close together, or that whales all feed on the same range of prey but forage on different prey in discrete bouts. The existence of 'specialists' could only be established by using methods, such as fatty-acid analysis (Olsen and Grahl-Nielsen 2003), that assess the long-term diet of whales.

It is also possible that certain categories of whales may have distinct MSFRs. While previous work suggests that whales of different sizes do not have significantly different prey preferences (Haug *et al.* 1997), net energy consumption is expected to be related to size (Tjelmeland and Lindstrom 2004). The size of an individual minke whale is therefore likely to influence its maximum consumption rate. Gender may also be an important factor affecting energetic requirements and prey choice (Haug *et al.* 2002). Eighty percent of the whales sampled in this study were female, so the MSFR

documented here may not reflect the feeding behaviour of the entire population.

#### 5.4.6 The importance of $m$

The posterior distributions (Figure 5.10) indicate that  $m$  for all prey species was significantly greater than 1. This result is consistent with Tjelmeland and Lindstrom (2005) and with other studies in which MSFRs have been fitted to field data (Asseburg *et al.* 2006). If  $m > 1$ , then prey preference measured using Chesson's index (Chesson 1978) will change with prey abundance. Such changes in preference have been observed in many studies of vertebrate predation, e.g. Sundell *et al.* (2004), Rindorf and Gislason (2003). Preference changes were also noted in a previous analysis of the minke whale data analysed here, (Lindstrom *et al.* 2005). If  $m > 1$ , this also implies that the single-species functional response for individual prey species is sigmoidal. Sigmoidal functional responses may have significant implications for predator-prey dynamics, because they make it possible for predators and prey to persist at a stable low prey density equilibrium (Murdoch and Oaten 1975, Turchin 2001, Case 2004). The consequences of sigmoidal functional responses in a multi-species system, with mobile predators and prey, are more difficult to predict (Turchin and Hanski 1997, Matthiopoulos *et al.* 2006b). The finding that  $m > 1$  for all prey in this localized foraging study suggests that local persistence of prey populations is possible, but it does not in itself imply that it is inevitable at this scale *let al.* one on a whole-sea scale.

Although the consequences of  $m \leq 1$  (i.e. that there may be no stable predator-prey equilibrium) are well known, many multi-species models use this formulation to describe the consumption of prey by predators (e.g. Begley 2005). In the analysis reported here, model 3, which assumed that  $m=1$  for all prey species, was a poorer fit to the same data set than the equivalent model (Model 1) where  $m$  was allowed to vary. This suggests that such simplifying assumptions are probably not realistic.

In order to explore the implications of Models 1 and 3 for local prey population dynamics, simple simulations were used to predict the impact on prey populations of a single minke whale foraging within a 1n.mile square for 2 weeks. Prey was consumed at the rate predicted by the appropriate MSFR and prey abundance was re-calculated each hour. The results of one run are shown in Figure 5.16. Here, an 'aggregation' of capelin was simulated by picking starting values from the availability data set that were 'high' for capelin and 'low' for other prey.

Given identical starting values for prey abundance, and when the simulations were run for the same time period, the predictions of the two models were rather different.

Model 1 predicted considerable depletion of capelin, some depletion of krill, and very little consumption of herring. Under Model 3, with all  $m=1$ , all three species were consumed, but the impact on capelin was less than

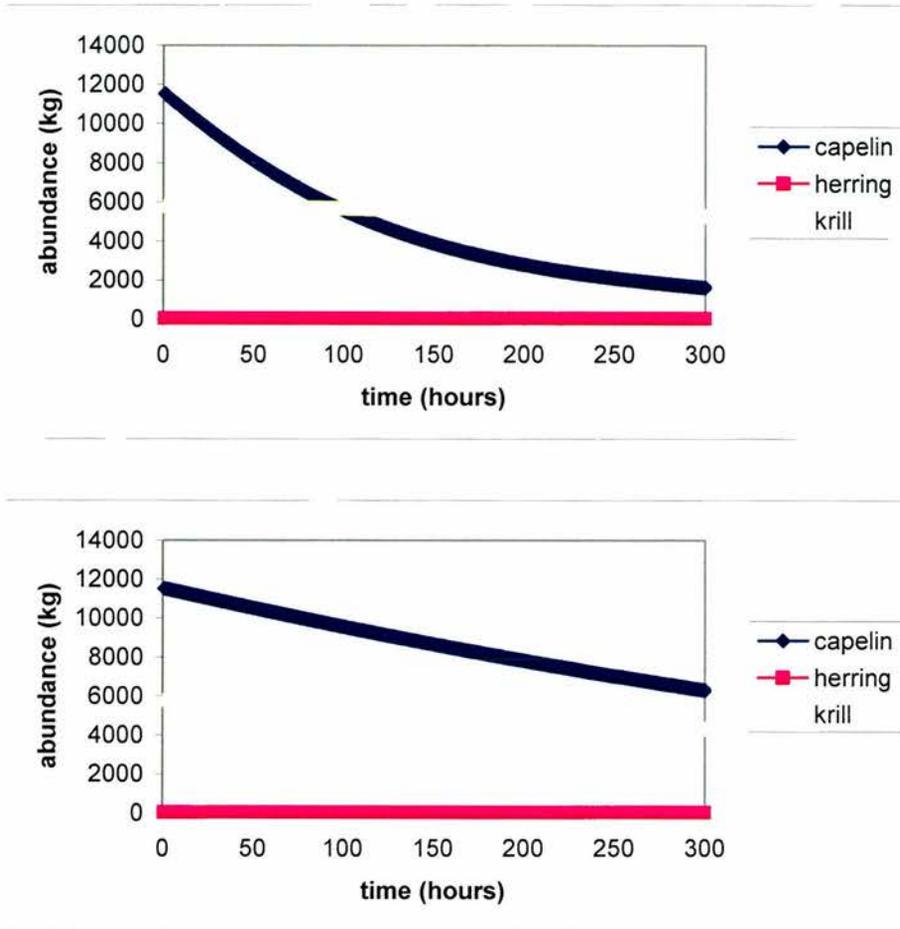


Figure 5.16: Simulation of the effects of minke whale consumption on prey abundance

One whale was assumed to forage in a square of area  $1n.mile^2$ . Consumption was calculated from the relevant MSFR model, and prey abundances were then re-calculated hourly to allow for the effects of depletion. Prey was assumed not to enter or leave the area during the simulation.

The top figure represents the predictions of Model 1 ( $m > 1$  for all prey), and the bottom row represents the predictions of Model 3 ( $m = 1$ ). Starting values for prey abundance were chosen from the range represented within the data set that was used to fit the MSFR models, with capelin abundant, and herring and krill both scarce.

under Model 1. Therefore it appears that assuming all  $m = 1$  may result in unrealistic predictions of the outcome of foraging by the whales, on the localised scale of this study.

#### 5.4.7 Implications for the Barents Sea ecosystem

Simple simulations using the MSFR models fitted to the data used here suggest that minke whales may cause local depletion of capelin stocks: if stochasticity were to be included in the simulations, local extinctions might occur within realistic time scales. However, similar depletion would not necessarily occur on a larger spatial scale. It is unlikely that whales distribute themselves precisely according to capelin distributions, because (a) capelin behaviour may well be anti-predatory (b) the number of whales is limited (c) whales may also be aggregating in response to different prey, which is differently distributed. Therefore, there are likely to be regions where capelin occur but whales are absent. Such regions would act as spatial refuges for capelin from minke whale predation, and could significantly influence the population-level dynamics of capelin (Krivan 1996, Ruxton 1995, Sih 1987).

To make inferences for the whole Barents Sea based on the localised MSFR, it would be necessary to estimate the distributions of prey and whales over the entire foraging season so that the spatial overlap between whales and their prey could be calculated. Distributions could be inferred from known migration patterns and seasonal distributional changes, or predicted using models of the relationship between the distribution of whales and their prey

and a range of environmental covariates. It would also be necessary to model the response of minke whales to finer-scale variations in prey density, ideally by parameterising an aggregative response (Asseburg *et al.* 2006).

It is hoped that the results of the present localized study can be used to inform multi-species models for the Barents Sea, such as GADGET (Begley 2005). Such models could then be used to explore the role of minke whales within this ecosystem and their effects on fish stocks. The results from this analysis could be used to parameterise a predation sub-model (Bogstad *et al.* 1997). However, they could also be used with time series of data from the entire ecosystem to provide starting values for a maximum likelihood fit (Koen-Alonso and Yodzis 2005), or to set priors for a Bayesian fit (Harwood and McLaren 2004).

#### **5.4.8 General conclusions**

The data used in this analysis were particularly well suited to fitting an MSFR because high quality data on local prey abundance were available. Computer-based sampling of smoothed prey abundance estimates in the area around each captured whale was used to provide an indication of the availability of prey, and the uncertainty in this availability. This approach could be used to assess prey availability to other situations where predation cannot be observed directly but must be inferred from stomach contents, provisioning of young, scat samples, or fatty acid analysis.

Some of the difficulties in fitting an MSFR using consumption rates estimated from stomach samples were overcome by using combined Bernoulli and Poisson error models. Again, this is a method that has considerable generality.

The Bayesian approach used here could easily be adapted, for example, to accommodate other mathematical formulations of functional response models (Gentleman *et al.* 2000). Fitting a MSFR to field data will always be a challenging exercise because of the need for data at a range of different combinations of prey abundances. The Bayesian approach allows additional information and expert knowledge to be formally incorporated into the analysis through the use of informative prior distributions in the fitting process. Although this makes it possible to estimate the parameters of an MSFR using relatively small data sets, the prior distributions must be chosen with care and must be based on sound principles or experimental evidence.

The results of the model fitting in this case highlight the importance of including all the important components of the predators diet, because changes in the abundance of other prey had a strong influence on the consumption of focal prey. It was also important to the shape parameter to vary among prey species because this parameter is critical in determining the predator's potential impact on prey dynamics.

## Chapter 6. Discussion

In this section, I examine the aims and objectives outlined in the Introduction and evaluate the progress I have made towards achieving them. I discuss some general interpretations and implications of my results, and plans for future research. A particular focus is the potential application of parameterised marine mammal consumption models within ecosystem based fisheries modelling.

**6.1 Is it possible to obtain sufficient field data to parameterise the FR of a generalist? Issues of spatial and temporal scale, and details of predator and prey behaviour, suggest that multi-species FRs should be parameterised using field data rather than laboratory experiments.**

#### 6.1.1 Sparse data, and the use of informative priors

The data sets used in both the grey seal and minke whale analyses were sparse: the number of separate data points was not very much greater than the number of parameters to be estimated (approximately three times in the case of the minke whales and two times in the case of the grey seals). However, sparse data are often all that are available to ecologists, and studies of the feeding behaviour of generalists demand considerable quantities of data. At present, the data sets used in this thesis are some of the best available for parameterising models of marine mammal predation. For the grey seals, two detailed diet studies based on samples from multiple sites and collection dates were available, and there was an exceptional long time-series of prey survey data which had been collected in a consistent way and included all likely prey species. For the minke whales, detailed prey surveys were carried out in the immediate vicinity of the sampled whales, and within a short time after the whale captures. It is therefore likely that any further attempts to model the functional responses of marine mammals using field data will face similar or greater difficulties in terms of the quantity of data that is available to fit a consumption model. The methods described in

this thesis for fitting consumption models using Bayesian methods may therefore have much wider generality for other generalist predators.

In order to fit sparse data-sets, auxiliary data were used to provide informative priors (Carlin *et al.* 2000). Since the fitting process was enabled by the use of these priors, the results were necessarily sensitive to them. An important question for the present study is, therefore, whether or not the choice of priors was appropriate.

For the minke whale study, priors for maximum consumption rates were obtained by bootstrapping over a larger stomach data set. This approach, based on measurements of consumption that were directly comparable to those that were used to fit the FR, seems appropriate provided the data set (400 stomachs) was sufficiently large. Priors for the shape parameter  $m$  were obtained from the results of an independent modelling exercise (Tjelmeland and Lindstrom 2005) in which a different FR model was fitted for minke whales. This model was applied over a larger spatial scale than the localised minke whale foraging study, but included the same suite of prey species.

For the grey seals, uniform priors were used for the 'attack rate'  $a$ , with limits set by information on the abundance of sandeels and the general nature of seal diets.

Experimental results were used to set priors for the shape parameter,  $m$ . This parameter determines the relationship between attack rate and prey abundance for a given prey, where

$$\text{attack rate} = aN^m \quad (1)$$

Evidence from telemetry studies suggests that individual seals spend an approximately constant proportion of their time away from haul-out sites (McConnell, pers com) and therefore foraging. This implies that the average consumption rate of a free-living animal would then be a fraction ( $1/Q$ ) of the consumption rate that would be observed for actively foraging seals, so that the FR would become

$$c = \frac{QaN^m}{1 + aN^m} \quad (2)$$

Equation (2) can be rearranged as

$$c = \frac{QaN^m}{1 + Qa\frac{t}{Q}N^m} \quad (3)$$

Although the values of  $a$  and  $t$  for a free-ranging animal will be rescaled versions of the values estimated for a captive animal,  $m$  is unaffected and a

value estimate from a captive animal should also be appropriate for a free-ranging one.

This simple argument suggest that, provided the parameters of a single-species FR measured in the absence of alternative prey correspond with the equivalent parameters of the multi-species FR (Joly 2003)) then studies of prey switching by individual captive seals can provide valid priors for fitting a multi-species FR for wild seals(Gallon, pers com).

#### 6.1.2 Modelling consumption - future directions

##### *Updating the grey seal model*

When data from the grey seal diet survey conducted in 2002 becomes available, along with new estimates of coefficients needed to correct the otolith data for the effects of digestion and otolith loss, then the grey seal consumption model will be updated. With more data, it is hoped that it will be possible to parameterise a model that includes more of the main fish species in grey seal diets. The choice of species to include in the model will in any case have to be reviewed in the light of the new data, since the composition of diets may have changed significantly in 2002. If more prey species can be included, it is hoped that predictions of consumption based on the model will become more accurate because the proportion of the diet that is composed of 'other' prey (i.e. prey species that were not included in the

model) will be smaller. With a larger data set, there is also the possibility of checking the predictive power of the consumption model using cross-validation - i.e. to test the model's ability to predict 'missing' data. A particularly interesting application would be to subset the data by area, and to try to predict consumption by West Coast grey seals, based on East Coast (North Sea) diet data. If the foraging behaviour of the seals is not itself strongly influenced by habitat (which is a strong assumption), then it might be possible to explore whether estimates of the abundance of fish off the West of Scotland are biased downwards because current fish abundance surveys are unable to explore the rocky regions of the seabed around the Hebrides which may be important nursery areas for fish. This suggests the intriguing possibility of using a parameterised consumption model for grey seals, together with diet data, to estimate the availability of prey.

#### *Up-dating the minke whale model*

For minke whales, work is in progress to fit a multi-species FR to a longer-term, wider spatial scale data set than the one used in Chapter 5. Stomach data are available for 6 years from whales captured in the western and eastern areas of the southern Barents Sea, along with estimates of prey abundance based on annual surveys.

The larger-scale FR model, may be more appropriate for inclusion in an ecosystem based fisheries model (EBFM) of the Barents Sea than the present

model, because the latter is based on fine scale observations and represents very localised foraging behaviour.

#### *Using other information on diet composition*

The methodology used to estimate the parameters of a grey seal FR could also be applied to estimates of diet composition obtained from quantitative fatty acid structure analysis (QFASA - see Iverson *et al.* 2004). QFASA requires the setting-up of a library of prey fatty-acid compositions, and calibration of uptake using data from captive animals. However, if these requirements can be met, it has the advantage that it provides estimates of the diet of individual animals averaged over a much longer time scale than either stomach contents or scat analysis can provide. It may therefore be useful for determining if there is significant variation in the diet composition of individuals or age and sex classes (Bennet 2005). In addition, QFASA can also be used in situations where killing animals to collect stomach samples is unacceptable for conservation or welfare reasons, and where scats are difficult to collect. QFASA is still at an early stage of development for UK grey seals, but I hope to investigate the feasibility of using the data on grey seal diet derived from QFASA that has already been collected by Walton and Pomeroy (2003), to parameterise a consumption model for grey seals preying on sandeels and other prey around one haul-out site in the North Sea for which detailed prey availability data is available (Greenstreet *et al.* in prep.).

### *Extending the FR model to other predators*

There are many potential applications for modelling consumption by generalists in both terrestrial and marine ecosystems. One project for which preliminary investigations have already been carried out involves modelling consumption by North Sea fish, based on data from stomach sampling (Floeter and Temming 2003). Prey availability can then be estimated from the contents of the trawl in which the predatory fish were caught (Rindorf 2003). Alternatively, the methodology developed in Chapter 2 could be used to estimate local prey availability. Because prey fish may in some case avoid predators, or prey may be locally depleted by predation (Temming *et al.* 2004), the spatial modelling approach to calculating availability may be better suited to this case than the direct use of the trawl data.

A project currently in the planning stage will seek to fit a FR to data on the quantities of different fish species brought by guillemots *Uria aalge* on the Isle of May to feed their chicks (Wilson *et al.* 2004). Some information on the use of space by adult birds is available from telemetry studies, and prey availability information is available from acoustic surveys (Greenstreet *et al.* in prep.). A model for the changing availability of sandeels over the guillemot breeding season, which takes into account changes in the vertical distribution of the sandeels, will also be applied.

The possibility of modelling consumption by North Sea fish and seabirds is particularly attractive because these organisms form an important part of a complex food-web that also includes grey seals. Parameterised models of consumption by fish, seabirds and seals could thus potentially contribute to an EBFM for the North Sea (Vinther 2004, Lewy and Vinther 2004, ICES 2005).

## **6.2 How can the availability of prey be calculated for a mobile predator?**

Where the usage of space by predators and prey is approximately uniform within the area of interest, prey abundance alone can be a satisfactory indicator of availability (Asseburg 2005). However, when the usage of space by predators and prey is complex, and in particular where the spatial range of a predator is limited, then it may be necessary to determine prey availability by estimating the overlap between predator and prey distributions. If availability cannot be calculated correctly, e.g. if information about the prey distribution is not available, then it may be impossible to determine a relationship between consumption and prey abundance. For example, prey may appear to be plentiful but be located in regions that are inaccessible to a predator. The correct estimation of availability is therefore a crucial step in discovering the true relationship between predator consumption and prey abundance (ICES 2005, Floeter 2005).

### 6.2.1 The use of space by predators

Matthiopoulos (2003) describes how the usage of space by grey seals around the UK can be estimated from telemetry data. I used the results of his analysis to calculate the availability of space to seals and to estimate the extent of overlap with prey distributions. The available information in the literature on minke whale movement patterns, however, is presently very limited. For this study I had to estimate parameters describing minke whale movement using telemetry data that was collected from one individual whale, with an average of three locations per day. Further tagging studies or, alternatively, information from direct follows of foraging whales, are needed to provide more comprehensive information. If such work is combined with prey surveys, it will be possible to investigate the relationship between whale spatial usage and fine-scale prey distributions. This could prove particularly useful in interpreting the long-term consequences of the localised MSFR model (Matthiopoulos *et al.* 2006 b).

### 6.2.2 The use of space by prey

General additive models (GAMs) provide a flexible framework for predicting abundance surfaces for prey, and I used this approach in Chapter 2. A realistic error model for biological survey data was available within the MGCV package for GAM fitting, and environmental correlates could be included to improve

the fit of the models and their predictive power. It was also possible to include time as a covariate. This proved particularly useful in the case of the IBTS data because this was available as a long time series.

The limitations of the GAM approach are:

- i. GAMs, even more than some other methods used to carry out spatial smoothing, tend to predict extreme values at the edge of the prediction area, and extrapolation outside the hull of the original data is ill-advised. This was not generally a serious problem for the calculation of predator prey overlap, because the range of the predators in the minke whale and seal studies fell almost entirely within the hull of the prey data. This might not be the case in future studies.
- ii. In GAM fitting, spatial interpolation was based on Cartesian coordinates and distances between points were therefore Euclidian. This is not necessarily appropriate for fish distributions, where land intervenes between locations and fish may have to swim considerably further than the Euclidian distance in order to travel from one point to another. 'Biological distances', which take the presence of intervening obstacles into account, can be calculated for any pair of points (Matthiopoulos pers com, Matthiopoulos 2003). It is possible to incorporate these calculations into a simple program which calculates a prediction surface based, for example, on local polynomial

smoothing. This approach was tried with some success for the IBTS data, but had the disadvantage that it could not easily incorporate the effects of covariates other than location. Unfortunately, the existing GAM-fitting packages do not easily allow for smoothing based on biological distances.

- iii. It would be useful to incorporate prior knowledge about fish behaviour into the spatial modelling, because a considerable amount of information about habitat use by fish is available from sources outside the IBTS surveys, for example from dedicated surveys of factors influencing sandeel abundance (Wright *et al.* 2000). An adaptation of model-supervised kernel smoothing (Matthiopoulos 2003) might provide an alternative framework for including the effects of environmental covariates to model the spatial distribution of prey.

In future, I plan to include detailed oceanographic covariates into the GAMs in order to investigate the relationships between fish distributions and the physical variables that drive primary production (Schrum, pers com).

### 6.2.3 Reconciling spatial scales

It is useful and informative to consider predator prey overlap when calculating prey availability, and it may be essential if a meaningful multi-species FR model is to emerge from the analysis (Floeter and Temming 2005). However, when the usage of space by predators and prey is complex, the calculation of

overlap is not straightforward and the relationship between prey availability and prey abundance may not have a simple form. As a result, an FR based on availability cannot be directly incorporated into a model of prey dynamics unless the intervening steps that are needed to calculate availability from prey abundance are coded explicitly in that model.

However the results of the present study and others (Floeter 2005) suggest that considerations of spatial effects are very important in estimating predator prey relationships. It may be possible to calculate availability from abundance in a straightforward way provided that predator and prey distributions do not vary between years. It may therefore be possible to incorporate this complexity into EBFMs (ICES 2005).

### **6.3 Can the uncertainties in consumption and prey availability be modelled appropriately?**

Using Bayesian methods to fit FRs made it possible to use appropriate statistical distributions to model uncertainty. For example, a simple model allowing for stomachs to be empty for a predictable proportion of time was incorporated in the minke whale FR fitting procedure.

By bootstrapping the prey data (in the case of the grey seals) and spatially sampling prey abundance surfaces (for the minke whales), uncertainty estimates were developed for the prey availability data. These were used in

the subsequent Bayesian fitting procedure. I believe that this is the first time that such uncertainty ('measurement error', Stephans and Dellaportas 1992) has been incorporated into models of prey consumption.

#### **6.4 What conclusions can be drawn from FR models about the role of a generalist predator in a complex food-web?**

##### 6.4.1 Parameter inspection and simple calculations

Where  $m$  is close to 1, a simple examination of the value of  $a$  for each prey species gives a crude indication as to which prey are preferred, if preference is calculated using Chesson's alpha index (Chesson 1978). Preference is one indicator of the strength of trophic links between a generalist predator and the prey species in its diet, provided that the relationship between availability and prey abundance is clear.

If  $m$  is greater than 1, preference for a given prey increases with the availability of that prey ('positive switching'), the FR will be sigmoidal, and there is the possibility that the predator and its prey can coexist at a low-density stable equilibrium. However, the actual existence of any such equilibria will depend on other factors also such as the form of the prey's intrinsic density dependence. If  $m$  is equal to 1, no switching occurs and there is no low-density equilibrium. This makes it difficult to explain how the two species can coexist. If  $m$  is less than 1, 'negative switching' is implied and this

has pathological consequences for prey dynamics at low densities (Rindorf 2003).

If maximum consumption rates for each prey type can be predicted directly from a multi-species FR, they can be compared and may indicate that some prey are 'easier' for a predator to consume or to digest than others. The impact of a predator on a prey population (in terms of net predation mortality) is likely to be greatest if the maximum consumption rate is high (i.e. if  $c_{max}$  is high and/or the handling time  $t$  is low) and the value of  $a$  is high.

Given any appropriate FR model and a set of parameter values, point estimates of the consumption of a prey of interest for different levels of prey availability can be made. Managers could utilise such a model to predict how general changes in prey availability (such as a drastic reduction in sandeel abundance in the North Sea) would be expected to influence predator diets. The posterior parameter distribution that results from a Bayesian analysis of consumption can also be used to indicate the uncertainty associated with the calculated values of consumption.

Knowledge of predator numbers is essential if the total quantities of prey consumed by predators are to be calculated. Even for UK grey seals, which are well studied, there is considerable uncertainty in the current population estimates (Thomas and Harwood 2004). The total number of whales present in

the Barents Sea in summer each year is believed to depend on the availability, and probably the distribution, of prey (Haug *et al.* 2002, Bogstad pers com). Uncertainties in predator numbers may therefore be an important component of uncertainty in estimates of the total consumption of prey by predators.

The ability of fish stocks to recover from low stock sizes depends on many factors, including mortality caused by all their predators, fishing mortality, and disease. The reproductive potential of the prey population must also be considered. Recruitment of fish is often highly variable, unpredictable and may be driven by abiotic factors.

A consumption model is therefore only one step, albeit an important one, in the sequence of calculations required to explore the implications of predation by a marine mammal on a fish stock. An examination of the parameters of the predator's FR may provide some indication of the nature of its impact on prey dynamics, this approach cannot be used to quantify these interactions (Yodzis 2000).

## 6.5 How can consumption models be incorporated into ecosystem-based fisheries models (EBFMs)

### 6.5.1 Do EBFMs need marine mammals at all?

EBFMs can be categorised in various ways (Hollowed *et al.* 2000), one useful working distinction is between models that are based on equilibrium flows of energy or carbon through a food web (e.g. ECOPATH, see Plaganyi and Butterworth 2004), and those that attempt to model the dynamics of a subset of all known species and trophic interactions ('minimum realistic models' or MRMs).

MRMs may not need to model the activities of higher predators explicitly in order to predict the trajectories of fish populations (Fulton *et al.* 2003). Marine mammals are long-lived and their populations tend to be slow to respond numerically to changes in prey abundance. As a result, their effects can be modelled, as a first approximation, by assuming that they are responsible for a constant background level of mortality (Hollowed *et al.* 2000).

If the conservation of marine mammal populations is the primary concern for managers, it may be sufficient to build an MRM that involves only the key fish species in the system. The effects of the changes in prey abundance predicted by the MRM can then be calculated under different scenarios (e.g. catch

quotas, which might impact on fish stocks) and the marine mammal FR used to link the predictions of the MRM to the dynamics of the marine mammal population, provided that the effect of consumption on the life history of the marine mammal - its numerical response - is known.

However, such an approach would not be adequate where marine mammal consumption is responsible for a large proportion of the natural mortality of fish or if it shows large scale changes with prey availability (Mori and Butterworth 2004, Bogstad and Haug 2000). In these circumstances, an explicit marine mammal FR should then be included within the MRM. Changes in the abundance of the marine mammals due to a numerical response (e.g. Matthiopoulos *et al.* 2006) or migration (Haug 2002) might also need to be modelled explicitly if they are expected to be large.

### 6.5.3 Incorporating models of consumption by marine mammals into EBFMs

A parameterised consumption model may play two roles in setting up an EBFM.

Independent studies of consumption by a predator may suggest the most appropriate form of the FR. For example, the results of the present study suggest that sigmoidal functional responses may be characteristic of marine mammal predation, and the consumption models used in EBFMs should allow for this. This result is also consistent with observations that fish predation is characterised by changes in suitability over time (Kempf 2005, ICES 2005).

Work to modify the form of the FRs used in existing EBFMs is presently in progress in collaboration with colleagues working on models for the North Sea and Barents Sea (Begley 2005, Vinther 2004, ICES 2005).

An EBFM can be entirely based on sub-models of consumption, growth, etc that have been parameterised independently or built from first principles. Such a model can then be used to simulate, for example, the qualitative effects of different management decisions or the likely impacts of climate change (Vichi *et al.* 2003). The sensitivity of outcomes of interest to the input parameter values can then be examined.

Some or all of the parameters of the EBFM may, however, be fitted using appropriate data sets, such as a time series of abundance measurements based on fishery and/or survey data. If the parameters of the consumption model are to be fitted as part of this process, then the original parameters of the consumption model can potentially be used as starting-values and/or to suggest constraints for parameter values during the fitting process. Koen-  
Alonso and Yodzis (2005) provide an example of this approach. Alternatively, posterior parameter distributions derived from a Bayesian fitting process for the individual sub-models could be used as priors for fitting an EBFM to the data set using Bayesian methods (Harwood and McLaren 2004).

#### 6.5.4 Scale-dependence of consumption models

For a given vector of prey abundances, a multi-species FR will indicate the quantity of food taken by an individual predator in a given time interval, the preferences of the predator and the composition of the diet. However, the estimates of consumption and preference will be scale-dependent. Therefore the consumption sub-model that is used in an EBFM must be matched to the temporal and spatial scale of the ecosystem being modelled.

##### *The scale-dependence of consumption rate*

Ideally, the consumption rate of a predator should be measured directly in the field and modelled with a full MSFR. The effects of changes in total prey availability on overall consumption can then be observed. For example, where prey is very abundant, more food may be taken than is required to fulfil the predator's energetic requirements. Predators may become 'choosy' and consume only those parts of killed prey items that are preferred. Care must also be taken in case field observations of consumption rates represent foraging over inappropriately short time scales. For example, animals which are observed when they are actively foraging may spend a proportion of their time engaged in activities which preclude foraging, such as resting, breeding, or migrating. Only if a detailed time-budget is available for these animals would it be possible to re-scale the estimates of consumption rates from the MSFR model, to match them with the monthly or annual time scales more

usually adopted in EBFMs. In practice, such detailed information is available only for well-studied species such as seals and seabirds, and is more difficult to obtain for cetacean species (McConnell *et al.* 1999, Boyd 2002, Benoit-Bird 2004).

Even when a full multi-species FR, the temporal and spatial scale of this model may not be appropriate, and modellers may be forced to resort to models of predator energetic requirements to set the maximum predator consumption rate. This will inevitably be the case if the only consumption data available is diet composition, as was the case for grey seals in Chapter 4.

The energetic requirements of marine mammals performing different activities can be estimated by direct or indirect measurements of metabolic rate in the laboratory (Sparling 2003) and, under special circumstances, in the field (Williams *et al.* 2004). Measurements of body composition can be used to estimate fat deposition (Reilly *et al.* 1996, Biuw *et al.* 2003) and the costs of reproduction can be estimated from measurements on individual mothers (Pomeroy *et al.* 1999). Average energetic requirements can then be inferred from the activity budgets of individual animals (Sparling 2003).

However, for large marine mammals such as baleen whales, energetic costs are virtually impossible to measure, either in the field or the laboratory.

Models then have to be based on assumed relationships between body size and metabolic rate or costs of reproduction, etc (Tjelmeland and Lindstrom 2005).

If it is impossible to measure consumption or energetic expenditure directly, then the uncertainties associated with models of energetic requirements should be accounted for explicitly when drawing inferences from the model.

### *The scale-dependence of preference*

Preference or suitability may well act as a surrogate variable for predator-prey overlap, when consumption models are fitted to data that have been collected over a large spatial area. This appears to be the case, for example, for the models fitted to fish prey consumption data for the North Sea (Floeter 2005, Floeter and Temming 2003). A predator will appear to have a strong preference for prey whose distribution is closely matched to its own. However, if predators or prey contract their range as their abundance declines, or if predators radically change their usage of space in response to changes in prey abundance, then predator preference may appear to change in a way that cannot easily be captured by a FR. The consequences of prey switching due to changes in prey abundance and due to changes in prey location are confounded (Trenkel *et al.* 2005). This might lead to difficulties in fitting a large-scale FR model directly to the prey abundance data.

There is some precedent for examining the spatial variation in the abundance (Kircher and McAllister 2002, Maury and Gascuel 2001) and prey consumption data (Bulgakova *et al.* 2002) that are used to parameterise EBFMs. It may be most appropriate to parameterise the FRs of marine mammals on a spatial

scale that is most relevant to the predator, having calculated the availability of prey to predators by means of spatial overlap. Predicted consumptions can then be incorporated into an EBFM using the methodology of Chapter 4.

#### 6.5.5 Incorporating consumption models for grey seals into EBFMs

Fish stocks in the North Sea have traditionally been assessed using single species Virtual Population Analysis. However, the population dynamics of a community may not be correctly represented by considering species in isolation (Mangel and Levin 2005), and single species approaches may be unable to predict important interactions. One example in the North Sea is the effect of increasing mesh size to facilitate the escapement of smaller fish. This resulted in increased populations of some predatory fish, which then inhibited the recovery of their prey (Pope 1991). The outcome from recent EU management decisions designed to conserve cod stocks predicted by EBFMs are quite different from those predicted by a single species model (Vinther 2004, ICES 2005).

Early EBFMs for the North Sea were based on a version of VPA (MSVPA - Vinther 2001). In MSVPA, total predator intake is assumed to be constant, and predator preference is allowed to vary between quarters but not between years. However, it is known that total intake is variable (Adlerstein *et al.* 2002), and that preference may also vary. The model 4M built upon the MSVPA approach, incorporating a variable total intake by predators that was a function of total prey availability (Gislason 1999). 4M has recently been

applied by the ICES multi species working group for the North Sea (ICES 2005), with predation by seals and seabirds included.

SMS, a multi-species stochastic version of 4M, (Vinther 2004, Lewy and Vinther 2004) is currently under development as part of an international EU-funded project (BECAUSE 2003). SMS allows for uncertainty in input data to be modelled explicitly, and fitting is carried out using a maximum likelihood method. Uncertainty in output predictions can also be explored. SMS is being used to explore the role of grey seals in the North Sea ecosystem and their impact on the recovery of the cod stocks.

#### 6.5.5 Incorporating consumption models for minke whales into EBFMs

Models of the interactions between minke whales, capelin, herring and cod in the Barents Sea are being constructed by Bogstad (pers com) using the GADGET framework (Begley 2005). GADGET is a multi-area, size-structured, monthly time-step model. Parameters are fitted to time series of abundance indices, diet and migration data using maximum likelihood methods. A simple population model for minke whales is under construction and will be fitted to a historical time series of fish stock data. It will use a growth model and a size-based energetic model for the whales (Lindstrom, pers com), with preferences and switching modelled using the multi-species FR developed in Chapter 5. The effects of different scenarios, for example the impacts of variations in the number of whales resident in the Barents Sea in summer or

the dramatic fluctuations in fish abundance that have occurred within the Barents Sea, on the life history of the whales will be explored using this model.

Future work will involve the fitting of a model that allows for trophic interactions between whales and fish, and between fish species, to a larger data set including fish stomach contents and fish abundance indices. This should indicate the importance of any indirect interactions, such as trade-offs for a given prey species between direct consumption by whales, and decreases in the numbers of fish predators which are also consumed by the whales (Bogstad 1997). Given the uncertainty in whale numbers, it will be particularly important to explore the impacts of changes in whale numbers on the predictions of this model

## 6.6 Recommendations and Aspirations

Fitting multi-species FR models to field data is difficult: a large amount of data is required, there is likely to be significant uncertainty in measurements of both consumption and availability, and standard statistical techniques are unlikely to be suitable. Bayesian methods offer solutions to these difficulties and are easily applied using freely-available software. They have the additional and important advantage that the output of the Bayesian fitting process is a full joint posterior distribution that can be used to explore the uncertainty in the inferences made from the model.

In order to obtain a realistic model of the relationship between prey abundance and consumption, it is crucial to consider the spatial and temporal scale over which these quantities are measured, to ensure that consumption and prey availability are measured sufficiently closely in time, and to consider whether spatial effects should be taken into account in modelling the availability of prey to predators. Ideally, uncertainty in prey availability should be incorporated directly into the fitting process. If this cannot be done because, for example, fitting is carried out using standard software, the sensitivity of the fitted parameters to uncertainty in prey abundance should be investigated.

A fitted multi-species FR can be used to identify which prey species are most important to marine mammals, and to predict the predation mortality that

they will impose on a focal prey species, under a given regime of predator and prey abundance. Thus a consumption model may add significantly to arguments concerning marine mammal - fisheries conflicts that are based on spatial overlap alone (Reid *et al.* 2004, Kaschner *et al.* 2001).

This may, in itself, inform decisions for the management of predator or prey populations. However, the true implications of predation for predators and prey, such as the size of population cycles and the outcome of indirect effects such as apparent competition, can only be inferred if all the trophic links in the system are accounted for in sufficient and appropriate detail (Yodzis 2000, Fulton *et al.* 2003, Collie and Gislason 2001, Gislason 2000). If marine mammals are of interest, either because they are to be conserved or because they are competitors with commercial fisheries, their multi-species FRs should be incorporated into EBFMs.

In order to do this, the spatial scales of whole ecosystem models, predator and prey spatial distributions, and foraging, must be reconciled (Babcock *et al.* 2005). For example, foraging by some predators may be highly localised within a large ecosystem. Reliable models of the spatial distribution of predators and prey are needed in order to meet this challenge. The spatial modelling of prey distributions based on abiotic factors (Hedger *et al.* 2004, Blanchard *et al.* 2005) and the parameterisation of the aggregative responses of higher predators to these distributions (MacLeod *et al.* 2004, Trenkel *et al.* 2005, Temming *et al.* 2004, Yen 2004) may provide this important link

between spatial scales. For marine mammals, studies of habitat use, which are often motivated by conservation concerns (for example, Canadas *et al.* 2005, Hastie *et al.* 2005, Gregr and Trites 2001), may find new applications in modelling and predicting consumption.

In systems where prey populations are particularly difficult to assess, information contained in predator diets might be used to monitor prey availability and abundance (Bunce 2004). If the effect of energy or nutrient intake on predators is known, changes in predator life history parameters such as reproductive rate could be used to indicate changes in prey availability (Reid *et al.* 2005). Predators might thus be used to provide 'ecological quality metrics', defined as 'measurement scales or dimensions by which ecological quality may be measured' (OSPAR 2002a,b). However, careful modelling of the relationship between prey abundance, predator consumption and predator performance is essential if predators are to be used as ecosystem indicators (Boyd *et al.* 2006).

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## Appendix 1: WinBUGS code for fitting grey seal functional responses

### Model 1

```

# WinBUGS model for fitting an MSFR to seal data
#
# input availability as gamma distributions, with shape and
# rate in the data set
#
# input consumption data (consumption in kg per day)
#
# parameterisation of the MSFR is due to Real (1975)
#
# First part - the model
# loop over data points
# and then over species

model{

for ( j in 1:Ndata){

  for(h in 1:Nspecies){

N[j,h]~dgamma(nshape[j,h],nrate[j,h])
product[j,h] <- t[h]*a[h]* pow(N[j,h],m[h])

  }

denom[j] <- 1+sum(product[j,])

for (k in 1:Nspecies){

  mu[j,k] <- (product[j,k])/(denom[j]*t[k])

  c[j,k]~dpois(mu[j,k])

}

} # end of model

```

```
## setting priors

# fix the value of handling time according cmax = 1/t
# and the seal's energetic requirements

t[1]=1/7.44
t[2]=1/7.44
t[3]=1/7.12
t[4]=1/5.86
t[5]=1/7.34
t[6]=1/6.69
t[7]=1/4.02

# for all prey, set m based on SSFR from the pool experiments
# and a broad prior on a

for(i in 1:7){

m[i]~dgamma(20,16)
a[i]~dunif(0,1000)

} # end of priors section

}# end of program
```

## Model 2

```

# WinBUGS code for fitting consumption model
#
# based on proportions of prey in the diet
#
# derived from the MSFR model of Real (1975)
#
# input data is in the form of:
#
# the number of species in the model (Nspecies)
#
# distributions of availability N (shape and rate
# parameters for each species)
#
# total biomass of prey inferred from scat samples at
# each site/date
#
# biomass of each class of prey inferred from the scat
# samples
#
# the number of samples (Ndata)
#

model{  ### main model

for ( j in 1:Ndata){

  for(h in 1:(Nspecies) ){

n[j,h]~dgamma(nshape[j,h],nrate[j,h])
N[j,h]<-n[j,h]

product[j,h] <-a[h]* pow(N[j,h],m[h])

  }

denom[j]<-sum(product[j,1:Nspecies])

for (k in 1:(Nspecies)){

  mu[j,k]<- (product[j,k])/(denom[j])
  expected.mass[j,k]<-mu[j,k]*total.biomass[j]
  c[j,k]~dpois(expected.mass[j,k])

}

} # end of model

```

```
### priors

# a for sandeels is fixed
a[7]<-1

# other a priors are uniform
for(i in 1:6) { a[i]~dunif(0,1) }

# m priors are based on pool experiments
for(i in 1:7) { m[i]~dgamma(80,50) }

} # end of code
```

## Appendix 2: WinBugs code for fitting functional response model for minke whales

```

# minke whale functional response model
# repeated values of N1, N2, N3 are based on bootstrap resampling of
# prey data

# c = biomass, assumed to be consumed over a 2 hour period

# error model is bernoulli*poisson, allowing for extra 0's in the data

#####
# main model #
#####

model{

for ( j in 1:Ndata){

  for(rnumber in 1:1000){

div1[j,rnumber]<-N1[j,rnumber]/nhalf[1]
div2[j,rnumber]<-N2[j,rnumber]/nhalf[2]
div3[j,rnumber]<-N3[j,rnumber]/nhalf[3]

product[j,rnumber,1] <- pow(div1[j,rnumber],m[1])
product[j,rnumber,2] <- pow(div2[j,rnumber],m[2])
product[j,rnumber,3] <- pow(div3[j,rnumber],m[3])

denom[j,rnumber]<-sum(product[j,rnumber,]) +1

for (k in 1:Nspecies){

eat.it[j,k,rnumber]-dbern(prob.eat)
mu[j,k,rnumber]<- eat.it[j,k,rnumber]*(2*cmax[k]*product[j,rnumber,k])/denom[j,rnumber]

c[j,k]-dpois(mu[j,k,rnumber])

} # end loop over species

} # end loop over repeated measures

} # end loop over whales

#####
## setting priors ##
#####

nhalf[1]-dgamma(3,0.0001)
nhalf[2]-dgamma(3,0.00005)
nhalf[3]-dgamma(3,0.00005)

cmax[1]-dgamma(31,0.3)
cmax[2]-dgamma(15,0.3)
cmax[3]-dgamma(30,0.5)

prob.eat-dunif(0,1)

m[1]-dgamma(76,20)
m[2]-dgamma(19,10)
m[3]-dgamma(35,11)

}

```

**Appendix 3: the data that were used to fit the functional response for minke whales**

*i) This is the table of data that results for the 1.8 n.m. case:*

whale ID	availability of capelin		availability of herring		availability of krill		consumption rate		
	mean	sd	mean	sd	mean	sd	capelin	herring	krill
1	4200	1483	7530	5166	39376	7491	0	0	1.545
2	6281	1351	4099	2910	30010	7627	0	0	5.32
3	4349	775	1696	700	33705	4781	0	0	9.601
4	3231	822	863	509	27086	5503	0	0	17.533
5	3275	865	826	570	26486	5457	0	0	9.271
6	337	771	9777	5055	13596	7976	0	0.285	6.826
7	2868	677	13677	5811	13868	6455	0.411	4.434	0
8	2192	857	1341	587	23795	10041	1.759	0	1.3
9	2166	844	1287	532	23725	9767	3.958	0	5
10	733	672	1256	781	30483	10650	0	0	15.092
11	5696	1863	132	1379	16379	5825	10.559	0	19.53
12	11058	2595	26	151	16006	2416	7.843	0	0.2
13	8545	3119	7	11	20299	4691	10.207	0	0
14	11439	2843	32	149	20242	3851	0	0	0
15	11533	2827	35	148	20239	4070	0	0	0
16	6137	2238	0	0	22975	4156	0	0	0
17	1650	251	1	5	23151	4026	0	0	56.242
18	1350	286	0	0	16020	4017	0	0	42.199
19	1276	566	3401	4005	5835	5019	0	0	2.146
20	3159	752	54	799	6020	5253	19.192	0	0
21	11119	3307	315	590	12686	2164	0	0	57.655
22	6991	3334	310	540	20548	9287	0	0	0.99
23	4111	691	72	248	12703	3877	30.615	0	6.955
24	5293	1423	13	32	27155	8401	0	0	0
25	2118	484	5228	3300	10269	5085	0	1.133	24.192
26	2263	604	8254	4580	8901	5929	0	9.151	0

ii) *For the 2.5 n.m. case*

whale ID	<i>availability of capelin</i>		<i>availability of herring</i>		<i>availability of krill</i>		<i>consumption rate</i>		
	<i>mean</i>	<i>sd</i>	<i>mean</i>	<i>sd</i>	<i>mean</i>	<i>sd</i>	capelin	herring	krill
1	4230	1914	8634	8397	36596	8886	0	0	1.545
2	6192	1716	4385	3711	30038	8665	0	0	5.32
3	4321	1106	1684	1278	32537	6073	0	0	9.601
4	3187	1144	835	727	25620	6799	0	0	17.533
5	3298	1222	896	955	24963	7014	0	0	9.271
6	637	1466	9505	6271	16347	11556	0	0.285	6.826
7	2793	876	12632	6946	14241	7568	0.411	4.434	0
8	1938	956	1558	1113	21986	11889	1.759	0	1.3
9	1943	938	1547	1247	22777	11735	3.958	0	5
10	747	732	1504	1432	29198	12676	0	0	15.092
11	5518	2080	628	2962	16425	6228	10.559	0	19.53
12	10252	3403	65	266	16132	3347	7.843	0	0.2
13	8377	3849	22	167	19573	5831	10.207	0	0
14	10803	3492	77	353	19799	5149	0	0	0
15	10934	3578	78	272	19726	5002	0	0	0
16	6750	3893	0	0	23124	4994	0	0	0
17	1713	357	5	33	22939	5491	0	0	56.242
18	1457	379	0	3	16547	5016	0	0	42.199
19	1529	768	4067	4569	7856	6780	0	0	2.146
20	3254	943	348	2093	7672	7197	19.192	0	0
21	10294	3940	427	907	13437	3019	0	0	57.655
22	6999	3702	403	841	20677	9978	0	0	0.99
23	4206	1046	146	590	13944	6380	30.615	0	6.955
24	5342	2032	22	133	25776	9173	0	0	0
25	2063	608	5557	4484	10759	6557	0	1.133	24.192
26	2250	744	8295	5531	10073	7769	0	9.151	0