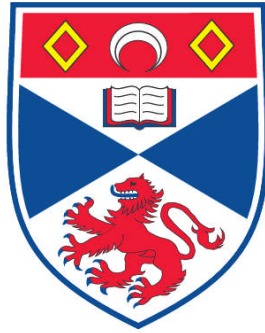


**A BAYESIAN APPROACH TO MODELLING FIELD DATA ON
MULTI-SPECIES PREDATOR PREY-INTERACTIONS**

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A Bayesian approach to modelling field data on multi-species
predator-prey interactions

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30 September 2005
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Declarations and statements

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I, Christian Asseburg, hereby certify that this thesis, which is approximately 35,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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I was admitted as a research student in September 2001 and as a candidate for the degree of PhD in September 2002; the higher study for which this is a record was carried out in the University of St Andrews between 2001 and 2005.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of PhD in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

date: _____ signature of supervisor: _____

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Abstract

Multi-species functional response models are required to model the predation of generalist predators, which consume more than one prey species. In chapter 2, a new model for the multi-species functional response is presented. This model can describe generalist predators that exhibit functional responses of Holling type II to some of their prey and of type III to other prey. In chapter 3, I review some of the theoretical distinctions between Bayesian and frequentist statistics and show how Bayesian statistics are particularly well-suited for the fitting of functional response models because uncertainty can be represented comprehensively. In chapters 4 and 5, the multi-species functional response model is fitted to field data on two generalist predators: the hen harrier *Circus cyaneus* and the harp seal *Phoca groenlandica*. I am not aware of any previous Bayesian model of the multi-species functional response that has been fitted to field data.

The hen harrier's functional response fitted in chapter 4 is strongly sigmoidal to the densities of red grouse *Lagopus lagopus scoticus*, but no type III shape was detected in the response to the two main prey species, field vole *Microtus agrestis* and meadow pipit *Anthus pratensis*. The impact of using Bayesian or frequentist models on the resulting functional response is discussed. In chapter 5, no functional response could be fitted to the data on harp seal predation. Possible reasons are discussed, including poor data quality or a lack of relevance of the available data for informing a behavioural functional response model.

I conclude with a comparison of the role that functional responses play in behavioural, population and community ecology and emphasise the need for further research into unifying these different approaches to understanding predation with particular reference to predator movement.

In an appendix, I evaluate the possibility of using a functional response for inferring the abundances of prey species from performance indicators of generalist predators feeding on these prey. I argue that this approach may be futile in general, because a generalist predator's energy intake does not depend on the density of any single of its prey, so that the possibly unknown densities of all prey need to be taken into account.

1 Introduction

1.1 Ecological modelling

Ecological modelling is a tool with two major purposes: to elicit an understanding of the interactions between species and better knowledge of their biology, and to predict future states of ecosystems, for example as a consequence of human actions. Gurney and Nisbet (1998) provide a technical introduction to ecological modelling and Hilborn and Mangel (1997) introduce the reader to the investigative approach to ecological modelling. However, a model necessarily is a reduced view of nature. Due to computational limitations, we cannot model ecosystems to the fine resolution at which they operate, and, even if we could, the detailed information required for this is usually not available. Uncertainty enters the modelling process at various stages, and a successful modeller needs to be aware of these uncertainties. Many ideas of how uncertainty can be incorporated into mathematical models and used for risk management are summarised in Morgan and Henrion (1990).

1.2 Why model ecosystems?

Apart from human curiosity, the study of ecosystems is motivated by several reasons. People interact with their environment in many ways, ranging from aesthetic contemplation and leisure activities to intense exploitation of natural resources. We are drastically changing the ecosystems around us, and ecosystem models can provide some insight into the effects that we have on ecosystems. By feeding back into management mechanisms, an ecological model can help us sustain the benefits that we derive from our position in nature, for example by allowing us to assess whether we harvest sustainably. Common management objectives are the conservation of endangered species, the maintenance of biodiversity (Sainsbury *et al.* 2000), or the maximising of economic returns (Murawski 2000).

The starting-point of this PhD thesis was the question on how to improve the management of human intervention in marine ecosystems. Because of the dangers of over-fishing a common resource (cf. the “tragedy of the commons”, Hardin (1968)), fisheries models have been in place in many countries to limit the amount of fish removed from the sea. A prevalent concept in fisheries management models is that of “maximum sustainable yield” (MSY, see Beddington and Cooke (1982)), i. e. a maximum amount of fish that can be harvested before the fish stock suffers from the adverse impacts of exploitation. In theory, MSY summarises the possible coexistence of humans interacting with the ecosystem without harming it.

But, if a predator preys on a species of interest also to humans, this predator will be seen as a competitor. To increase yield further, without causing higher mortality to the target species, culls of predators are usually suggested. However, leaving ethical questions aside, it is unclear whether such a cull actually has any beneficial influence on prey abundance. Taking the above simplified position on the interactions between one prey and one predator ignores the ecosystem setting. Resulting surplus prey production may be simply unavailable for human exploitation, or other predators may step in to consume it. Removal of a predator may even have adverse effects on the target species, when other of its prey become more abundant and compete with the target species. This effect is known as mesopredator release, and its importance was seen as particularly striking in Punt and Butterworth (1995).

Two conclusions can be drawn from these predator-prey considerations. First, predator-prey interactions are an important component in the assessment models of harvested populations. The current lack of knowledge on trophic links in the context of stock assessment models can be seen in the contribution of this component to the uncertainty inherent in current predictions of future stock sizes. In stock assessments for the Newfoundland cod stocks, for example, predation of other species on cod is the model component that contributes the most to the overall uncertainty of the cod population estimates (Shelton *et al.* 1995). Second, the need for explicit multispecies modelling in setting total allowable catch quotas is well established (Murawski (2000), Gislason (1999)), but the current lack of understanding of ecosystem processes such as predator-prey interactions make it difficult to obtain precise conclusions from multispecies models (Ripa *et al.* (1998), Sainsbury *et al.* (2000)). In this PhD thesis I extend the theory on multi-species predator-prey interactions by introducing a new mathematical model (Chapter 2) and showing how it can be fitted to field data on predation by a terrestrial predator (Chapter 4) and by a marine predator (Chapter 5).

In marine environments, predators may be easier to observe than their prey because they are larger or show more conspicuous foraging behaviour. It has therefore been suggested to observe these more conspicuous predator populations and deduce prey abundances from observations on predator fitness. For example, within the Convention on the Conservation of Antarctic Marine Living Resources, a range of variables on the population dynamics of nine predators on krill (*Euphausia superba*) are monitored with the aim of informing models of krill abundance (Constable *et al.* 2000). I have contributed to the analysis of the theoretical viability of such an approach, and because this relies on multi-species predator-prey theory, the results of this analysis are included as an Appendix to this thesis. However, throughout the Chapters of this thesis, I will limit myself to studying the link from prey abundances to inform predator consumption.

1.3 Uncertainty in ecological modelling

Managers do not like uncertainty, to them high uncertainty means high risk. The precautionary approach translates this point of view into action: when the results of management actions are unclear, choose a management option that avoids undesirable outcomes (for a review of definitions see Francis and Shotton (1997)). Scientists and managers, however, have come to acknowledge that predictions about the future of ecosystems necessitate the use of methods that account for uncertainty. Accordingly, there is a need for scientists to communicate their findings on uncertainty in accessible form (Bradshaw and Borchers (2000), Geromont *et al.* (1999)). In Chapter 3 I show that Bayesian statistics is a suitable tool for modelling uncertainty in ecological contexts and that decision-makers may find it easier to understand results from Bayesian methods than from “classical”, frequentist statistics.

The precautionary principle is the managers’ incentive for reducing uncertainty, because predictions with high uncertainty do not translate into management guidelines. However, ecological systems are highly unpredictable (Harwood and Stokes 2002), and predictions will always contain some uncertainty (Dovers *et al.* 1996). There is thus a trade-off between investing resources into reducing uncertainty, and accepting that results will always be imprecise but management decisions still have to be made (Harwood and Stokes (2002), Bradshaw and Borchers (2000), Hodges (1987)).

Trying to model ecosystems in all their complexity is thus driven not only by curiosity, but also by the need to make sense of the multitude of factors that constitute an ecosystem (Lubchenco *et al.* 1991). However, current understanding of marine ecosystems is sparse—data are available on key species of commercial or conservation interest, but an understanding of the overall functioning of marine life is still missing (Sainsbury *et al.* 2000). Uncertainty is fundamental to all scientific activities (Ellison 1996), and it is vital to know how it enters the modelling process (Ludwig *et al.* 1993). Widely diverging views among ecologists on the likely outcomes of management actions are an indicator of a lack of understanding of the environment (Dovers *et al.* 1996). By taking into account various sources of uncertainty, science may possibly overcome this confusion or at least direct future research (Cochrane 1999).

1.4 Summary

Through modelling, we try to improve our understanding of the interactions between species and of their biology, and we aim to predict future states of ecosystems, for example as a consequence of human actions such as ecosystem disturbance or harvesting. Harvesting of natural populations is usually directed towards a target species, as in game hunting or in fisheries, although fisheries

also harvest indiscriminate other species through incidental take. If a predator preys on the species of interest also to humans, it can be seen as a competitor because it causes additional mortality to the prey. To understand the role of the target species in its ecosystem fully with the aid of a model, predator-prey interactions are thus a required component. Also in the assessment of the impact of human disturbance on a rare species the ecosystem context needs to be recognised, because human actions affect not only the species of interest, but all its predators and prey, too. The need for an ecosystem approach thus pervades in ecological modelling regardless of the purpose of the model.

The amounts of prey consumed by a predator are quantified by the functional response. In Chapter 2, I introduce the theory of functional response modelling in a multi-species context. However, nature is always more complex than a model. Uncertainty enters the modelling process from several sources, and these uncertainties have to be taken into account in any statistical model. In Chapter 3, I present the foundations of Bayesian statistics and show why it is suitable for modelling uncertainty in ecology. In Chapters 4 and 5 I show how Bayesian statistics can be used to fit models of the multi-species functional response to field data.

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2 The functional response and prey switching

2.1 Predator–prey interactions

Trophic interactions between predators and their prey are a key to understanding dynamic processes in ecosystems. To analyse the effects of changing prey numbers on predator populations, three components of the predator-prey interaction can be distinguished (e. g. Turchin (2003)). Changes in prey density affect the rate at which prey are killed by an individual predator—this predator “response” is called the **functional response** (Solomon 1949). Predators also tend to move to areas of higher prey density—this is called the **aggregative response**. Finally, variations in prey consumption affect predator population sizes—this is known as the predator’s **numerical response**.

The functional response, together with predator abundance, determines the predation mortality suffered by each prey individual. Other processes that affect predation, such as predator population growth, operate on a slower time-scale and primarily through the numerical response (Oaten and Murdoch 1975b). It is therefore the functional response that has received a lot of attention when the prey population forms the focus of an ecological study (for a review of functional response theory, see e. g. Gentleman *et al.* (2003), Jeschke *et al.* (2002)). Below, I outline some of the factors determining a predator’s functional response (section 2.2), introduce the concept of functional response types (section 2.3), prey switching (section 2.4), and return to the question of the ecological impact of a predator’s functional response (section 2.5), before suggesting a general multi-species functional response equation and describing its properties (sections 2.6 and 2.7).

2.2 Factors influencing the functional response

2.2.1 Prey densities

The higher the prey density, the more likely a randomly-foraging predator is to encounter prey. Accordingly, the predator’s consumption rate is likely to increase with prey density, up to a maximum consumption rate determined by the time predators have available for foraging, which is inevitably limited (see e. g. Holling (1965)). When a functional response is specified in a model, this relation to prey abundance is quantified. Usually prey densities are the key inputs to any functional response model, and only very few models of population dynamics ignore the relationship between prey consumption and prey availability by assuming a constant rate of prey intake across all prey densities.

2.2.2 Other factors

Many factors other than prey densities can influence predation (see e. g. Ivlev (1961) for a comprehensive overview). For example, **prey behaviour** can affect predation, because prey may exhibit defensive behaviour at high prey densities (e. g. Khan *et al.* (2004)), thus reducing the predator's consumption rate. Also, at very low prey densities prey may escape consumption entirely because the predator may be unable to detect them. Similarly, **predator density** can impact on the functional response. At higher predator densities, competition for the available supply of prey makes it inevitable that predators will impede each other in their foraging (Abrams and Ginzburg 2000). Predator species may also show facilitative interactions, for example by hunting in groups when predator densities are sufficiently high. The **spatial distribution** both of prey and of predators can also affect the functional response—this is a complex issue that has generated a lot of research (for some starting-points, see e. g. Cuddington and Yodzis (2000), Durrett and Levin (1994), Murdoch (1994), or a general text such as Murray (1989)). For example, a heterogeneous prey distribution could result in higher consumption rates for those predators that are adapted to discovering prey that occurs in patches. Other predators may be able to detect single prey regardless of local prey densities, and consumption rates for these predators may be expected to vary little with distribution of prey. Even for these predators, however, a heterogeneous prey distribution may introduce a higher variance into the functional response, as predators may be lucky or unlucky in finding patches of high prey density. **Differences between individual predators** may be important in modelling the functional response, too, because individual predators are not identical, and assuming a common functional response for predators is, then, a theoretical approximation that is made necessary by the decision to use population models, rather than individual models. Finally, **environmental factors** such as weather, time of day, season, pollution and environmental stresses, interactions with human or other animal populations, the presence of hyper-predators, and other environmental variables may change the predator's functional response.

A functional response model will always be a simplified representation of real predator-prey interactions. The decision to include any of the factors listed above can be guided by reflecting on their importance in the context of each study. For example, in quantifying the overall annual predation mortality of a prey population, the effects of weather that favour or impede predation may cancel each other on average. On the other hand, if it is desired to understand daily changes of predation rates, weather may be an essential factor in the model. By failing to model such a factor, the remaining components of the model have to account for this unexplained variability, and estimates of the functional response may show higher uncertainty. But at the same time the model becomes simpler.

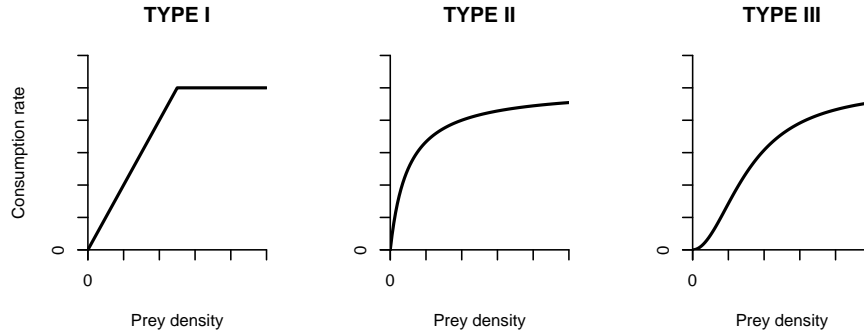


Figure 2.1: **Functional response types I, II and III.** Relationship between prey density and consumption rate for an individual predator. The numbering of these types is due to Holling (e. g. Holling (1959)).

2.3 Functional response types

2.3.1 Holling’s classification of functional response types

Leaving aside for now the debates introduced above and returning to the form of the functional response itself, we can distinguish different shapes in the relationship between prey consumption rate and prey density. Holling (e. g. Holling (1965)) identified three distinct possible shapes and named these **types I, II and III**. His classification is in widespread use (see e. g. Turchin (2003) or Trexler *et al.* (1988)). All three Holling types have in common a satiation of the predator at a maximum consumption rate (see Figure 2.1), for sufficiently high prey densities. However, whereas type I approaches this limit linearly and changes suddenly to a constant consumption rate, type II reaches the satiation limit asymptotically. Type III is a modification of type II which assumes lower predation rates for low prey densities, accelerating predation rates and the levelling-off at satiation. The type II response is also known as the hyperbolic functional response, and type III is also called the s-shaped or sigmoidal functional response. Holling also defined a type IV functional response that is characterised by a reduction of predation rates when prey abundances increase beyond a threshold (Holling 1959), thought to arise through anti-predator defence when prey occurs in large groups (e. g. toxicity or schooling in fish) – but the examples studied in this thesis do not require the recourse to type IV responses.

To model each type of functional response shape, many different mathematical equations have been proposed that relate prey density N to consumption rate F . A common choice for the type II functional response is Holling’s original model (called the “disc equation”, Holling (1959)):

$$F = m \frac{N}{k + N} = \frac{aN}{1 + atN}. \quad (2.1)$$

Holling’s disc equation has a very explicit and clear underlying behavioural model (Holling 1959). In the first parameterisation, m is the maximum consumption rate that is reached asymptotically as prey density increases, and k is the “half-saturation constant”, i. e. the prey density at which consumption is at half its maximum value (cf. Gentleman *et al.* (2003)). In the second parameterisation, a is a parameter representing the rate of successful attacks and t is the time required to attack, capture and digest a prey item. Depending on a model’s scope and applications other formulations for the type II functional response may be chosen that take into account different covariates or mechanistic explanations. Likewise, there is not just one mathematical equation to represent the type III functional response, and many models have been suggested. Jeschke *et al.* (2002) includes a comprehensive review of some type II and type III functional response models and their properties.

2.3.2 Generalist predators

Generalist predators, which consume more than one prey type, have to choose between the different prey types available to them. When a generalist predator consumes more of one prey (for example, because it has become more available), it may have to eat less of other prey accordingly. The consumption rate of one prey by a generalist predator can thus change even when this prey’s density remains unchanged. Functional responses like these, which depend on the abundances of more than one prey, are known as **multi-species functional responses**.

2.4 Prey selection in generalist predators

2.4.1 Prey switching

Many predators consume abundant prey at disproportionately higher consumption rates. Such behaviour is known as **prey switching**, and it has been observed in many generalist predators (for example, Murdoch (1969), Greenwood and Elton (1979), Akre and Johnson (1979), Joly and Patterson (2003)). For the two-prey case, Murdoch (1969) identified “switching” by comparing the ratio of the two prey types i and j in the predator’s diet to the ratio of their abundances: $F_i/F_j = C(N_i, N_j)N_i/N_j$. If the factor of proportionality $C(N_i, N_j)$ increases for higher relative abundance of prey i , the predator is directing disproportionately more attention to the more abundant prey i . Murdoch (1969) did not distinguish between numbers of prey attacked and numbers of prey eaten, but switching is more commonly applied to relative consumption rates rather than to encounter rates (e. g. Real (1977)), to link it to the functional response.

In a two-prey system, a switching predator thus has non-constant preference for both prey i

and prey j . Murdoch defines switching only for two-prey systems, but his definition can be extended to predators of more than two prey by defining proportionality factors $C_{i,j}(N_i, N_j) = (F_i/N_i)/(F_j/N_j)$ for every pair of prey types. In cases with more than two prey, it is possible for a predator to switch from or to a prey i for which it exhibits constant prey preference as measured on the scale of Chesson (1978)'s index of selectivity α_i .

2.4.2 Switching and the functional response

I challenge the view that type III functional responses are linked to predators that switch. Murdoch (1973), for example, argues that type III functional responses emerge from the predator's switching behaviour as follows. At constant abundance of prey i , the predator consumes relatively little of prey j when this prey is at low abundance, but at higher densities of prey j the predator devotes disproportionately more foraging effort to it, resulting in an s-shaped relationship between the consumption rate of prey j and its density. This s-shape is characteristic of single-species type III functional response curves. Because type III functional responses, at low prey densities, define a low prey consumption that increases with the prey population size and thus mimic the prey consumption pattern implied by prey switching, the type III functional response has been called the "switching response" (e. g. Gismervik and Andersen (1998)).

However, this argument is weak on several counts. First, prey switching is defined with reference to the relative abundances and relative amounts consumed of two prey i and j , whereas the functional response refers to absolute abundances and consumptions. The argument above glosses over this incongruity. Second, the argument above does not carry over easily to a multi-species modelling context, in which the abundances of both prey i and prey j vary independently. In the example above, the abundance of prey i was assumed to be constant, and any single-species functional response for prey i would thus predict constant consumption of this prey, but the example has the predator switch away from prey i when the abundance of prey j increases. By the same reasoning that suggests a type III functional response to prey j , we would expect a single-species functional response to prey i that can produce different consumption rates of prey i relating to the same abundance of prey i , which is impossible. The example above must thus be understood in an explicitly multi-species context. But then it is the multi-species component (availability of alternative prey i , measured absolutely or relative to availability of prey j) that results in the predator consuming disproportionately more prey j when switching to it, and not the functional response to the density of prey j itself, whose type is not determined in this example. Switching, therefore, does not necessarily imply a type III single-species functional response (see also Oaten and Murdoch (1975a)).

What is more, switching can occur even with some type I or type II functional response models.

For a very simplistic example, assume that a predator has a type I functional response to two prey i and j . Assume also that, when exposed to prey i at densities above $N_i = 50$, the predator's consumption of prey i satiates at $F_i = 5$, whereas for prey j the numbers are $N_j = 100$ and $F_j = 20$. A generalist predator described by these type I functional responses is a switching predator, according to Murdoch's definition of switching, because its switching coefficient $C(N_i, N_j)$ changes with prey abundance. For example, at densities of $N_i = 20$, $N_j = 20$, the consumptions predicted by the (linear) functional response are $F_i = 2$, $F_j = 4$, giving $C(N_i, N_j) = 1/2$. But at densities of, say, $N_i = 80$, $N_j = 40$, the corresponding consumptions are $F_i = 5$ (satiated) and $F_j = 8$, giving $C(N_i, N_j) = 5/16 \neq 1/2$, which indicates switching.

Some type II functional response models also allow switching. For example, switching is observed when two prey satisfy the type II "random predator equation" (see Colton (1987)), where consumption rates F_1 , F_2 and prey abundances are related as follows.

$$F_1 = N_1 \{1 - \exp[-a_1(T - t_1F_1 - t_2F_2)]\} \quad (2.2)$$

$$F_2 = N_2 \{1 - \exp[-a_2(T - t_1F_1 - t_2F_2)]\} \quad (2.3)$$

Here, just as in Holling's Disc model (equation (2.1)), a are constant parameters that represent the rate of successful attacks, and t are the times required to attack, consume and digest one prey item. T represents the time available for foraging. In this model, Murdoch's factor of proportionality

$$C(N_i, N_j) = \frac{F_1/N_1}{F_2/N_2} = \frac{1 - \exp[-a_1(T - t_1F_1 - t_2F_2)]}{1 - \exp[-a_2(T - t_1F_1 - t_2F_2)]}$$

changes with prey densities N_1 , N_2 , unless one can assume that $t_1F_1 + t_2F_2$ is constant. A constant $t_1F_1 + t_2F_2$, however, would indicate that the total time spent on predation does not change with prey densities, which is unrealistic. The "random predator equation" is thus a type II functional response model that allows switching.

Some type II functional responses, however, do not allow switching. For example, the two-prey generalisation of Holling's disc equation (Murdoch 1973),

$$F_1 = \frac{a_1N_1}{1 + a_1t_1N_1 + a_2t_2N_2} \quad (2.4)$$

$$F_2 = \frac{a_2N_2}{1 + a_1t_1N_1 + a_2t_2N_2} \quad (2.5)$$

gives Murdoch's factor of proportionality

$$C(N_i, N_j) = \frac{F_1/N_1}{F_2/N_2} = \frac{a_1}{a_2},$$

i. e. equal to the ratio of the constant attack rates on either prey, which is constant.

Without specifying a particular functional response model, there is thus no generally applicable link between switching and functional response type.

2.4.3 Mechanisms that can cause a type III functional response

At the level of an individual predator, two mechanisms are often suggested that can cause predation rates to show functional responses of type III. The “learning” theory assumes that predators gain experience at hunting abundant prey, for example by forming a search-image, by learning to look for prey in particular types of area, or by adjusting their search paths (see e. g. Real (1979)). Accordingly, at low prey densities the predator is not attuned to capturing the prey. Real (1979) shows mathematically that a type III functional response represents this mechanism. On the other hand, the “refuge” theory postulates that prey have limited places available in which to hide from the predator, or are difficult to detect in small numbers, and thus escape predation at low prey densities (see e. g. Murdoch (1973)).

Hassell (quoted in Abrams (1982)) suggested that a change in the total time spent foraging with prey density is one mechanism that could convert a type II response into a type III response. Abrams (1982) shows mathematically that, if predators optimise time spent foraging (and with it the energetic return of foraging) against a trade-off such as mortality and reproductive ability depending on foraging time, then an overall functional response of type III could emerge for an individual predator that forages with a type II functional response. Dunbrack and Giguère (1987) extended Abrams’ argument to show that, in predators that actively search or filter for prey, a dependence of the energetic cost of searching or filtering on prey density can imply a type III functional response because the costs associated with foraging for each prey item are higher at low prey densities.

Type III functional responses can arise when the handling time, i. e. the time a predator requires to catch, consume and digest one prey item, or the predator’s attack rate change with prey density (e. g. Hassell *et al.* (1977), Abrams (1990), Joly and Patterson (2003)). Holling’s disc model (equation (2.1)) of the type II functional response defines two parameters that represent constant attack rate and constant handling time. Type III functional responses that are the result of predator behaviour causing density-dependence to arise in these parameters can be described mathematically by replacing the constants in Holling’s type II model by prey density-dependent expressions. Foraging effort that varies with prey density can also result in an overall type III functional response. This can be modelled by multiplying the foraging effort by the consumption rate predicted from a type II model (e. g. Abrams (1990)).

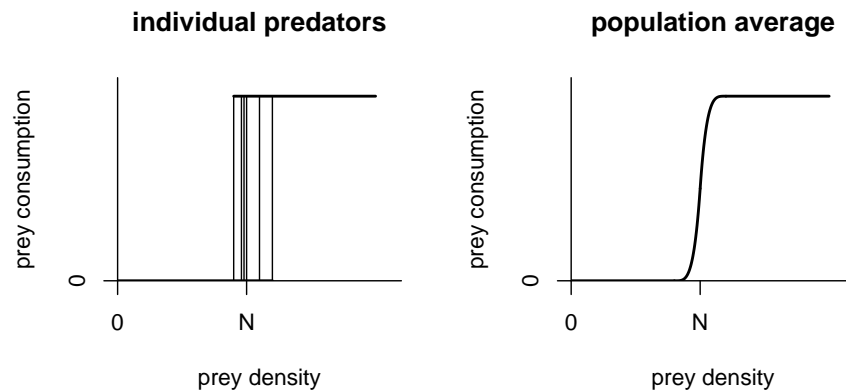


Figure 2.2: **Emergence of type III functional response at the population level from individual step functions.** The graph on the left illustrates the functional response of six predators who forage only when prey densities are above a threshold N . Because individual predators may have different thresholds and their knowledge of these is imperfect, each predator makes the switch at a prey density close to, but not exactly equal to, N . On average, the functional response of this predator population will have a type III shape, as shown on the right.

However, type III functional responses can also emerge at a population level, such that the population’s overall “average” functional response to prey densities differs in type from the functional response of a typical individual predator (Abrams 1982). These emergent functional responses are generated either by taking account of spatial processes or by averaging across similar predators. For example, Turchin (2003) describes a population of hypothetical predators that either forage if prey densities are sufficiently high, or do not forage at all at low prey densities (see Figure 2.2). But an individual predator has imperfect knowledge and will not make the switch between foraging and not foraging at exactly the required prey density (N , say). One predator may switch at a density slightly less than N , another may switch at a density slightly higher. On average, a population of these predators will exhibit a type III functional response, because the stepwise section is blurred into a sigmoid shape in the averaging process (see Figure 2.2). Van Baalen *et al.* (2001) apply a similar argument to a population of optimal foragers. A population-level sigmoid functional response emerges because individual predators make the switch at prey densities close to, but not exactly at, the threshold density N . If predation on a prey is energetically optimal regardless of the prey density (i. e. if predators always try to catch prey regardless of prey density) but is more likely to succeed at higher prey densities, then there is no positive threshold density N and the corresponding emergent functional response is type II.

2.4.4 Negative switching

“Negative switching” denotes the case in which a predator reacts to an increase in the relative abundance of prey i by eating relatively less of it and more of prey j instead. At first sight, this concept sounds counter-intuitive, but Rapport (1971) gives a straightforward explanation and an example: Higher abundance of prey i could allow the predator to eat a sufficient amount of prey i in a shorter time, leaving it more time to spend foraging for prey j , with the result that the proportion of prey j in its diet increases. Negative switching thus denotes a synergism between two prey (Gentleman *et al.* 2002) that allows the predator to gain more energy by focussing its foraging effort away from the prey whose abundance has increased. Gentleman *et al.* (2002) call such predator behaviour “anomalous”, but it is consistent with prey group defence mechanisms or a type IV functional response (see section 2.3.1).

2.5 Functional response in context

2.5.1 Absolute versus relative prey densities

Some ecologists (see Abrams and Ginzburg (2000) for a review) object to the use of relative abundances in defining prey switching or preference because a predator’s preference may be determined by absolute prey abundance. They ask the question: “If enough of the preferred prey is available, why consume anything else, even if there’s a lot of it?” Imagine two prey populations that are both highly abundant, such that a predator can live by consuming only the preferred prey 1. Now imagine another scenario, with the same two prey occurring at the same relative abundances, but at sharply reduced absolute abundances. The predator can no longer find enough of prey 1 and has to eat prey 2 in order to survive. The proportion of prey 2 in its diet will change as will its selectivity for prey 2, but the relative abundances of prey 1 and 2 and the predator’s strategy (eat prey 1 as much as possible) are unchanged. Predators that behave like this are not described by Murdoch’s definition of switching (see section 2.4.1). In order to model this predator, it is necessary to use functional response models that specify the influence of predator numbers on prey consumption explicitly (see Huisman and de Boer (1997) for an example).

2.5.2 Ecological implications of the functional response type

The three functional response types (see section 2.3.1) give rise to different relationships between the instantaneous prey mortality rate induced by an individual predator, and prey density (see

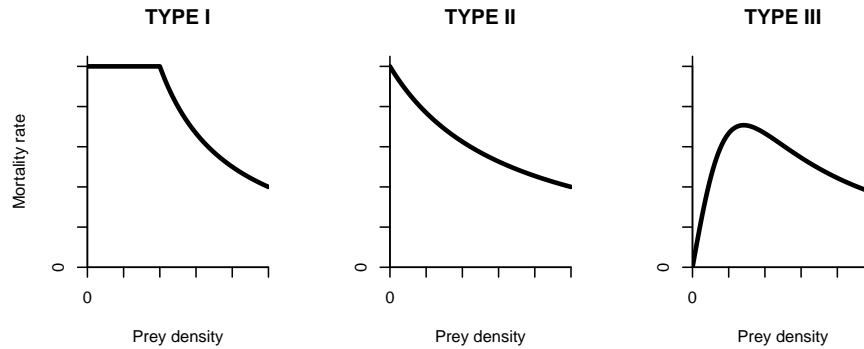


Figure 2.3: **Per-capita prey mortality caused by functional response types I, II and III.** The per-capita prey mortality rate due to an individual predator is plotted against prey density (see e. g. Murdoch (1973)). Note: These mortalities correspond to the functional responses shown in Figure 2.1.

Figure 2.3). Type I implies a constant predation mortality for the prey, up to the density at which the predator satiates, after which prey mortality decreases. Type II assumes a prey mortality that decreases over the full range of prey densities. Type III describes a predation mortality that rises up to a maximum at an intermediate prey density and then decreases asymptotically at higher prey densities.

Ecologically, the difference between the prey mortalities implied by type II and type III functional responses can be very important. In a type III functional response mortality rates increase at low prey densities, up to the mortality peak. In contrast, in type II, an increase in prey density results (in the short term) in reduced prey mortality, at any prey density. Type II predation is thus an example of negative density-dependence between prey mortality and density. Negative density-dependence between mortality and density implies a positive density-dependence of overall fitness on population density. Such a relationship between fitness and population density, known as an Allee effect, can arise from predation or other population processes such as reproduction and can contribute to prey extinction (Gascoigne and Lipcius 2004). Type II predation may thus contribute to extinction of a prey population, because it introduces an Allee effect. Extinction risks of a prey population that is exposed to type III predation, however, are not exacerbated by a predatory Allee effect because per-capita predation mortality decreases with decreasing population density.

A switching predator is believed to facilitate the coexistence of several prey (Comins and Hassell (1976), Greenwood and Elton (1979)). May (1977) notes that, when the type III functional response can be attributed to a predator that switches away from a prey species at low densities, then a depressed population of this prey receives disproportionately less predation, and suggests

that this mechanism can facilitate the coexistence of prey. But May’s argument will not apply to all predators that switch because a switching predator does not necessarily have a type III functional response (see section 2.4.2).

2.5.3 Evolutionary stability of type III functional responses

Specialist predators must satisfy their energetic need from consuming their prey. Because prey abundances vary, and could be low, it seems unlikely that even specialist predators will switch away from any prey species at low overall prey densities. Otherwise they would starve during prolonged periods of prey scarcity. Murdoch (1973) calls specialist predators with such a type III functional response “naive”. These predators would have a higher food intake if they had a type II functional response to their only prey species.

Generalist predators are seen as more likely to have type III functional responses because, when they switch away from one prey, they presumably switch to another prey and thus still satisfy their food intake. Also, they are less dependent on the consumption of one prey.

However, the argument from energetic optimality suggests that generalist and specialist predators should exhibit “zero-one” switches in their functional response to prey densities (see e. g. Dunbrack and Giguère (1987), Corbett and Newsome (1987) for field examples). A specialist predator should stop hunting and eating one prey when this is no longer energetically optimal (i. e. when resting and engaging in other physiological processes would conserve more energy than could be gained through the net benefit of hunting). A generalist predator should switch totally to whichever prey species provides the highest net benefit or rest if the net benefit of resting is greater. A type III functional response is only an approximation of this behaviour.

However, type III functional responses appear to be common in nature (e. g. Hassell *et al.* (1977) or Gismervik and Andersen (1997)), and it can be argued that a type III functional response is evolutionarily stable. First, type III functional responses can emerge as the average functional response of a group of predators even when individual predators have other functional responses (see section 2.4.3). Second, predation must be seen in the long-term context of co-evolution of the predator and its prey, because the predator could not live without its prey. If predator behaviour is energetically optimal during an individual predator’s life-time, the predator population may be too good at killing and drive their prey to extinction. Van Baalen *et al.* (2001) show how individual predators that forage sub-optimally can stabilise a community of two prey and one predator that has no stable equilibria if the predator forages optimally. The arguments against the existence of the type III functional response discussed above all act within a predator’s life-time and may therefore not apply in the context of predator-prey coexistence and evolution.

Finally, it remains an open question whether type II functional responses are characteristic of specialist predators, and if generalist predators are more likely to show type III responses. A generalist predator might have evolved to depend on one or a few prey species as its “staple” prey (and therefore show type II functional responses to these), while supplementing its diet with “opportunistic” prey species when these occur at very high abundances (following the pattern of type III functional responses). Below, I develop a functional response model that can be used to investigate this kind of behaviour.

2.6 Characteristics of multi-species functional responses

A multi-species functional response is a function that relates prey abundance and consumption for a generalist predator, whose diet includes $n > 1$ prey species. Mathematically, a multi-species functional response is a function from the n -dimensional space of prey abundances $\{N_1, N_2, \dots, N_n\}$ to the n -dimensional space of prey consumption rates $\{F_1, F_2, \dots, F_n\}$.

For an ecological modeller to harness the functional response concept, the relationship between prey consumption and resource availability needs to be quantified mathematically. However, the many-dimensional nature of multi-species functional response equations makes it difficult to recognise, at a glance, what properties any particular mathematical formulation of the functional response may have. Gentleman *et al.* (2003) suggest seven diagnostics that can help modellers identify the assumptions that are implicit in various formulations of the multi-species functional response.

2.6.1 Diagnostic I: Effective preference

Gentleman *et al.* first define a diagnostic quantity E_i that they call “effective preference”, defined as the simplest quantity that can be written in place of F_i/N_i when calculating Chesson’s index of preference α_i for prey i (Chesson 1978). In other words $F_i/N_i = kE_i$, where k is the greatest factor common to all of the F_i/N_i , $i = 1 \dots n$. This definition implies that $\alpha_i = E_i / \sum_j E_j$.

Based on this criterion of “effective preference” E_i , Gentleman *et al.* distinguish three categories of functional response. In the “no prey switching” category, they group formulations of the functional response that imply a constant relative preference for any pair of resources i and j , i. e. the relative preference given by E_i/E_j does not change with prey abundances for any combination of prey i, j . The second category, called “passive prey switching”, encompasses those formulations that allow the relative preference to vary with prey abundances, but only in such ways as can be predicted from the relevant single-species functional responses. Finally,

“active prey switching” occurs when the relationship between relative preference and prey abundances cannot be predicted from individual single-species functional responses. In other words, the “active prey switching” functional responses have $E_i = E_i(N_j)$, i. e. prey preference for prey i varies with the availability of some other prey j . If $E_i = E_i(N_i)$ only and does not depend on any N_j , then this functional response may be of the “active prey switching” or of the “passive prey switching” class, and diagnostic II needs to be investigated.

2.6.2 Diagnostic II: Implied single resource response

A multi-species functional response F predicts consumption rates of the n prey species for any combination of prey abundances $\{N_1, N_2, \dots, N_n\}$. In particular, it predicts consumption rates for the case that only the abundance of prey i changes, while the densities $N_{j \neq i}$ of all other prey j are held fixed. Gentleman *et al.* define the implied single-species functional response $F_i^{*\text{imp}}$ to prey i by

$$F_i^{*\text{imp}} = F_i(0, \dots, 0, N_i, 0, \dots, 0),$$

i. e. the consumption rate of prey i predicted by F when only prey i is present.

If all parameters of a “switching” multi-species functional response could, in theory, be estimated from a series of single-species functional response experiments, then the functional response is said to describe “passive prey switching”. However, if some of the multi-species functional response parameters cannot be estimated in this way because they do not occur in any of the implied single-species functional responses $F_i^{*\text{imp}}$, the functional response is said to be of the “active prey switching” class. Diagnostic II thus helps recognise whether a given multi-species functional response model can describe a predator whose behaviour changes between a single- and a multi-species setting.

2.6.3 Diagnostic III: Change in intake of one resource as its density increases

The third diagnostic that Gentleman *et al.* define concerns the change in consumption F_i of a particular prey i when this prey’s density N_i changes and all other prey densities N_j , $j \neq i$, remain constant. If $\partial F_i / \partial N_i > 0$ always, then consumption of prey i always increases when it becomes more available, whereas $\partial F_i / \partial N_i < 0$ indicates decreasing consumption with more abundant prey, which could be due to prey toxicity or other group defensive behaviour.

2.6.4 Diagnostic IV: Change in intake of one resource as the density of another increases

Just as diagnostic III looks at the change in prey intake F_i when that prey density N_i changes, diagnostic IV concerns the change in prey intake F_i when another prey density N_j changes and all other prey densities (including N_i) remain constant. If $\partial F_i / \partial N_j < 0$ always and for all j , then consumption of prey i always decreases when another prey becomes more available, whereas $\partial F_i / \partial N_j > 0$ indicates that there exists a mechanism that allows the predator to consume more of prey i when another prey j becomes more available.

2.6.5 Diagnostic V: Change in total nutritional intake as resource density increases

With their fifth diagnostic, Gentleman *et al.* study the relationship between total nutritional intake $F_{\text{tot}} = \sum_j F_j$ and the change in availability N_i of any one prey. If $\partial F_{\text{tot}} / \partial N_i > 0$, the predator is feeding optimally: higher availability of any single prey results in higher total prey consumption. Negative values of this diagnostic indicate sub-optimal foraging: despite higher availability of prey i the total consumption is reduced.

2.6.6 Diagnostic VI: Nutritional benefit (or cost) of generalism

Next, Gentleman *et al.* analyse if the predator is benefitting from the generalist predation described by the multi-species functional response, or if it could increase its total prey intake by specialising on one of its prey using the implied single-species functional response (and ignoring the remaining prey). For example, the quantity

$$B_{\text{gen}} = \sum_{g=1}^{n_g} (F_g) - F_s^{\text{*imp}} \quad (2.6)$$

is the benefit in prey intake that is associated with the predator's generalist predation on all n_g prey types, compared to specialist foraging for prey s (using the implied single-species functional response, see diagnostic II). If $B_{\text{gen}} < 0$ the predator would gain more energy by consuming exclusively prey s instead of being a generalist predator.

2.6.7 Diagnostic VII: Nutritional cost (or benefits) of selection

Finally, Gentleman *et al.* define the cost of generalism, which arises when the predator distinguishes prey that are not distinct in terms of their single-species functional responses. This diagnostic only applies to those prey i, j for which the single-species functional responses $F_i^{*\text{imp}}$, $F_j^{*\text{imp}}$ implied by the multi-species functional response in the absence of all other prey are identical. If we denote by $N_t = N_i + N_j$ the total abundance of those preys that share the same implied single-species response $F_i^{*\text{imp}}$, and by $F_t = F_i(N_i, N_j) + F_j(N_i, N_j)$ the total consumption predicted by the multi-species functional response, then the cost of distinguishing between these two indistinct prey is

$$C_{\text{sel}} = F_i^{*\text{imp}}(N_t) - F_t \quad (2.7)$$

and $C_{\text{sel}} > 0$ indicates that the generalist predator is incurring nutritional costs by selecting between prey i and j .

2.6.8 How to use these diagnostics

The diagnostics defined in Gentleman *et al.* (2003) help recognise the assumptions implicit in multi-species functional response models. For example, predators are usually thought to increase their total energy intake when any individual resource density increases. Likewise, generalist predators should not derive an energetic benefit by excluding any of their prey from their diet. These two properties are desirable in functional response models and can be quickly checked by reference to diagnostic criteria V and VI.

Gentleman *et al.* (2003) note that many of the commonly used multi-species functional response models show “anomalous” properties. For example, total prey consumption (diagnostic V) is expected to increase with an increase in prey abundance. In some predator-prey systems, prey group-defence mechanisms or predator confusion could result in total prey consumption decreasing with an increase in prey abundance. But if the multi-species functional response model implies type II or type III single-species functional responses to all prey species, total prey consumption should not decrease with an increase in the abundance of any prey species. If diagnostic V indicates that it does, Gentleman *et al.* call this “anomalous” because, at these combinations of prey densities, and with implied single-species functional responses of type II or III, the model includes no explicit mechanism for reducing the consumption of any one prey when its density increases, so a decreasing overall consumption in such a model seems contradictory.

To verify the suitability of a multi-species functional response model, Gentleman *et al.* advocate

to check it for “anomalous” dynamics, aided by their diagnostics. The modeller should also verify that the implied single-species resource responses (diagnostic II) is of a functional response type appropriate for describing the foraging behaviour of the predator in question.

2.7 A generalised “passive switching” multi-species functional response equation

In their survey of multi-species functional responses, Gentleman *et al.* (2003) have identified which of the commonly used multi-species functional response equations belong to each of the types “no prey switching”, “passive prey switching”, and “active prey switching”.

I think that a generalist predator may well be relying on a “staple prey” in its diet, to which a type II functional response is exhibited, yet at the same time the predator may be taking other prey opportunistically with a functional response that would best be described by a type III function (see section 2.5.3). To describe such a predator mathematically, a functional response model of one of the “switching” classes is required. However, all of the “passive prey switching” functional responses reviewed by Gentleman *et al.* assume that either all marginal single-species functional responses are of Holling type II or all of Holling type III. Furthermore, Gentleman *et al.* conclude in their review that it is hard to justify the use of “active prey switching” models because these have wider regions of anomalous dynamics (see section 2.6.8) than the “passive prey switching” models. There is thus a lack of a functional response model that is sufficiently flexible to describe such predator behaviour, as sketched above, without being overly flexible to fall into the “active prey switching” class.

To make up for this current lack of functional response model, I propose to use the following multi-species functional response equation (2.8, called **MSFR equation** below) of a generalist predator to the densities N_i of its prey types, and I analyse its properties according to the criteria laid out in Gentleman *et al.* (2003). This equation is based on a single-species functional response suggested first by Real (1977), generalised to the multi-species context in analogy with Murdoch (1973). Gismervik and Andersen (1997) have used a functionally equivalent form of this equation with the constraint that $m_i = m_j$, but it is desirable to be able to detect through model-fitting which species are subject to type III predation (e. g. Trexler *et al.* (1988), Abrams and Ginzburg (2000)). Koen-Alonso and Yodzis (2005) have studied a reparameterisation of this MSFR equation to compare the performance of several multi-species functional response models as part of a dynamical model describing time-series data on predator and prey populations from a marine ecosystem, and they found that this MSFR equation gives good model fit and results in realistic consumption rates. I am not aware of any published formal presentation of the properties of this MSFR equation.

$$F_i = \frac{a_i N_i^{m_i}}{1 + \sum a_j t_j N_j^{m_j}} \quad (2.8)$$

The consumption rate F_i of prey species i is determined by its density N_i , as well as by the densities of all other prey (N_j in the denominator). The MSFR equation has three parameters per prey species: $a_i \geq 0$ is related to the attack rate, $t_i \geq 0$ denotes handling time for one item of prey i , and $m_i \geq 1$ is a shape parameter. When $m_i = 1$, the MSFR describes a type II functional response to changes in the density of prey i alone, whereas $m_i > 1$ gives a type III shape.

The MSFR equation is capable of modelling type II and type III functional response curves, depending on the parameter values of m_i . By setting $m_i \neq m_j$ for two species i, j , the MSFR equation can describe a predator that shows a sigmoidal functional response to one prey but a hyperbolic response to another one.

With three parameters per species, the MSFR equation is relatively parsimonious in the number of parameters that need to be estimated (Gentleman *et al.* 2003). Also, some of its parameters have a clear biological meaning. Handling times t_i , for example, are the times that a predator requires to “process” one prey item exclusively. For handling-time limited specialist predators, the biological meaning of this is obvious, but the concept of a generalist predator dedicating time exclusively to each prey type is less applicable in a multi-species context. It is likely that a generalist predator could be digesting prey of one type while foraging for prey of another type. Jeschke *et al.* (2002), for example, argue that a model can only define handling time adequately when it models digestion explicitly.

The attack rate parameters a_i can be related to the rate of observable attacks γ_i by $\gamma_i = a_i N_i^{m_i-1}$ (Real 1977). Real (1977) suggests that, if the sigmoidal shape of a Holling type III functional response is the result of learning alone, the value of m_i corresponds to “the number of encounters a predator must have with a prey item before becoming maximally efficient at utilising the prey item as a resource” (Real 1977). However, this mechanistic explanation does not apply to the parameters m_i in equation (2.8) because the generalist predator may switch to a different prey at any time during this hypothesised learning process. In short, some of the parameters of equation (2.8) represent biological mechanisms, even if the mechanistic derivation of the MSFR equation as a whole is unclear.

Equation (2.8) stands out from other models of the “passive prey switching” class because it can represent functional responses of different type to different prey. Only three parameters need to

be fitted for each species, which is parsimonious compared to some other models of sigmoidal functional responses (Trexler *et al.* 1988). Therefore, equation (2.8) is a good model choice when sigmoidal functional response processes are expected.

2.7.1 Diagnostic properties of the MSFR equation

I now evaluate the properties of equation (2.8) using the diagnostics of Gentleman *et al.* (2003).

Diagnostic I: Equation (2.8) gives $E_i = a_i N_i^{m_i - 1}$, which is a function of primary prey density, N_i , only. E_i/E_j , accordingly, is not constant, and equation (2.8) belongs in the class of switching models.

Diagnostic II: The implied single-species functional response in the absence of all other prey, $F_i^{*\text{imp}}$, is

$$F_i^{*\text{imp}} = \frac{a_i N_i^{m_i}}{1 + a_i t_i N_i^{m_i}}. \quad (2.9)$$

Thus, all parameters of equation (2.8) can, in theory, be estimated from the implied single-species responses for each species in the absence of any other prey species. Accordingly, equation (2.8) is in the class of passive switching models.

Diagnostic III: When the density N_i of a resource i increases, equation (2.8) always gives an increase in the consumption of F_i : $\partial F_i / \partial N_i > 0$ always.

Diagnostic IV: When the density N_j of a resource j increases, the consumption F_i of any other prey i is reduced, i. e. $\partial F_i / \partial N_j < 0$ always, for $i \neq j$.

Diagnostic V: $\partial F_{\text{tot}} / \partial N_i$, the change in total nutritional intake predicted by equation (2.8) as the density of resource i increases, is usually positive, but (depending also on the other parameter values and on prey abundances) it can be negative if $t_i > t_j$, i. e. if the resource i whose density increases has a longer handling time than another resource j .

Diagnostic VI: B_{gen} for equation (2.8) is usually positive, i. e. generalism is beneficial, but it can be negative for some combinations of parameter values and prey abundances.

Diagnostic VII: $C_{\text{sel}} > 0$ if $m_i > 1$, and $C_{\text{sel}} = 0$ otherwise, i. e. there is a cost to selecting between two prey types that are indistinguishable in terms of their parameter values, if they are subject to type III predation.

Other assumptions: Equation (2.8) also implies that, for any single prey i for which $m_i > 1$, the rate of increase in the consumption of that resource is zero when its abundance is extremely low (i. e. at $N_i = 0$, $\partial I_i / \partial N_i = 0$). This assumption may or may not be biologically justified (van Baalen *et al.* 2001), and models with this property may not approximate predator behaviour very well at extremely low prey abundances.

Using equation (2.8), Murdoch's constant of proportionality for two prey i and j (cf. section 2.4.2) is

$$C(N_i, N_j) = \frac{F_i/N_i}{F_j/N_j} = \frac{a_i N_i^{m_i}}{a_j N_j^{m_j}}.$$

If $m_i \neq 1$ or $m_j \neq 1$ (or both), $C(N_i, N_j)$ is thus not constant, and equation (2.8) describes a predator that switches between prey i and j .

2.8 Choosing a multi-species functional response model

The choice of functional response model should be a case-by-case decision. For example, predator density-dependence in consumption rates should be recognisable through observation of a predator's foraging behaviour. Depending on the evidence for a relationship between predator densities and consumption rates, a prey density-dependent, a ratio-dependent or an intermediate (Arditi *et al.* 1991) model can be chosen. But this choice must be made in conjunction with decisions about the scope of the model and the availability of data. For example, suppose that data on predator and prey abundance through time indicate that predator numbers are limited by some unidentified mechanism, but that no data on the relationship between predator behaviour and prey abundance are available. Given this limited biological knowledge, a dynamical model that limits prey consumption through a ratio-dependent functional response might seem just as good a modelling choice as one in which predator mortality is density-dependent (Arditi *et al.* 1991). In this example, goodness of fit could be used to decide whether or not to include a ratio-dependent functional response.

Similar considerations must apply to the choice of functional response equation. In multi-species contexts, predation by a generalist predator on one resource is bound to be influenced by the predation effort spent on other resources, so it appears reasonable to model predation by way of a multi-species functional response, rather than treating each prey-predator pair in isolation using single-species functional responses.

Colton (1987) fitted a two-species type II functional response model that allows prey switching (based on Murdoch (1973)), but with this model he observed a lack of fit to his experimental data. Colton amended Murdoch's model by incorporating additional density-dependence on

both prey in the equation for one prey species. This “active switching” model (see section 2.6.1) resulted in much improved model fit, leading Colton to discourage the use of “passive switching” models.

In Colton’s case, the need for an “active switching” model was indicated by the complex density-dependence of the predator’s behaviour to one prey species. However, data both from single-species studies as well as from studies with several prey present at the same time is needed to detect that an active switching model is necessary to model a predator (Gentleman *et al.* 2003). In other applications, there may be no evidence that this level of complexity is required. Depending on the biological realism desired in any given application and on the available data, a passive switching model may be a better choice than other models because it requires fewer parameters than an active switching model (Gentleman *et al.* 2003). A complex model has higher data requirements and may be able to explain more of the observed variance, but it may also over-fit to spurious peculiarities in the data-set. A simpler model requires a higher abstraction from reality and may thus not represent the knowledge of any given system in all its detail, but it requires fewer data to fit and may be applicable in other settings too. Model fitting always involves this trade-off between model complexity and generality (Hilborn and Mangel 1997).

2.9 Fitting a multi-species functional response model

Few attempts have been made at fitting multi-species functional response models to field data (Gentleman *et al.* 2003). I think researchers may have perceived the multi-dimensional nature of multi-species functional response models as a difficulty that may only be overcome using complicated, computer-intensive statistics and large amounts of data. In the rest of this thesis, I show how the MSFR equation I have chosen (section 2.7) can be fitted to relatively sparse data-sets for both a terrestrial generalist predator (Chapter 4) and a marine generalist (Chapter 5), hoping that other researchers may hereby be encouraged to fit multi-species functional responses to their field data.

Functional responses can either be fitted directly to data on consumption (see e. g. Akre and Johnson (1979), Real (1979), Colton (1987), Gismervik and Andersen (1997), Buckel and Stoner (2000), see Jeschke *et al.* (2002) or Gentleman *et al.* (2003) for a review), or they can form part of a dynamical model, which is fitted to time-series data on population sizes (see e. g. Jost and Arditi (1999), Heikinheimo (2001), Koen-Alonso and Yodzis (2005)). Direct fitting of functional responses requires careful thought about the statistical properties of functional response data (Trexler *et al.* 1988). For example, poor quality of data may mask type III shapes in the functional response (Joly and Patterson 2003). The fitting approach chosen also depends on the

interest of the modeller: If an improved understanding of the functional response is required, data collected on the functional response itself should be fitted directly (Abrams and Ginzburg 2000). But when the quantities of concern are population sizes and the functional response is simply a part of the dynamical model, it may be more appropriate to fit the dynamical model directly, especially when no data are available to inform the functional response component. But it is not often that all components of predator-prey dynamics are well understood (Abrams and Ginzburg 2000). In the absence of data to inform the functional response in particular, it is then difficult to assess different hypotheses about the functional response by inference from the available data, because an alternative assumption on another component of the predator-prey interaction may explain the available data equally well as a particular hypothesis on the functional response. Abrams and Ginzburg (2000) therefore suggest that functional responses can only be estimated reliably from data relating directly to predation and prey consumption.

2.10 Conclusion

In this chapter, I suggest a possible model for the multi-species functional response. A better understanding of the predator's functional response translates to better understanding of predator-induced prey mortality. For example, determining the functional response type of a predator to its prey can help recognise whether predator-induced Allee effects are present (see section 2.5.2), which may be of relevance in prey populations under threat of extinction. But the predator's functional response also describes the predators' energy intake, such that changes in prey densities affect predator growth, predator reproduction and predator mortality (Beddington *et al.* 1976). In systems with a generalist predator, its multi-species functional response is thus an important component to the predator and prey population dynamics, and therefore the functional response deserves an important place in the choice and fitting of dynamical population models. Nevertheless, a model of both the functional as well as the numerical response is required to assess the population dynamics of predator and prey, which are not determined by the functional response alone (see Gascoigne and Lipcius (2004), Turchin (2003)).

For predators that switch, the knowledge of particular prey preferences at different combinations of prey densities says little about the predator's functional response. In particular, the definitions of selectivity in common use (e. g. Chesson (1978), Manly *et al.* (1972)) are insensitive to scaling the consumption of all prey by a constant. Selectivities by themselves thus leave the magnitude of consumption rates totally undefined. Estimates of prey preferences are therefore of little use in describing prey mortalities at different prey densities. Also, as both prey preferences and prey switching are defined with regard to proportions of prey in the diet of the predator, and not in terms of absolute consumption, it is difficult to integrate these directly into models of population

dynamics. The argument from optimal foraging theory, which describes foraging behaviour with regard to absolute, rather than relative, prey abundances (Holt 1983), further marginalises the relevance of prey preferences in switching predators, whereas functional response models can be adjusted to represent optimal (step-wise functional responses) or almost optimal foraging (e. g. type III models of the functional response, see section 2.4.3). I think that preferences do have an important place in describing the consumption of non-switching predators, and in relatively constant environments they may be successfully used in describing the average diet of switching predators, but I advocate against their use in generalist predators because the relationship between non-constant preferences and the shape of the functional response is unclear (see section 2.4.2). Rather, I recommend the use of functional response models. When data are available to fit models of prey selectivity or prey preference (e. g. Murdoch (1969), Manly *et al.* (1972), Greenwood and Elton (1979), Joly and Patterson (2003)), models of the multi-species functional response should be fitted. They require no more data but have an immediate and observable interpretation in terms of the amounts of prey taken by a predator.

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3 Bayesian statistics in ecological management

3.1 Uncertainty in ecological modelling

Ecological theory can be applied to many management issues, including the harvesting of natural resources, their conservation, the protection of habitats and biodiversity, as well as the control of hazards. A successful application of ecological theory to management usually requires the conciliation of opinions from stakeholders who have very different value systems. In multi-species functional response models, for example, stakeholders may disagree on the importance of a particular prey species to a predator's diet.

However, ecological and environmental processes are not fully understood, and management decisions have to be made despite the lack of complete knowledge (Dovers *et al.* 1996). The false security arising from an ignorance of these uncertainties has been recognised as a cause of past management failure (e. g. Wade (2001), Ralls and Taylor (2000)). Nowadays the importance of decision-making in the face of considerable uncertainty has become part of the mainstream attitude to ecological management (see e. g. Ludwig *et al.* (1993)). The **precautionary principle** states that, by default, uncertainty in the knowledge of environmental processes must be taken into account in decision-making (see e. g. FAO (1995)), with a view to erring on the side of caution (see e. g. Butterworth and Punt (2003) or Dovers *et al.* (1996)).

Below, I summarise different sources of uncertainty (section 3.2), and I describe how these sources are relevant to functional response modelling (section 3.2.5). Later, I outline some distinctions between Bayesian and frequentist statistics (section 3.3) and give an overview of different methods that are available for the fitting of Bayesian models (section 3.4). Finally, I discuss why the Bayesian paradigm may be better suited to the modelling of functional responses (section 3.5).

3.2 Types of uncertainty

Various authors have classified uncertainty in the modelling process in terms of its sources (e. g. Harwood and Stokes (2003), Regan *et al.* (2002), Cochrane (1999)) or according to the mechanisms that generate it (e. g. Dovers *et al.* (1996)). From a more applied point of view, these types of uncertainty manifest themselves as components of risk (Francis and Shotton 1997).

3.2.1 Types of statistical uncertainty

Measurement uncertainty arises at the point of observing the system under study, because human observers and measuring devices are inherently imprecise. In principle, this source of uncertainty can be reduced, for example by increasing the precision of the measuring mechanism or improving the training of human observers, but no measurement will ever be completely certain.

Parameter uncertainty summarises the degree of confidence in the available estimates of particular model parameters, which are unknown quantities that represent some state or function of the natural system, such as a mortality rate or the rate of change in temperature. Some parameters are measurable directly, others are inferred in the modelling context, and all of these are usually not known exactly.

Structural uncertainty arises because the knowledge about the processes that generate the observed data is limited. Thus, a model is only an approximation to reality (or “All models are wrong, but some are useful” (Box 1979)), and scientists have to choose between different descriptions of the natural processes that are being modelled (Hilborn and Mangel 1997). Often, different models with a claim to describing the data-generating process exist, and the most appropriate model (or combination of models; e. g. Draper (1995)) has to be chosen. The uncertainty about this choice and about the amount of detail that goes into a model is known as structural uncertainty (see McAllister and Kirchner (2002) for a good review, and see section 3.3.3 for existing methods that address structural uncertainty).

Implementation uncertainty An additional source of uncertainty enters models that are designed to inform management decisions and predict their consequences. It is known that recommendations by scientists are not always adopted as policy (Hilborn 2003). Even when they are, their implementation may be difficult to achieve. For example, through accidental take and bycatch, actual fishing effort in a managed fishery may result in catches higher than allowed even when the total allowable catch is set in accordance with scientific guidance (Stefansson 2003). This type of uncertainty can be addressed in models by extending the scope of the model to include implementation mechanisms explicitly.

3.2.2 Process error

Also known as environmental variance, process error denotes the effect of those environmental processes that are known to affect the quantities of interest, but that seemingly vary at random. For example, weather affects a predator’s hunting behaviour but, because weather cannot be

predicted precisely, there will always be some residual uncertainty about predictions of hunting behaviour. In other cases, high unexplained variation in the observed quantities may be evident, but the causal mechanism cannot be identified. Because the residual variation inherent in the environment cannot be explained with current knowledge, it is impossible to extend the model to explicitly account for it (Jonzén *et al.* 2002).

If the processes that cause the additional variation are identified, they could be incorporated into the model structure – some of the process error is then represented by structural or parameter uncertainty. In this sense the boundaries between process error and the uncertainties defined earlier become blurred. However, modelling all processes occurring in nature is usually impossible and outwith the available resources and time frame of the model’s application, especially in the “new” field of ecological modelling (Dovers *et al.* 1996), so some process error will always remain unresolved.

3.2.3 Issues that can be confused with statistical uncertainty

The following three major themes are sometimes confused with the statistical concept of uncertainty.

Bias refers to systematic deviations in a description from what is known to be true. For example, a measuring device is said to be biased if its readings consistently over- or underestimate the observed quantity. Likewise, a model is said to be biased when predictions systematically over- or undershoot their targets. If a model is known to be biased, it needs to be corrected because it gives wrong answers, just like measurements taken from a biased measuring device need to be adjusted (or discarded). If the model’s bias is unknown, the uncertainty in predictions due to unknown bias is already included in the other components of uncertainty, such as parameter and structural uncertainty, and there is no reason to call the model biased when no evidence of such bias exists.

Language also gives rise to concepts that are easily mistaken for uncertainty. For instance, vague or ambiguous wording can make it difficult to be precise about something. When, for example, a management aim is to “prevent the extinction of a threatened animal population”, without specifying precisely what these terms mean, the intended interpretation of “population” is unclear—does this mean the whole population of that animal, or a particular subpopulation? Likewise, does “extinction” here mean the death of the last individual, or is a minimum population size implied, below which a population would be doomed to extinction? This lack of precision can be confused with uncertainty. However, in these cases, it is not our understanding that is uncertain but simply our expressions. These linguistic issues cannot be modelled

probabilistically (Francis and Shotton 1997).

Institutional uncertainty A final source of uncertainty arises when the purposes of a model are not stated explicitly at the outset. However, without a clear remit, a model can only give uncertain answers. By definition, there is nothing that can be done within a model to quantify this source of uncertainty. It is therefore essential for a modeller to elicit the purpose and required design before starting to build a model.

3.2.4 Methods for modelling uncertainty

To capture explicitly process error and the types of statistical uncertainty, several statistical tools have been developed. Wade (2001) reviews some of these, that include: classical hypothesis testing and confidence intervals, Akaike's information criterion (AIC), fully Bayesian methods, likelihood inference, empirical Bayes, fuzzy numbers, and sensitivity analysis using bootstrapping. He concludes that, among those approaches having solid statistical foundations, Bayesian statistics uses distributions to describe uncertainty and can incorporate both model uncertainty as well as uncertainty from alternative sources that are not explicitly included in the model. The advantages and disadvantages of using Bayesian methods for quantifying uncertainty in ecology are reviewed in section 3.5.

3.2.5 Applications to functional response theory

The aim of a functional response model is usually to extend the knowledge on the functional response of a predator. As such, a functional response model aims to reduce both the structural and the parameter uncertainties that are inherent in the current understanding of the predator's functional response. Structural uncertainty may arise from various considerations, for example: Is a multi-species functional response required, and which prey species should be included in the model? Do spatial aspects play an important role in the predator's foraging behaviour? What other covariates, such as predator density or ambient temperature, may be useful in informing the functional response? What structural assumptions can be made regarding the shape of the functional response curve?

Some of these questions may be investigated by formulating different models for the functional response. Then, their performance in explaining the observed functional response data can be assessed using methods of model comparison or model averaging (see section 3.3.3). Alternatively, it may be possible to represent some of these structural issues by parameters in the model. For example, the functional response model given in section 2.7 is capable of distinguishing between

type II and type III functional responses through the parameters m_j , and the values of m_j in the posterior indicate the shape of the functional response to each prey species. Likewise, the question of including a covariate in a model could be studied by verifying whether the parameters that relate this covariate to the prediction of consumption take non-trivial values. A successful functional response model accommodates all the questions of structural uncertainty that are deemed to be important, be it in the form of competing models or of model parameters, but the degree of complexity allowed to the modeller may be limited by the availability of data and by the resources allocated to the modelling process. In the functional response models presented in chapters 4 and 5, the principal question of interest was the shape of the predator’s functional response to various prey species—other structural questions were not investigated.

When data on consumption, prey density and other covariates are available to inform the functional response model, measurement uncertainty needs to be considered. Prey abundance, for example, may be known exactly in a laboratory experiment, but in field studies it is an observed quantity. Measurement uncertainty in the prey abundances may thus be relevant to a functional response model that is informed by field data. Prey consumption is usually observed and is thus prone to observation error, too. The choice of how to represent these uncertainties in the model should be made according to the nature of the observation process: for instance, count data of items consumed could be modelled using a Poisson process, whereas data on the rate of consumption per time-unit must be modelled using methods for continuous variables.

Finally, implementation uncertainty does not enter the functional response model *per se*, because a functional response model does not result in management decisions. However, a functional response model may be part of a bigger model to predict, for example, fish abundances and thereby inform decisions on the regulations of a fishery. Implementation uncertainty may be relevant within the wider scope of the extended model.

3.3 A brief contrast of Bayesian and classical frequentist statistics

3.3.1 Probability statements and the role of data

In **frequentist** (“classical”) **statistics**, data D are compared to a model M using the probability of observing the data given a particular model, $p(D|M)$, and models are fitted to data by maximising this likelihood. The actual observed values D are seen as one among many potential values of D , and to infer the adequacy of model M in explaining the data frequentist statistics relies on tools such as *hypothesis testing* and *p-values*, which build on the concept of repeatability of observing the data D given M . That is, by repeatedly assuming certain fixed values for model parameters and calculating the frequency of observing data D under repeated,

identical circumstances, a frequentist judges whether a model using these fixed values adequately represents the observed data D (Efron 1986). In chapter 1 of his textbook, D’Agostini (2003) reviews these fundamental assumptions of frequentist statistics in more detail.

In **Bayesian statistics**, a probability is a mathematical representation of the degree of belief in an event happening or a statement being true. In Bayesian statistics, data D are compared to a set of K models by calculating, for each model k , the probability $p(M_k|D)$ that the model M_k is true, given the observed data D . Bayes’ theorem

$$\begin{aligned} p_{\text{post}}(M_k|D) &= \frac{p_{\text{prior}}(M_k) \times p(D|M_k)}{\sum_{j=1}^k p(D|M_j)p(M_j)} \\ &= \frac{p_{\text{prior}}(M_k) \times p(D|M_k)}{p(D)} \end{aligned} \tag{3.1}$$

is used to combine the prior subjective belief in model M_k and the likelihood $p(D|M_k)$ of observing D according to model M_k . $p(D)$ is a normalising constant. Bayes’ theorem updates a prior subjective belief in the truth of M_k to give a posterior subjective belief in the truth of M_k that is consistent with the observed data D . In Bayesian statistics, model M_k is treated as unknown whereas the data D are taken as fixed and known. Bayes’ theorem states the posterior probabilities of M_k directly. Because Bayesian statistics gives the subjective probability of a particular model M_k (Efron 1986), no further tools need to be invoked to draw conclusions about M_k . Howson (1997) gives an extensive introduction to the meaning of “probability” in Bayesian statistics, and many textbooks devote a chapter to defining the foundations of Bayesian statistics (e. g. chapter 2 in D’Agostini (2003)).

3.3.2 Prior information

Conceptually, the most striking advantage of the Bayesian paradigm and also its greatest weakness is the use of prior knowledge. In a Bayesian model, prior information about all quantities of interest is combined with the observed data to give an updated posterior (e. g. Punt and Hilborn (1997)). Models thus no longer exist in isolation from previous studies (Prato 2005). Instead, Bayesian modelling explicitly represents the scientific process of repeatedly collecting data and updating the level of knowledge about a system. Accordingly, sample size of each single experiment becomes less of an issue (Ellison (2004), Ghazoul and McAllister (2003)). The ability of a Bayesian model fit to combine old and new data (Ellison 2004) makes Bayesian modelling particularly suitable for adaptive management (Prato 2005), i. e. management in which model results are reviewed whenever new data become available.

Additionally, where disagreement exists about the admission of prior evidence or where stakeholders have different prior opinions, a Bayesian model can easily be calculated for each prior in turn (D’Agostini 2003). This exchangeability of prior information provides different stakeholders with an established method for calculating the posterior opinions that they should rationally subscribe to, given their own priors and the common data that enter a model. Reconciliation between different stakeholders’ points of view can thus centre on the posterior beliefs of each stakeholder, which are based on common data and thus less divergent than their prior beliefs. The exchangeability of prior information in Bayesian models thus introduces additional transparency into the modelling process and can facilitate agreement between stakeholders.

However, with its use of prior information, a Bayesian model fit is based not only on the available data, but also on the choice of prior. For this reason many scientists see Bayesian statistics as being at odds with the principle of scientific objectivity (Howson 1997), whereas the frequentist model is free from subjective judgments (apart from the decision on which hypotheses to test (Ellison 1996), which is a subjective decision common to all scientists).

Among Bayesian statisticians, different points of view prevail on this issue of objectivity. **Subjective Bayesians** are happy to dismiss the idea of objectivity and welcome the fact that priors are essentially subjective judgments that may be employed to enter prior knowledge into the model, for example where earlier studies or common knowledge can inform a subset of the parameters in the current model, or where experts have been asked for their opinions on particular model quantities. **Objective Bayesians** challenge the interpretation of Bayesian probabilities as subjective by defining reference priors that avoid the need of subjective judgments (e. g. George and McCulloch (1993)). In this approach, criteria of objectivity are used to choose a particular prior (e. g. Jeffreys priors, see Box and Tiao (1973)). Usually, these criteria include the resilience of a prior to the scale of the model parameters. An objective prior should not influence model fit, regardless of the parameterisation chosen for a model. Another criterion is that a reference prior should favour simpler models over more complex ones, if both describe the data adequately.

Howson (1997) shows that the objective Bayesian approach does not fully answer the objection against subjectivity in Bayesian models, because reference priors that have been defined for common models often fail to result in proper prior distributions and thus do not guarantee that the posterior model distributions will exist. While it is possible to use reference priors as a starting-point even when these are improper, the need to approximate them by proper prior distributions (for example by truncating their support to a range of parameter values that are deemed “realistic”) involves a subjective judgement that makes them no longer objective (Howson 1997). Efron (1986) claims that “subjective Bayes” is the only philosophically coherent standpoint within the realm of Bayesian statistics.

3.3.3 Model specification

Bayesian methods allow more flexibility in the model design and specification (Punt and Hilborn 1997). For example, Bayesian model fitting is capable of fitting overspecified models (Nielsen and Lewy 2002), which is very difficult to do in frequentist statistics (Omlin and Reichert 1999). Bayesian methods also facilitate the use of complex models that are designed and fine-tuned for each individual purpose, whereas frequentist teaching can look back on a long history of well-established models. The novelty of many Bayesian models and the trade-off between complexity and transparency thus often makes Bayesian models appear opaque to non-Bayesians. However, whereas the flexibility of designing Bayesian models to fit each individual application is an advantage compared to off-the-shelf frequentist methods, “Bayesian theory requires a great deal of thought about the given situation to apply sensibly” (Efron 1986), and this can be seen as a hindrance. Because Bayesian models are often highly complex, they are also more computer-intensive to analyse, which can impede the verification and independent review of model implementation and make some Bayesian models computationally too expensive to be useful (Punt and Hilborn 1997).

Structural uncertainty can be addressed by model selection and model averaging. Model selection aims to identify one model that best explains the data, whereas model averaging is a method for assigning weights to different models based on how well they fit the data. Within the Bayesian paradigm, a good overview of methods in model selection and model averaging is Hoeting *et al.* (1999), whereas a good reference text for addressing structural uncertainty in frequentist statistics is Burnham and Anderson (1998). Model averaging over all competing models results in better average predictive ability than using only the “best” model for making predictions (Hoeting *et al.* 1999).

In Bayesian model averaging, the posterior likelihood of each potential model is used to weight the contribution of this model in making predictions (Draper (1995), Hoeting *et al.* (1999)). Frequentist statistics does not assign probabilities to a model, because in frequentist statistics it is the data that are assumed to be random, not the model (see section 3.3.1). Thus, in frequentist statistics the weights used to average competing models need to be taken from other goodness-of-fit measurements, such as the AIC (see Buckland *et al.* (1997)). This leads Hodges (1987) to conclude that structural uncertainty can be addressed more straightforwardly in a Bayesian modelling context than in a frequentist one.

3.3.4 Presenting the model results

According to the theoretical distinctions between Bayesian and frequentist statistics (see section 3.3.1), statements about the probability of particular events occurring or of model parameters taking values in a particular interval can be made immediately within the Bayesian paradigm, but to express model results within the frequentist paradigm the assumption on repeatability and the use of hypothesis testing and p -values, with associated levels of significance, are required. Output on a particular quantity (a rate of reproduction m , say) from a Bayesian model is summarised in a posterior distribution, which can be presented graphically or which can be used to make statements such as “There is a probability of 81% that $m < 2$ ”, and the meaning of such statements is clear to anyone who understands the concept of subjective probability. Following a frequentist modelling approach, however, results on the same quantity m can only be expressed by statements such as “At a 95% level of significance, a confidence interval for m is [1.8, 5]”, and to make sense of this information, knowledge of both the frequentist interpretation of probability (as the frequency of observing an event under repeated, identical conditions) and of the means of a particular level of significance is required. Likewise, any graphical representation of output from a frequentist model has to be understood within the frequentist concept of probability, whereas a graph of a Bayesian posterior distributions immediately gives the probability distribution of interest.

3.4 Numerical methods for the fitting of Bayesian models

In some simple Bayesian models the posterior likelihood resulting from Bayes’ theorem (equation (3.1)) is of a form that allows the modeller to recognise parametric distributions for the quantities of interest—the posterior likelihood of this quantity is then said to be analytic. However, in most applications of Bayesian theory to ecology, the posteriors of interest cannot be evaluated analytically, and numerical fitting methods are required. In the last decades, powerful numerical algorithms have been developed to provide an approximate sample from the full joint posterior distribution, and even complicated, possibly multivariate models have become tractable computationally. Brooks (2003) provides a detailed review of these methods, below I give a brief introduction.

3.4.1 Markov chain Monte Carlo (MCMC)

MCMC is the general name given to several algorithms that generate a Markov chain in parameter space whose limiting distribution is the non-analytic, possibly multivariate posterior of

interest to a Bayesian modeller (Gilks *et al.* 1995). MCMC is commonly employed to sample from Bayesian posteriors, but it can also be applied to any likelihood function arising in frequentist statistics. At each iteration of the algorithm, all parameters are updated to new values, either taking each parameter in turn or grouping correlated parameters (known as *block sampling*). The sequence of parameter values is recorded, and ergodic theory ensures that, once the chain has converged to its limiting distribution, these parameter values retained by the chain are distributed according to the probability distribution of interest.

To update each parameter or parameter group, the transition kernels of the Markov chain are set to be the full marginal posterior probabilities, which derive from the full joint posterior. The default sampling scheme for MCMC is called *Metropolis-Hastings*. This is based on proposing a new “candidate” value, calculating its posterior probability relative to the current value, and either accepting the candidate or keeping the old value (Hastings (1970), Gamerman (1997)). When the full marginal posterior probability for a parameter or group is analytic, a special case of Metropolis-Hastings, called *Gibbs sampling* (Tierney (1994), Gelfand and Smith (1990)), provides an efficient updating method, in which the new values are drawn directly from the full marginal posterior and their acceptance probabilities are always 1. Gibbs sampling thus does not suffer from the need to find adequate candidate generators, which propose candidates “close enough” to the current values so that areas of high posterior probability may be explored well, but at the same time “different enough” from the current values to ensure sufficient coverage of the whole posterior probability region. The need for tuning a Metropolis-Hastings sampler to achieve “good” acceptance rates is the main drawback of Metropolis-Hastings methods, and this has led to a discussion on the convergence properties of Metropolis-Hastings samplers (see Cowles and Carlin (1996) or Brooks and Roberts (1998) for reviews). Alternative sampling schemes have been proposed, usually based on independence sampling and data augmentation, which require less tuning (e. g. the *slice sampler* (Neal 2003)).

Several freely available software packages provide easy access to the numerical algorithms required for fitting Bayesian models using MCMC (e. g. WinBUGS (Spiegelhalter *et al.* 2004), JAGS (Plummer 2005)). Also, packages exist for monitoring that the sampler has converged and samples the target distribution efficiently (e. g. the CODA package (Plummer *et al.* 2006)). Alternatively, the MCMC algorithm and convergence assessments can be carried out using any programming language with mathematical capabilities (e. g. C, Fortran, or a statistical package such as R).

3.4.2 Alternatives to MCMC

Bayesian models that involve structural uncertainty can be implemented using *reversible jump Markov chain Monte Carlo* (Green 1995), which extends the basic MCMC algorithm to a set of competing models, each with their own parameter space. Developing more efficient samplers for complex Bayesian posteriors and improving the convergence properties of current algorithms are active areas of research (see e. g. the WinBUGS/OpenBugs development website <http://mathstat.helsinki.fi/openbugs/>).

Another area of current research are *sequential Monte Carlo (SMC)* algorithms, such as the *particle filter* (e. g. Doucet *et al.* (2001)). Here, instead of first applying Bayes' theorem (equation 3.1) to calculate the full posterior likelihood from the prior and the likelihood of all data, and then using Metropolis-Hastings to sample likely parameter values one at a time, sequential importance sampling starts from a large set of random samples that are propagated over time using simple importance sampling and resampling mechanisms. The weights used in the resampling at each propagation are based on the likelihood function in such a way that the distribution of the particles approaches the distribution of interest asymptotically. For example, an SMC algorithm can be designed such that the Bayesian prior corresponds to the initial distribution of particles, and the resampling weights at each propagation are based on one datum each. This facilitation of sequential processing of individual data makes SMC the numerical algorithm of choice for time-series data, for example in a state-space modelling framework (Buckland *et al.* 2004) or when data are modelled in real-time.

3.5 Discussion

Having briefly outlined some distinctions between Bayesian and frequentist statistics, I discuss below why Bayesian statistics may be more applicable to ecological modelling. I also outline some of the challenges that must be faced when using models to help evaluate the role of uncertainty in decision-making.

3.5.1 Applicability of Bayesian statistics to functional response modelling

In ecological modelling, it is rarely possible to repeat an experiment under identical circumstances (Ellison 1996), because external influences such as weather cannot be controlled. Also, in large-scale ecological experiments or in experiments involving rare species, the observed changes, for example the growth or decline of a particular species in nature, cannot be made undone in order to repeat the experiment under identical conditions. Repeatability, which is the theoret-

ical basis of the frequentist interpretation of probabilities, can therefore rarely be assumed in ecological models. Hence, the theory of frequentist statistics is not well adapted to handling the uncertainties inherent in managing natural resources (Prato 2005). This theoretical objection does not apply to Bayesian statistics, which interprets probabilities as degrees of belief, without requiring any assumptions about repeatability. Based on their theoretical underpinnings, Bayesian methods are therefore more suitable for ecological applications.

Regarding the issue of objectivity in functional response modelling, the choice between the frequentist and the Bayesian paradigms has to be made on philosophical grounds. However, I believe that the possibility of using prior information to represent “current knowledge” of a system in a Bayesian model is a blessing especially in functional response modelling, because field data on a predator’s functional response is often sparse. Bayesian priors provide a statistically sound method for incorporating results from similar studies or from laboratory experiments into a model of a predator’s functional response, which may be difficult to fit to field data alone. In chapter 4 I give an example of using ancillary data in the form of an informative prior on one of the model parameters (section 4.6.1).

As for the differences between the Bayesian and the frequentist paradigms regarding structural uncertainty, both schools of thought provide methods for model averaging or model selection. However, I perceive Bayesian statistics as offering more freedom in designing models and in specifying error distributions, and as such it may be easier to fit functional response models within the Bayesian paradigm.

Because of the different definitions of “probability” used in the Bayesian and the frequentist paradigms, the output from Bayesian models has been variously described as being more intuitive (Ghazoul and McAllister 2003), easier to understand (Wade 2000), and more presentable to managers (Ellison 1996) than frequentist model results. This is not of especial relevance to functional response modelling, but it may influence the choice between Bayesian and frequentist models, particularly so when the results of the functional response model feed in to any kind of management model.

3.5.2 Fitting functional response models

Functional response models usually involve non-linear functions that map prey availability to prey consumption, and such models are usually not analytic. In chapters 4 and 5, I use MCMC to fit functional response models based on the MSFR equation (2.8). The models presented in the following chapters were fitted using Fortran and R, and to verify that the fitting algorithm written in Fortran for chapter 4 was correct, its output was compared to numerical samples of

the model posterior generated by WinBUGS. In both examples, the data collection had already been completed before the modelling began, so MCMC was chosen to fit the models. But in cases where functional response data are gathered continuously, model-fitting methods such as SMC, which allow the fitting of real-time data, may be used more advantageously.

3.5.3 Uncertainty in ecological modelling

Cochrane (1999) suggests that policy-makers are reluctant to base decisions on models that fully account for all uncertainties, because output from these models is considered to be less useful than the “definite answers” of deterministic models that ignore uncertainty. However, this reluctance to take action, even when the ecological system is not understood fully, is seen as an excuse by many ecologists, who believe that management action must be taken now to avoid future damage (e. g. Dovers *et al.* (1996), de la Mare (1996)). In any case, the explicit modelling of uncertainties has been recognised as an important component of ecology (Ludwig *et al.* (1993), Harwood and Stokes (2003)).

In multi-species contexts it is essential to state explicitly the cost-benefit functions such that different outcomes for different species may be evaluated jointly. This both makes the decision-making process more transparent and allows modellers to include all the details in a model that are relevant to the decision. When the differences between management options in terms of costs and benefits are given as probability distributions, Bayesian decision theory (e. g. Raiffa and Schlaiffer (1967) or DeGroot (1970)) can be used to choose that management decision which yields the highest expected net benefit (e. g. Wade (2000)).

In ecology, however, decision-makers may be reluctant to assign relative benefits to non-economic outcomes of their management actions (Ludwig *et al.* (1993), Francis and Shotton (1997)). For example, it may seem ethically wrong to associate a price tag with a probability of, say, 4% that elephants will be extinct in the wild by 2050, or simply impractical to evaluate the cost associated with such outcomes. However, even when these are not stated explicitly, managers usually follow a set of decision rules (de la Mare 1996), thereby making an implicit assessment of the trade-offs between economic and non-economic outcomes.

In particular, the precautionary principle needs to be re-evaluated in multi-species situations, because it does not extend easily to these problems (Stefansson 2003). For example, any multi-species predator-prey complex can present the problem of managing for a higher number of predators (at the risk of driving the prey population to extinction) or for a higher number of prey (by reducing the number of predators, at the risk of driving their population to extinction). The precautionary principle cannot be applied to two competing populations at once without

quantifying the relative benefits involved in this trade-off.

3.6 Summary

I have listed above the major components of uncertainty in functional response modelling (section 3.2) and given a brief overview of differences between the frequentist and Bayesian paradigms in statistics (section 3.3). Suitable numerical methods exist for fitting Bayesian functional response models (section 3.4), and I discuss how Bayesian statistics may be more suited for functional response modelling than to frequentist statistics (section 3.5). Bayesian modelling can thus help the ecological decision-making by summarising all information and their inherent uncertainty.

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4 The functional response of the hen harrier

The material presented in this section has been developed in collaboration with Sophie Smout, and under the supervision of Carmen Fernández, Jason Matthiopoulos and John Harwood. The presentation in this chapter is entirely my own.

4.1 Hen harriers and red grouse

The red grouse (*Lagopus lagopus scoticus*) is an important sports quarry in the United Kingdom, and moorlands are actively managed to maintain grouse populations (Redpath and Thirgood 1997). The hen harrier (*Circus cyaneus*), a rare predatory bird in the United Kingdom, provisions its young with grouse chicks, among other prey species. To alleviate the perceived predation pressure on grouse, moorland managers are known to kill hen harriers illegally (Etheridge *et al.* 1997).

Field voles (*Microtus agrestis*) and meadow pipits (*Anthus pratensis*) make up most of the harriers' diet (Redpath and Thirgood 1999). Instead of reducing the predation pressure of hen harriers on grouse by killing hen harriers, alternative management schemes attempt to reduce the proportion of grouse in the harrier diet. As grouse and pipits prefer different habitats (Redpath and Thirgood 1997), a straightforward implementation of this management option is the spatial separation of heather moorland (grouse habitat) and open meadows (pipit habitat), in the hope that hen harriers will prefer the pipit habitat. As an alternative method for maintaining a sufficient supply of non-grouse prey, it has been suggested to provide the hen harriers with additional food, for example by placing dead rats or chicks in harrier habitat (Redpath *et al.* 2001).

However, understanding hen harrier predation is complicated by the fact that populations of grouse and rodents show cyclic dynamics (e. g. Matthiopoulos *et al.* (1998), Krebs *et al.* (2001)). Whereas cyclic dynamics do ensure a wide coverage of prey densities, thereby providing ample data on the functional response at many different prey densities, there is no agreement on the cause of these population cycles in the grouse population (Matthiopoulos *et al.* 1998). These unknown underlying processes that cause the cyclic population dynamics may also influence the shape of the functional response, and it is in this sense that cyclic dynamics complicate the modelling of the functional response of the hen harrier.

4.2 Why model the multi-species functional response?

Currently, the relationship between the harriers' consumption of grouse chicks and the availability of other prey is unclear. Intuitively, a higher density of voles, pipits or other suitable prey should reduce the grouse mortality caused by harriers. The management approaches outlined above presuppose this effect, although it has never been quantified. The multi-species functional response is a precise numerical statement of the relationship between all prey abundances and consumption rates for each prey species (see Chapter 2). A fully fitted multi-species functional response model can estimate the number of grouse chicks killed each hour by a pair of hen harriers in a given moorland, and it can provide a measure of per-capita grouse mortality due to this predator. By incorporating this mortality into models of population dynamics for grouse, it may be possible to disentangle predation mortality from other sources of density-dependent mortality.

The functional response may also highlight combinations of prey abundances that cause particularly high grouse predation mortality. Managers could benefit from such information by ensuring that moorlands inhabited by harriers and grouse support alternative prey at densities that are associated with lower predation on grouse.

With this functional response study I also hope to identify whether the harriers have a “preferred” prey that is caught predominantly at high abundances, but ignored at low abundances. In earlier studies, hen harrier numbers have been observed to correlate with pipit and vole densities, but not with grouse (Redpath and Thirgood 1999). Given that hen harriers feed primarily on pipits and voles and that abundances of these prey are highly variable (Turchin 1993), they may have evolved to prey on grouse chicks “opportunistically”, for example in order to survive years of low vole availability. By identifying the type of functional response to each prey, the multi-species functional response model may provide evidence of this special status of grouse (see also section 2.5.3).

4.3 Available data

On six Scottish moorlands, data on hen harrier consumption and the abundances of their prey have been collected by Redpath and Thirgood. They have kindly given me permission to reanalyse the data underlying their own study on the functional response of the hen harrier (Redpath and Thirgood 1999). The analysis in this chapter uses data collected in 1993–1997.

4.3.1 Consumption data

During the harrier breeding season, parent harriers bring prey to their nests to provision their chicks. Observers watched these nests and recorded the number and type of each prey item for a certain number of hours. Consumption rates (in numbers per hour) for each prey type can be calculated from these data. The observation protocol is described in more detail in Redpath and Thirgood (1999). In this chapter, I denote the consumption counts by $F_{i,j}$, where i indexes one of the 43 combinations of harrier nest site and year that were used in this study, j represents the prey type, and T_i is the duration (in hours) for which each nest i was watched.

4.3.2 Abundance data

Prey abundances at each moorland site were measured using prey-specific methods (Redpath and Thirgood 1999). For meadow pipits, an observer walked line transects and recorded the number of pipits encountered. A live-trapping scheme was carried out to assess the density of field voles at each site. The number of voles captured during 100 ‘trap nights’ gives an index of vole density. For grouse, pointing dogs were used to discover grouse nests, and grouse chick abundance was estimated from counts of the number of chicks present in these nests.

For grouse, the abundance data represent an estimate of chick densities per km^2 . For voles and pipits, however, the figures are a relative rather than an absolute measure of prey density. Our multi-species functional response model does not strictly require abundances to be measured on the same scale for each prey type as long as one scale is used for each prey throughout. However, to facilitate the comparison of species-specific results we scaled the abundance data so that they represent prey densities per km^2 . For pipits, the approximate area surveyed during each line transect was $0.2km^2$ (Redpath and Thirgood 1999), hence the transect counts were scaled by the factor 5. A previous mark-recapture study (Redpath *et al.* 2002b) related voles caught per ‘trap night’ to density, giving a scaling factor of 520.

Some sets of consumption data relate to the same set of abundance data because abundances were measured at each moorland site only once a year and not separately for each individual harrier nest. For instance, I use the prey abundances measured at Langholm moor in 1993 to explain harrier consumption at all 4 harrier nests observed on that moor in 1993. Below, I denote the abundance measurements by $N_{k,j}$, where k identifies one of the 10 combinations of year and location for which abundance data had been collected, and j represents the prey type. The mapping $L(i) = k$ relates harrier nests i to their respective abundance data k .

No data were available to quantify the change of prey population densities within a year. How-

ever, the rate at which harriers provision their offspring with grouse chicks does not change significantly within a breeding season (Redpath and Thirgood 1999), suggesting that harrier predation does not deplete local prey densities. Hence, throughout this study, prey abundances were treated as fixed during each harrier breeding season.

4.4 Previous modelling approaches

Redpath and Thirgood (1999) have analysed their data to determine the (single-species) relationship between grouse chick abundance and the provisioning rate of grouse chicks by hen harriers. They found that a sigmoidal functional response explains their provisioning data slightly better than a hyperbolic curve, but residual variation was high ($R^2 = 43\%$). However, Redpath and Thirgood used the method of ordinary least squares to estimate the parameters in their functional response model. This method assumes that observations of consumption relate to the predicted consumption values by independent, identically distributed errors. Without making any explicit distributional assumptions, Redpath and Thirgood are thereby implying that errors in observing consumption are independent of the mean predicted functional response, and that negative values of consumption could be observed. Ordinary least-squares is thus not a statistically appropriate choice for functional response data. The model presented here (section 4.5) uses statistical methods that are appropriate for functional response modelling.

The influence of abundances of other prey on the consumption rate of grouse chicks may explain the high residual variation observed in Redpath and Thirgood's one-prey study. We are not aware of any attempt to incorporate alternative prey abundances into an analysis of the functional response of the hen harrier, even though the availability of other prey is believed to affect grouse consumption by the hen harrier (Thirgood *et al.* 2000).

4.5 A multi-species functional response model

A predator's predation history is composed of a sequence of successful or failed attempts at catching prey. The predator's functional response determines the underlying probability of successful predation. In a constant environment, the number of prey items caught is the result of a sequence of identical trials subject to this probability. Statistically, such data is conventionally modelled through a Poisson process.

Functional responses in general may incorporate quantities other than prey abundance. For example, age or sex of the predator or environmental variations can affect predation rates. For an overview, see section 2.2 above or Ivlev (1961). However, only 43 observations on harrier

consumption were available, so it was decided not to model variation between individual predators. Furthermore, interference from other predators can influence predation rates, but Redpath and Thirgood (1999) show that the hen harriers of this study did not change their feeding rates in response to changes in predator density. Hence, I assume that prey densities are the only variables affecting the functional response of harriers.

Let us denote by $\mu_{k,j}$ the mean hourly consumption rate of prey j predicted at location k . According to a Poisson process, consumption $F_{i,j}$ observed at location $L(i) = k$ in T_i hours is expected to follow the Poisson distribution:

$$F_{i,j} \sim \text{Poisson}(T_i \mu_{L(i),j}). \quad (4.1)$$

However, I found the data to be highly over-dispersed, as is often the case with data of this kind (McCallum 2000). To account for variation in the behaviour of individual predators or other external factors such as weather, which are known to affect harrier predation, but without explicitly including these variables in our model for lack of data, I used a negative binomial model instead. The negative binomial distribution generalises the Poisson distribution to have variance larger than its mean, and the ratio $v = \text{var}/\text{mean}$ summarises the over-dispersion that the Poisson process alone does not explain:

$$F_{i,j} \sim \text{NegBin}(\text{mean} = T_i \mu_{L(i),j}, \text{var} = v T_i \mu_{L(i),j}). \quad (4.2)$$

A first look at the available consumption data shows that over 60% of the harrier diet is made up of three prey species: the red grouse, the field vole, and the meadow pipit (Table 3 in Redpath and Thirgood (1999)). Analysis of the functional response was restricted to these three prey species because no abundance data were available for the remaining prey.

I use the functional response model presented in section 2.7,

$$\mu_{k,j} = \frac{a_j N_{k,j}^{m_j}}{1 + \sum_r a_r t_r N_{k,r}^{m_r}}, \quad (4.3)$$

with r summing over the three prey species.

The negative binomial model for the multi-species functional response of the hen harrier has 10 parameters – three functional response parameters (a , t , and m) for each of three species, and the over-dispersion parameter v . Theoretically, the over-dispersion ratio could vary by prey type, but with all prey being similar in size it was decided to assume one over-dispersion ratio v applying to all prey. Under both the frequentist and the Bayesian paradigms (see section 3.3),

there is no analytic solution to this model; numerical methods (see section 3.4) are required to find the best model fit.

Two different Bayesian models were fitted: the multi-species functional response model (MSFR), which fits to all available data; and the single-species functional response model (SSFR), obtained by using only the data on abundance and consumption of grouse.

Redpath and Thirgood’s (1999) best-fit functional response to grouse data only ($Y = 0.21x^{5.1}/(51^{5.1} + x^{5.1})$) can be represented in the single-species version of equation (4.3) by setting the grouse-specific parameters $m = 5.1$, $t = 4.76$, and $a = 4.11 \times 10^{-10}$. However, I did not expect the functional response models presented here to replicate Redpath and Thirgood’s results, either in the MSFR or in the SSFR model, because of differences in the statistical assumptions. The Bayesian models presented here use priors and assume a negative binomial error in the consumption data, whereas Redpath and Thirgood fitted a frequentist weighted least-squares model. The negative binomial functional response does equal the mean given by their model but, because best model fit is determined by the whole predictive distribution and incorporates Bayesian prior information, I would be surprised to see strong agreement between Redpath and Thirgood’s fitted functional response and the best fit of the models introduced here.

4.6 Priors

Both the SSFR and the MSFR models use the same priors. An overview is given in Table 4.1, and the prior choices are explained below.

parameter	prior	95%-CI
m grouse	$(m - 1) \sim \text{Gamma}(\text{mean} = 1, \text{var} = 0.9)$	(1, 3.9)
m other	$(m - 1) \sim \text{Gamma}(\text{mean} = 1, \text{var} = 0.9)$	(1, 3.9)
t grouse	$t \sim \text{Gamma}(\text{mean} = 0.36, \text{var} = 0.075)$	(0.035, 1.05)
t other	$t \sim \text{Gamma}(\text{mean} = 0.15, \text{var} = 0.035)$	(0.0006, 0.67)
a grouse	joint distribution with m grouse	$(1 \times 10^{-6}, 0.009)$
a other	$a \sim \text{Gamma}(\text{mean} = 1, \text{var} = 0.99)$	(0.026, 3.67)
v	$(v - 1) \sim \text{Gamma}(\text{mean} = 4, \text{var} = 2)$	(1.9, 7.34)

Table 4.1: **Overview of prior choices.** Parameters and priors are explained in detail in section 4.6. The single-species functional response model uses only the grouse-specific parameters and v , the multi-species functional response model uses all priors listed above. This table summarises prior distributions and the *a priori* 95%-credibility intervals.

4.6.1 “Attack rate” parameters a and “shape” parameters m

The numerator of functional response equation (4.3) represents the encounter rate, Q_j , between one predator and its prey j . The encounter rate is the product of prey density N_j and attack rate γ_j , i. e. $Q_j = \gamma_j N_j$. Because equation (4.3) defines encounter rate as $Q_j = a_j N_j^{m_j}$, it implies that attack rate $\gamma_j = a_j N_j^{m_j-1}$. Thus, when $m_j = 1$, $\gamma_j = a_j$ and a_j itself is the attack rate, with a clear biological meaning. When $m_j > 1$, a_j is a scaling factor in the density-dependent attack rate but, when m_j is unknown, the meaning of the parameter a_j is opaque. This dependence of a_j on the value of m_j suggests the specification of a joint prior on a_j and m_j , provided that additional data on prey-specific attack rates are available.

For hen harriers preying on grouse chicks, we found suitable independent data on the number of attacks G_i observed in ϑ_i hours, at various chick densities N_i in Redpath *et al.* (2002a) and Redpath (*pers. comm.*). With the relationship between prey density and attack rate that is implied in equation (4.3) ($\gamma_j = a_j N_j^{m_j-1}$, see above), the following regression model was fitted, conditional on a fixed value for m_j , to obtain a maximum-likelihood estimate for the mean and variance of parameter a_j , which was assumed to follow a normal distribution:

$$G_i \sim N(\vartheta_i a_j N_i^{m_j-1}, \sigma_G^2). \quad (4.4)$$

σ_G^2 was treated as a nuisance parameter, with no further relevance to the model. The mean of a_j in the above model (4.4) and the variance of this mean were estimated using maximum likelihood. These estimates were used as prior on the parameter a_{grouse} in the functional response model (4.2), conditional on m_{grouse} . However, as these additional data do not relate to the same individual predators observed in the functional response data, the variance of the least-squares estimator of a_j was multiplied by 5. Also, because of the constraint that $a_{\text{grouse}} \geq 0$, this prior distribution was truncated at 0. This modified least-squares estimator was used as a conditional prior for a_{grouse} conditional on m_{grouse} (see Table 4.1).

Regarding voles and pipits, I was unable to find data on the attack rate by hen harriers or related birds of prey. Therefore, several uninformative priors were tried. The model posteriors were reasonably robust to these choices, and a gamma prior with mean 1 and variance 0.99 was used (see Table 4.1).

By determining the density-dependent nature of the prey-specific attack rate γ_j , the parameter m_j specifies the shape of the functional response curve: $m_j \approx 1$ results in hyperbolic (type II) functional responses, whereas values of $m_j > 1$ produce sigmoidal (type III) shapes. ($m_j < 1$ implies “negative switching” (see section 2.4.4), i. e. the rate of attacks on a prey decreases when its abundance increases. I excluded the possibility of negative switching in the model because I

am not aware of any explanation for such predatory behaviour in the hen-harrier.) *A priori* the functional response shape for each species was unknown, but I expected a sigmoidal relationship, as these commonly apply in generalist predators (Turchin 2003). Thus I set a gamma prior on $(m_j - 1)$, with mean 1 and variance 0.9 for all three prey species (see Table 4.1). This gives a non-informative 95% credibility interval for m_j of (1, 3.9).

4.6.2 Handling time parameters t

I asked a hen harrier expert (Simon Thirgood *pers. comm.*) to estimate handling times (in hours) of individual prey items and used these to select priors for the parameters t_j . As handling times are constrained to be strictly positive, gamma distributions were chosen to define these priors. For grouse, I assumed a mean handling time of 0.36h/prey, with a variance of 0.075 (see Table 4.1). This gives a 95% credibility interval *a priori* around (0.035, 1.05). Voles and pipits are smaller in size than grouse chicks, and I was advised to choose a smaller *a priori* handling time. So, I set the prior mean at 0.15h/prey and variance at 0.035 – representing a 95% credibility interval around (0.0006, 0.67).

4.6.3 Over-dispersion ratio v

A priori, I only knew that the data were over-dispersed with regard to a Poisson process, but the proportionality factor that would best summarise the relationship between variances and means for the functional response model was unknown. As over-dispersion entails that $v > 1$ in equation (4.2), a fairly wide gamma prior on $(v - 1)$ was used (see table 4.1), which represents an *a priori* 95% credibility interval for v of (1.9, 7.34). Again, I tested for robustness to the exact prior choice for v and found no sensitivity of the results to changes to this prior.

4.7 Model fitting

Markov chain Monte Carlo methods (see section 3.4.1) were used to fit the hen harrier functional response model.

4.7.1 The full joint posterior probability

Writing $p_{\text{negbin}}(F_{i,j} | \mu_{L(i),j}, v)$ for the likelihood of the functional response data (where $\mu_{L(i),j}$ is given by equation (4.3) and depends on the abundances $\mathbf{N}_{L(i)}$ as well as the functional

response parameters \mathbf{m} , \mathbf{t} , and \mathbf{a}) and $\pi_{\text{parameter}}$ for the respective prior distributions, the full joint posterior probabilities for the parameters in this model are given by

$$p(\mathbf{m}, \mathbf{t}, \mathbf{a}, v, \mathbf{F}, \mathbf{N}) = \prod_i \left(\prod_j p_{\text{negbin}}(F_{i,j} | \mu_{L(i),j}, v) \right) \times \pi_v(v) \pi_m(\mathbf{m}) \times \\ \times \pi_{a_{grouse}}(a_{grouse} | m_{grouse}) \pi_{a_{vole}}(a_{vole}) \pi_{a_{pipit}}(a_{pipit}) \pi_t(\mathbf{t}). \quad (4.5)$$

Due to the complicated non-linear formula for $\mu_{L(i),j}$ (equation (4.3)), an analytical representation could not be found for any of the full marginal posterior probabilities.

4.7.2 MCMC algorithm

I implemented a Metropolis-Hastings algorithm (see section 3.4.1) to sample the model posterior numerically. At each updating step, the parameters t and v were sampled one by one. The parameters a and m were sampled in pairs, because I found them to be highly positively correlated in the posterior (see figure 4.1). For each parameter, candidates θ_{new} were generated based on the current parameter values θ_{old} by drawing from truncated Normal distributions $N^+(\theta_{old}, \sigma^2)$ with given parameter-specific variances σ^2 and truncated to obey the constraints on each parameter (i. e. $a_j > 0$, $t_j > 0$, $m_j > 1$, for all j , and $v > 1$). Because this truncation does not occur at the same quantile of the proposal distribution when the mean of the distribution varies, an appropriate correction factor was entered into the calculation of the relative likelihood of current and candidate parameter values in the Metropolis-Hastings updating step. At each iteration, thus, four factors enter the ratio that determines the probability whether the Metropolis-Hastings candidate is accepted: the likelihood function for all data, the priors on the model parameters, an adjustment to ensure reversibility of the candidate generator distributions, and an adjustment to take into account the truncation of the candidate generator distributions at their lower limit. In a preliminary run of the MCMC algorithm, suitable variances for these generalised Random Walk candidate generators for each parameter (or parameter block) were found, such that average acceptance rates were between 10% and 50% for each parameter.

Both the SSFR and the MSFR model were fitted in R, using handwritten code to carry out the Metropolis-Hastings sampling. For the SSFR model, the Metropolis-Hastings algorithm was run for 50,000 draws, and 10,000 of these were discarded to remove the bias caused by the choice of initial values. In the MSFR model I observed a much higher auto-correlation between subsequent draws, so I ran the Metropolis-Hastings algorithm for 4,000,000 draws, out of which the first 10,000 were discarded due to burn-in. By keeping every 200th value of the Markov chain for subsequent analysis, high auto-correlation was addressed successfully.

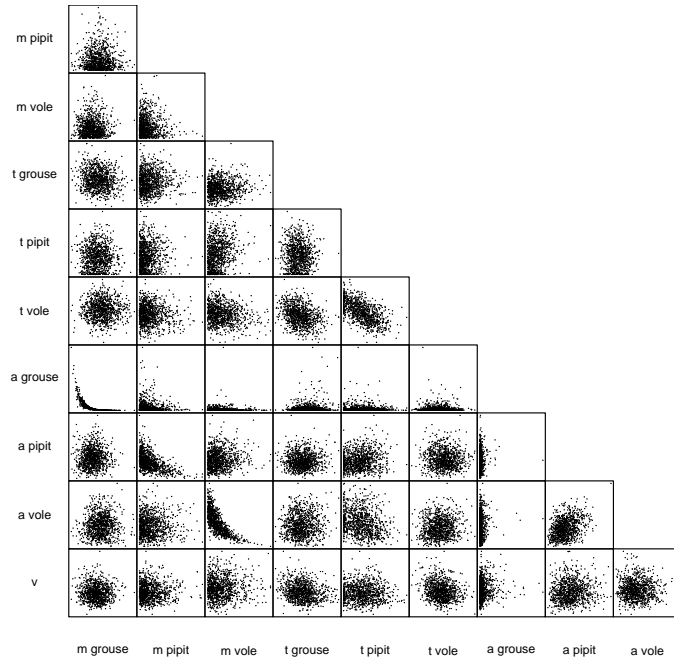


Figure 4.1: Correlation plots for all variables in the posterior distribution of the MSFR model fit.

The convergence and mixing properties of the MCMC sampler were verified graphically by plotting sequences of draws for each parameter. Model adequacy and distributional assumptions were checked using Q-Q plots (see figure 4.2), which contrast predictive and empirical quantiles. For both the SSFR and the MSFR model, the Q-Q plots indicate a good model fit.

4.8 Results

4.8.1 Single-species model

In contrast to the single-species functional response to grouse published by Redpath and Thirgood (1999), I found no clear evidence for a sigmoidal functional response to grouse. Figure 4.3 compares the SSFR functional response to Redpath and Thirgood’s results. The “probability cloud” represents not only the predicted mean values for consumption rate at a given density, but also the probability distribution predicted by the Bayesian model. Table 4.2 summarises the best-fit parameter values in Redpath and Thirgood’s and the SSFR models. Due to a different parameterisation in Redpath and Thirgood’s (1999) model, different assumptions on priors and consumption error, the estimates of individual parameters and parameter uncertainty are not directly comparable.

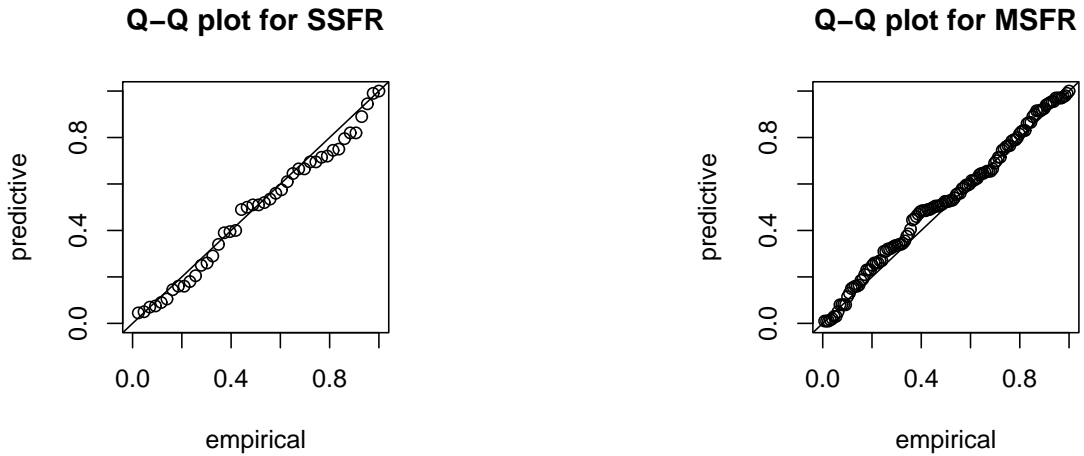


Figure 4.2: **Q-Q plots for the hen harrier models.** Predictive and empirical quantiles are compared for the SSFR (left) and MSFR models (right). In each iteration of the MCMC sampling, each datum is compared to its predicted distribution, and the average of these quantiles was taken to be the overall “predictive quantile” for this datum.

The SSFR model shows an over-dispersion ratio of $v = 3.86$, indicating that variances are almost four times the corresponding means. Compared to a Poisson model, which implies $v = 1$, this over-dispersion ratio is relatively high. The need to use one measurement of abundances to explain consumption rates at several harrier nests is probably the main source of this uncertainty. The high over-dispersion may also be due to ignorance of individual and environmental variation, which cannot be addressed without additional data. Model mis-specification or measurement errors can also cause high over-dispersion.

	Redpath and Thirgood (1999)		SSFR	
m_{grouse}	5.1	(0.16, 10)	1.09	(1.0, 1.2)
t_{grouse}	4.8 [†]	(3.2, 6.3) [†]	0.33	(0.049, 0.79)
a_{grouse}	4.1×10^{-10} [†]	$(-7.6 \times 10^{-9}, 8.4 \times 10^{-9})$	1.6×10^{-3}	$(7.9 \times 10^{-5}, 0.0023)$
explained variance	$R^2 = 0.43$		$v = 3.86$	(2.66, 5.42)
distributional assumptions	normal		negative binomial	

Table 4.2: **Comparison of parameter values in single-species models of grouse consumption.** Means and 90%-CI. [†]derived by reparameterisation of the figures quoted in Redpath and Thirgood (1999), confidence intervals approximated by the ‘delta method’ for normally distributed random variables, e. g. Serfling (1980).

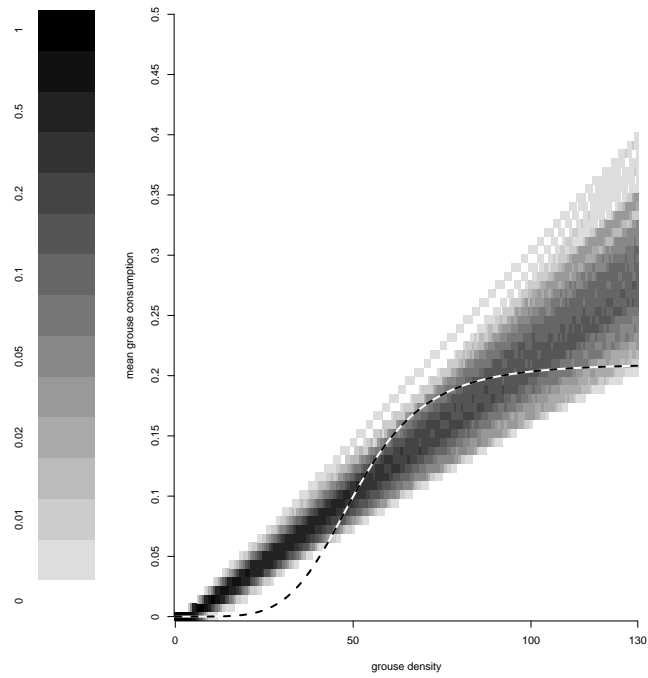


Figure 4.3: **The single-species functional response of hen harriers (in h^{-1}) to variations in the density of red grouse chicks (in km^{-2}).** The dotted white line shows the non-linear least squares fit reported in Redpath and Thirgood (1999). The grey shades (see legend) represent the posterior probability of observing a certain mean rate of grouse consumption at each level of grouse chick density, according to the SSFR model.

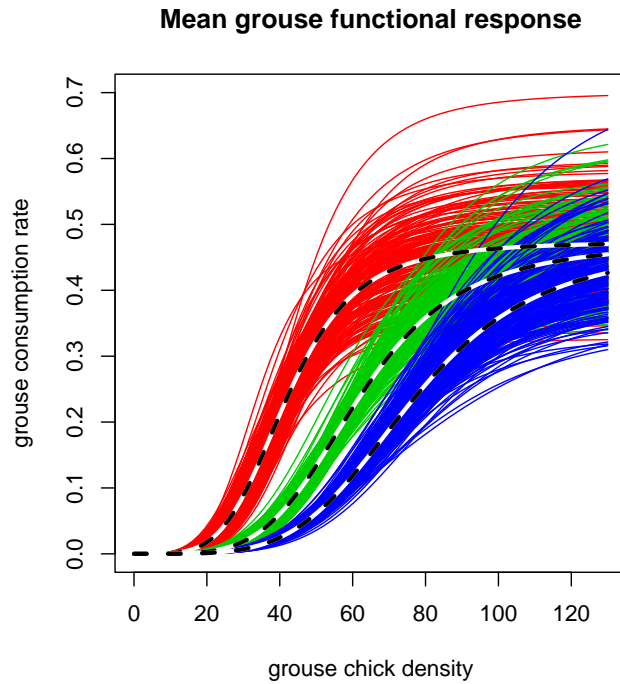


Figure 4.4: **The multi-species functional response of hen harriers (in grouse/h) to grouse chick density (in km^{-2}) at different densities of alternative prey.** Each colour represents a different combination of alternative prey densities: almost no alternative prey (red lines: 52 voles. km^{-2} , 10 pipits. km^{-2}), some alternative prey (green: 520 voles. km^{-2} , 45 pipits. km^{-2}), and high vole and pipit densities (blue: 2080 voles. km^{-2} , 100 pipits. km^{-2}). The individual lines demonstrate the uncertainty captured in the Bayesian model fit. The dashed lines indicate the respective mean predicted grouse consumption rates.

4.8.2 Multi-species model

The MSFR model predicts how the consumption rates of any prey species depend on the abundances of all three modelled species. It is impossible to present all of this multi-dimensional relationship (see section 2.6) visually in one graph. Instead, to plot the predicted functional response to the density of one prey, I have to fix the densities of the other prey. The effect on grouse consumption of changing the abundance of voles and pipits may be appreciated by plotting on one graph the grouse functional response curve for different fixed levels of alternative prey abundance – this is shown in Figure 4.4.

The fitted MSFR is strongly sigmoidal in response to grouse (Figure 4.4), but no s-shaped relationship was found in the functional response to either vole or pipit density (Figure 4.5).

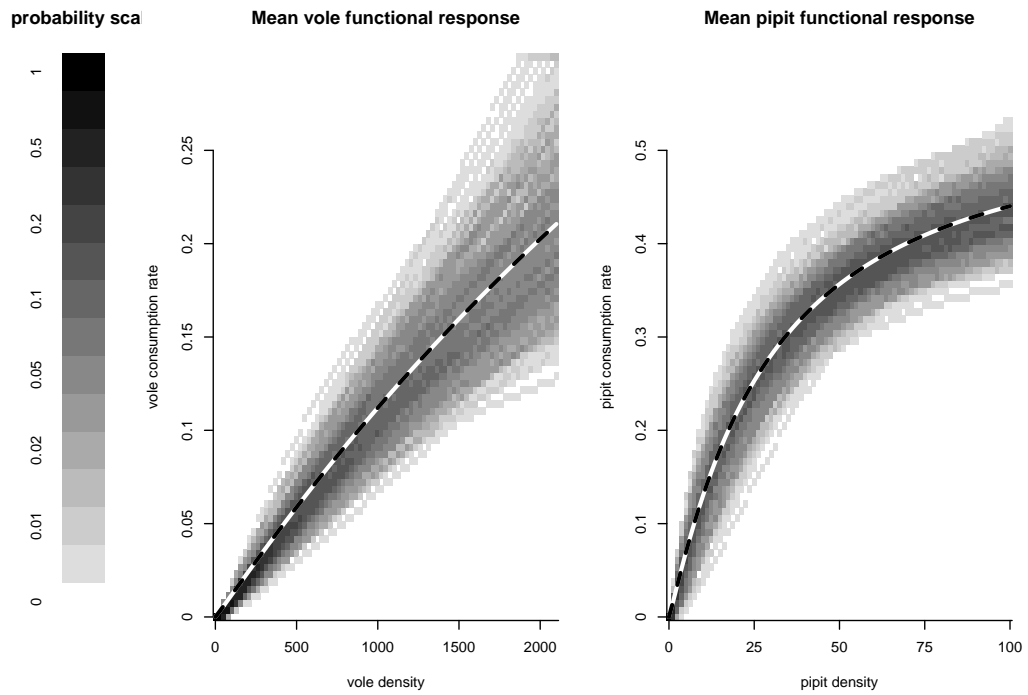


Figure 4.5: **The multi-species functional response of hen harriers to alternative prey.** The left graph shows how harriers respond to vole density (pipit density was held fixed at $45 \text{ pipits.km}^{-2}$, grouse at $50 \text{ chicks.km}^{-2}$), the right graph shows the functional response of harriers to pipits (vole density fixed at $520 \text{ voles.km}^{-2}$, grouse at $50 \text{ chicks.km}^{-2}$). The grey shading indicates the posterior probability of observing a particular consumption rate (in items/h) at any given prey density (in items. km^{-2}), and the dashed lines indicate the respective mean predicted consumption rates.

The model fitting results can also be presented in the form of histograms for each parameter posterior. The posteriors for the shape parameters m (Figure 4.6) confirm a clear distinction between the m_{grouse} , significantly greater than 1, compared to m_{pipit} and m_{vole} , which are both close to 1. Results for the MSFR posteriors for the other functional response parameters are shown in Figure 4.7. A numerical summary of the posteriors for individual parameters is given in Table 4.3. Because the correlation structure between parameters in the joint posterior is not represented in the marginal posteriors, predictions should not be made from these summary values, but only from the full joint posterior.

In Bayesian statistics, the deviance information criterion (DIC, Spiegelhalter *et al.* (2002)) is often quoted as a tool of model comparison. For the SSFR model, the DIC is approximately 75, whereas in the MSFR model, the DIC is around 245. These values are approximate because they are calculated from the posterior distribution, which is only known approximately through the numerical algorithm, MCMC. Furthermore, to calculate the DIC, assumptions of multivariate normality in the posterior are required, and these may be violated in the above example. Finally, because the data that went into the SSFR model is only a subset of the data in the MSFR model, namely the abundances and consumptions of grouse only, the terms that correspond to the data in the calculation of the DIC estimates do therefore not cancel out. Thus, the two DIC estimates may not be directly comparable, and I am not aware of any methods for comparing two Bayesian models that do not explain the same data-set. However, it may be possible to compare the following two models using the DIC: 1. the MSFR model; 2. a model in which three unrelated SSFR models are combined such that each prey species' consumptions are predicted from their corresponding prey abundances, but without taking into account any constraints on simultaneous consumption of more than one prey species. This approach would give two models that are comparable by the DIC, as they both explain the same data-set. However, the judgement whether the MSFR or the SSFR model yield a better model fit should be based not on the DIC, but rather on the structural distinctions between the two models.

4.9 Discussion

4.9.1 MSFR model

The functional response fit shows that hen harriers treat grouse as an “occasional” prey, which is taken at high prey densities but not at low ones, nor when alternative prey are readily available (see section 2.5.3). Especially at medium grouse densities, the influence of alternative prey can cause grouse consumption rates to vary up to fourfold. (Compare the red and blue curves in Figure 4.4 at any grouse chick density between 40–60 chicks. km^{-2} .) Alternative prey densities

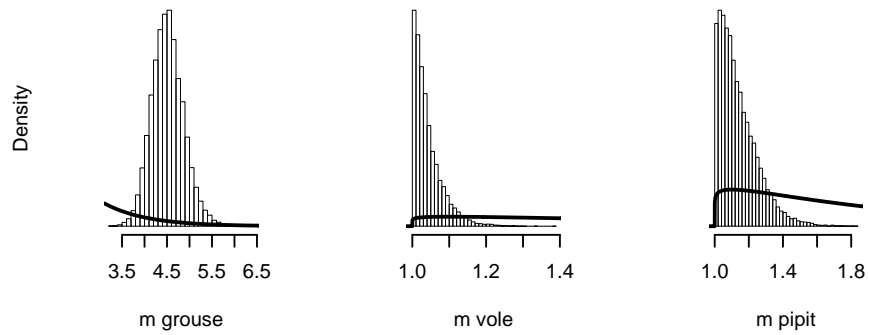


Figure 4.6: **Posterior distributions for the shape parameters m of the multi-species functional response.** The histogram shows the posterior probabilities, the black curve indicates the prior.

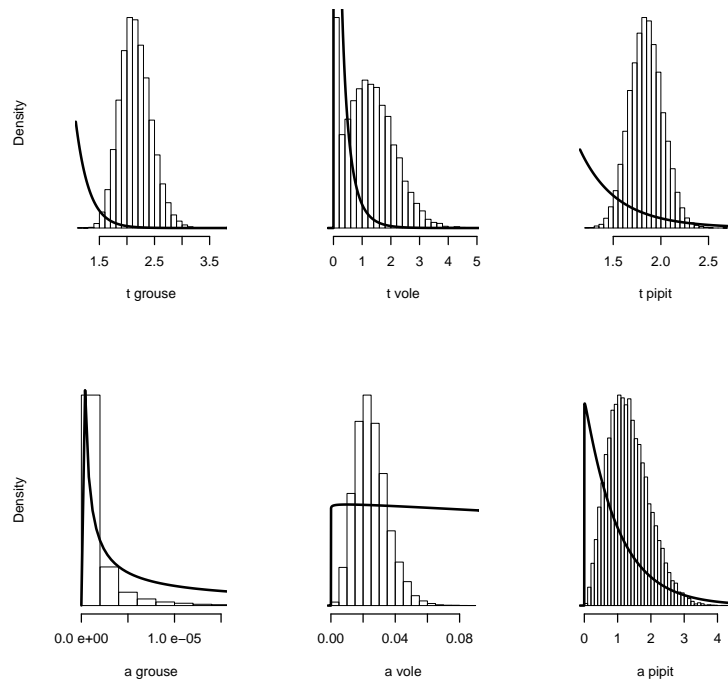


Figure 4.7: **Posterior distributions for parameters t and a of the multi-species functional response.** The histogram shows the posterior probabilities, the black curves indicate the priors.

	SSFR posterior		MSFR posterior	
m_{grouse}	1.09	(1.01, 1.24)	4.51	(3.96, 5.13)
t_{grouse}	0.33	(0.0489, 0.786)	2.16	(1.72, 2.64)
a_{grouse}	1.64×10^{-3}	$(7.86 \times 10^{-5}, 0.00232)$	1.89×10^{-6}	$(6.01 \times 10^{-8}, 6.92 \times 10^{-6})$
m_{vole}			1.04	(1.00, 1.12)
t_{vole}			1.24	(0.0152, 2.69)
a_{vole}			0.0252	(0.0106, 0.0437)
m_{pipit}			1.14	(1.01, 1.35)
t_{pipit}			1.85	(1.56, 2.14)
a_{pipit}			1.33	(0.436, 2.43)
v	3.86	(2.66, 5.42)	4.83	(3.84, 6.02)

Table 4.3: **Posterior parameter means in the multi-species model of hen harrier predation.** Posterior means and 90% credibility intervals for the multi-species functional response model, with a comparison to the corresponding parameters in the single-species functional response model.

have no perceptible impact on grouse consumption rates at high grouse chick densities.

I expected to see a sigmoidal functional response to all prey species because the hen harrier is a generalist predator (Redpath and Thirgood 1997). However, the MSFR fit shows that the sigmoidal functional response is specific to grouse: the best model fit for vole and pipit consumption rates is a hyperbolic (or type II) functional response. Hyperbolic responses are expected to apply to specialist predators (Murdoch 1973), so the results of the MSFR model suggest that hen harriers are specialist predators on voles and pipits that also act as generalist predators on other prey – including grouse (see section 2.5.3). Because hen harrier numbers have been observed to correlate with pipit and vole densities but not with grouse (Redpath and Thirgood 1999), this interpretation of the differing foraging behaviour seems plausible. However, I am not aware of any facts about hen harrier biology that could support or refute this claim.

Having fitted a functional response, I can predict how grouse chick mortality is affected by changes in the abundances of grouse and of alternative prey (Figure 4.8). The sigmoidal shape of the functional response implies the existence of a mortality peak (see section 2.5.2), which can be more or less pronounced according to the sharpness of the s-shape in the functional response curve. The MSFR model predicts that changes in alternative prey abundances will have a strong influence on peak grouse mortality, especially when alternative prey abundances are low. The grouse chick density at which mortality is at a maximum has a direct ecological significance. The peak mortality rate when alternative prey are scarce is approximately twice that when alternative prey are abundant. At medium and high abundances of pipits and voles, peak grouse chick mortality is much lower and occurs at higher grouse chick densities. The estimate of the grouse density for peak mortality in the absence of other prey ($55 \text{ chicks.km}^{-2}$)

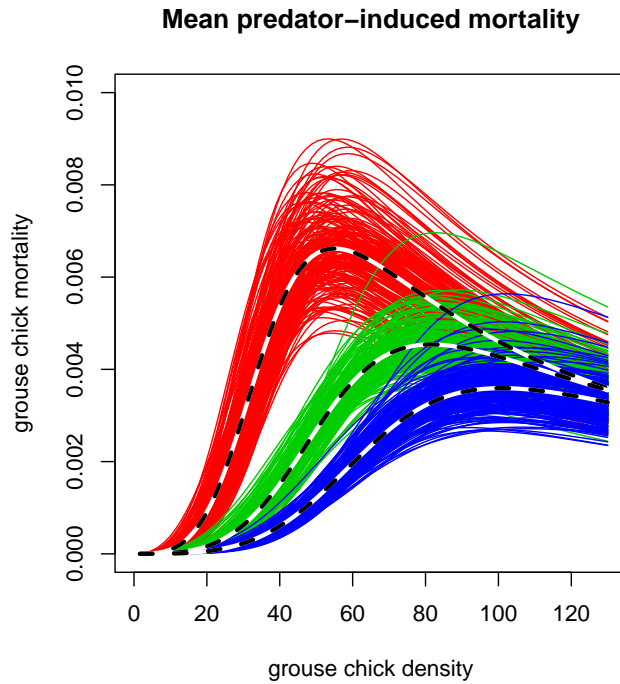


Figure 4.8: **Grouse chick mortality (in chicks/h) at different densities of alternative prey.** The colours red, green and blue indicate low, medium and high levels of alternative prey, respectively (as in Figure 4.4). The individual lines demonstrate the uncertainty inherent in the Bayesian model fit. The dashed lines indicate the respective mean predicted grouse chick mortality rates.

agrees quite well with Redpath and Thirgood (1999)'s estimate of $67 \text{ chicks.km}^{-2}$.

4.9.2 Single-species models

The SSFR model fit and Redpath and Thirgood's results differ in two important regards. Redpath and Thirgood observed a high value for the shape parameter m , and their handling time for grouse ($4.76h$) is much higher than that from the SSFR. The SSFR model does not suggest that hen harriers have a sigmoidal functional response to grouse, but Redpath and Thirgood's (1999) single-species model does. However, when all available data are taken into account in the MSFR model, it is clear that the hen harrier functional response to grouse is indeed sigmoidal.

Having fitted the MSFR model, I can predict the average single-species functional response to grouse alone that would arise from the multi-species data-set when all information on pipits and voles is ignored, as in the SSFR model. For each combination of alternative prey densities that

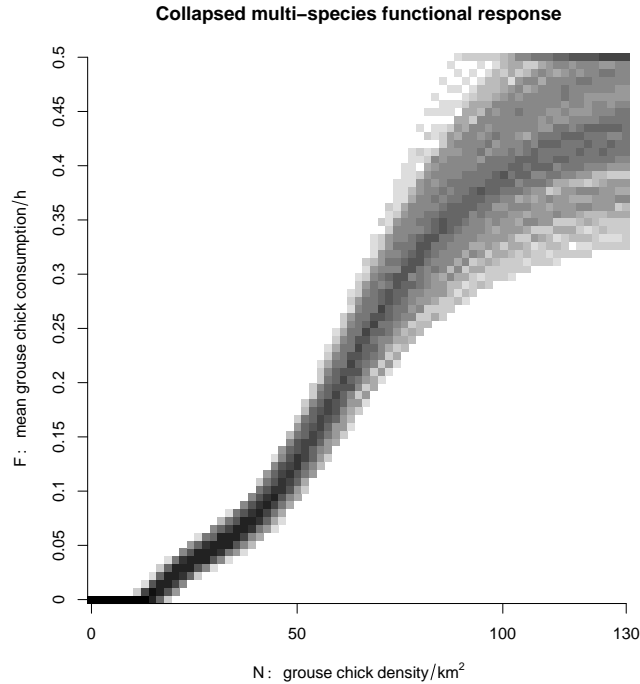


Figure 4.9: **The collapsed MSFR of hen harriers (in grouse/h) to grouse chick density (in km^{-2}).** This figure shows the single-species response to grouse that is implied by the MSFR model when functional responses to grouse at alternative prey abundances are averaged using the same alternative abundances and weights that are found in the data-set. The grey shading indicates posterior probability; see figure 4.3 for a legend.

occurs in the multi-species data-set, I use the MSFR model to predict the functional response to grouse over a range of grouse densities, and I average these functional response curves weighted by the hours of observation that correspond to each of these alternative prey densities in the data-set. By thus ignoring all information on the alternative prey densities, this “collapsed” MSFR (see figure 4.9) corresponds to the information on the single-species functional response to grouse that enters the SSFR model. Compared to the MSFR functional responses to grouse at various combinations of alternative prey densities (figure 4.4), where the sigmoidal shape is evident, a type III functional response is not clearly apparent in the “collapsed” MSFR (figure 4.9). It is thus not surprising that the SSFR model does not detect a type III functional response to grouse (figure 4.3).

In comparison, the results from the SSFR model and from Redpath and Thirgood’s (1999) single-species model differ markedly in their implications for the shape of the functional response to grouse. By collapsing the MSFR fit to yield the single-species response that is implied by the MSFR model, when ignoring all the information on alternative prey (figure 4.9), I have shown

that the SSFR model cannot be expected to detect a type III functional response. However, Redpath and Thirgood’s model does, and the only differences between their model and the SSFR model are distributional assumptions on consumption rates, and a different approach to modelling and model fitting, with the SSFR model using prior information within a Bayesian framework. The SSFR model thus addresses both parameter and measurement uncertainty in a wholly different way. I suspect that the disagreement in functional response shape that is evident in the two model fits is due to these differences in the statistical assumptions underlying the two models.

These conflicting results add support to the arguments outlined in section 2.3.2 that a single-species model is inadequate for modelling the consumption rates of a generalist predator. In this example of the hen harrier functional response, the fitted form of a single-species functional response model depends critically on the assumptions that are made about error distribution, and on the densities of alternative prey on each occasion that the density and consumption of the focal prey species were measured. The mixture of densities of the alternative prey will weight the predator’s single-species functional response in unpredictable and potentially highly variable ways. These problems can be overcome by fitting an MSFR, but it is important to have consumption data from a wide range of prey densities to avoid the need for extrapolation or extensive interpolation. By studying the “collapsed” multi-species functional response, one can understand whether a single-species functional response model is likely to fail to pick up sigmoidal signals that are only apparent in the multi-species functional response data-set. This question could be an area of further research, for example by repeatedly simulating multi-species data-sets which include a type III functional response and assessing whether the resulting collapsed single-species responses allow the detection of the type III shape, or by studying other multi-species data-sets from field studies or experiments.

4.10 Outlook

Generalist predators can dampen or eliminate cyclical interactions between specialist predators and their prey (Hanski *et al.* 1991) or hold prey populations at low-density equilibria (May 1977). One mechanism that could be responsible for such low-density equilibria is the **predator pit** (Hilborn and Walters 1992): when a prey population is subject to predation mortality from a generalist predator with a sigmoidal functional response and the prey abundance is below the value at which peak prey mortality occurs (see section 2.5.2), then an increase in prey density results in an increase in per-capita predation mortality, which may cancel out any increases in fitness coincident with the short-term population increase. But the functional response is a fast response compared to the processes that are involved in the numerical response. Thus, when

a fitted model indicates that a type III functional response is the explanation most consistent with the observed data, the effects of the sigmoidal functional response on population sizes must be evaluated within the context of the predator's numerical response, which quantifies the relationship between predation and predator population size. When predation results in more predators and thus higher predation mortality in the long term, the prey can become trapped in a predator pit by this predator population. If, in the long-term dynamics of predator and prey populations, the predation mortality is dominated by other processes (such as prey reproductive growth or predator migration), the type III predation does not limit prey population growth. Hence, a model of predator and prey dynamics together with a numerical response is required to assess the implications of the observed functional response on population sizes.

The MSFR presented here allows us to quantify the changes to grouse chick mortality that are likely to occur as a result of changes in grouse, vole and pipit densities. The MSFR model quantifies the consumption rate of grouse by hen harriers (in grouse chicks per hour). Redpath and Thirgood (1999) report that the average breeding pair of grouse has 5.5 chicks, which are subject to harrier predation for around 15h during the breeding season. These numbers provide a link between the grouse chick mortality estimates from the MSFR model and the mean chick mortality that applies throughout a grouse breeding season. The MSFR indicates that some combinations of prey densities result in predation mortality peaks for the grouse. So, the potential for a predator pit exists in cases of low alternative prey abundance. However, without a model for the hen harrier's numerical response and a dynamical model of grouse reproduction and all causes of mortality, we cannot ascertain how real this perceived threat to the grouse population is.

The MSFR presented here does not explain how harrier numbers are affected by either changes in the density of alternative prey or provisioning with supplementary food. Little is known about the hen harrier's numerical response (i. e. changes in hen harrier population through time) and, to complicate matters, hen harriers also show an aggregative response to their prey (i. e. they aggregate in areas of higher prey densities when selecting nesting sites: Redpath and Thirgood (1999), Redpath *et al.* (2002b)). Modelling hen harrier and grouse dynamics is outside the scope of this project, but Graham (2005) has laid the groundworks by designing a model that combines the hen harrier MSFR presented here with a model of the hen harrier's aggregative response and a number of different models of grouse dynamics in the absence of predation. More research is required into the harrier's numerical response, for example by documenting how the harrier's total population size changes according to the prey densities encountered in the previous breeding season. Combining this with dynamical models of each prey species would allow a full dynamical model of harrier, vole, pipit and grouse populations to be fitted, which would help in assessing the impact of different moorland management schemes on future numbers of harriers

and grouse.

Finally, grouse populations are known to cycle, and it may be possible to explain these population cycles through theories such as parasite load or kinship behaviour, but the exact mechanisms for the cyclic dynamics are not well understood (see Matthiopoulos *et al.* (1998, 2003) for an introduction). By incorporating the estimates of grouse predation mortality from the present study into models of population dynamics for grouse, it may be possible to disentangle harrier predation mortality from other sources of density-dependent mortality. A better understanding of mortality due to predation can aid in improving the precision of estimates on mortality due to other sources. This may help resolve the debate about the causes for population cycles in red grouse.

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5 The functional response of the harp seal

This aspect of the PhD was supervised jointly by John Harwood and Garry Stenson.

5.1 Introduction

5.1.1 Harp seals and the Newfoundland cod fishery

Historically, the Grand Banks off the south-east coast of Newfoundland have been very rich fishing grounds. European fishing vessels have frequented Newfoundland waters at least since the 16th century (Innis 1978), and the history of Newfoundland has been dominated by European powers fighting over the control of its productive waters. Commercially the most important fish species was the Atlantic cod (*Gadus morhua*), which, dried and salted, was known to the Portuguese as *bacalhao* (Kurlansky 1999). With the advent of powerful trawl fishing and preservation by deep freezing (Kurlansky 1999), the fish stocks were heavily exploited from the 1960s on (DFO 2003a). Fish stocks, in particular cod, had been reduced to numbers very close to extinction by the late 1980s, leading to a complete closure of the cod fisheries in Northwest Atlantic Fisheries Organisation (NAFO) divisions 2J3KL in July 1992 (DFO 2003a). A map of the NAFO area is shown in Figure 5.1.

Besides pressure from the fisheries, cod stocks may also be suffering through mortality from natural predation. The most numerous marine mammal in the north-west Atlantic is the harp seal (*Phoca groenlandica*) (Lawson and Stenson 1997), with a population of around 5.2 million in 2001 (see e. g. McLaren *et al.* (2001) or DFO (2003b)). Harp seals spend the summer in feeding grounds in Arctic waters and enter the study area around Newfoundland during the late autumn, where pups are born between late February and late March (DFO 2000). Harp seals stay in the study area to moult mid-April to mid-May before migrating northwards (DFO 2000), but the timing of their migrations varies from year to year (Stenson *et al.* 1997). Being generalist predators that prey on many fish species, harp seals may have significant impacts on their ecosystem (Lawson *et al.* 1998). However, because of the high mobility of harp seals and because they are marine predators that spend a lot of their time diving in the offshore waters, they are tricky to observe, and collecting data on predation by harp seals is a difficult task.

Contrary to scientific predictions, the fisheries closures of the 1990s did not result in the quick return of cod stocks to their previous high levels (Rose and O’Driscoll 2002). Cochrane (1999) reviews four causes for the failure of fisheries management, but the cause of this failure is still not clear (DFO (2003a), Stenson and Perry (2001)). Because their prey includes cod (Stenson

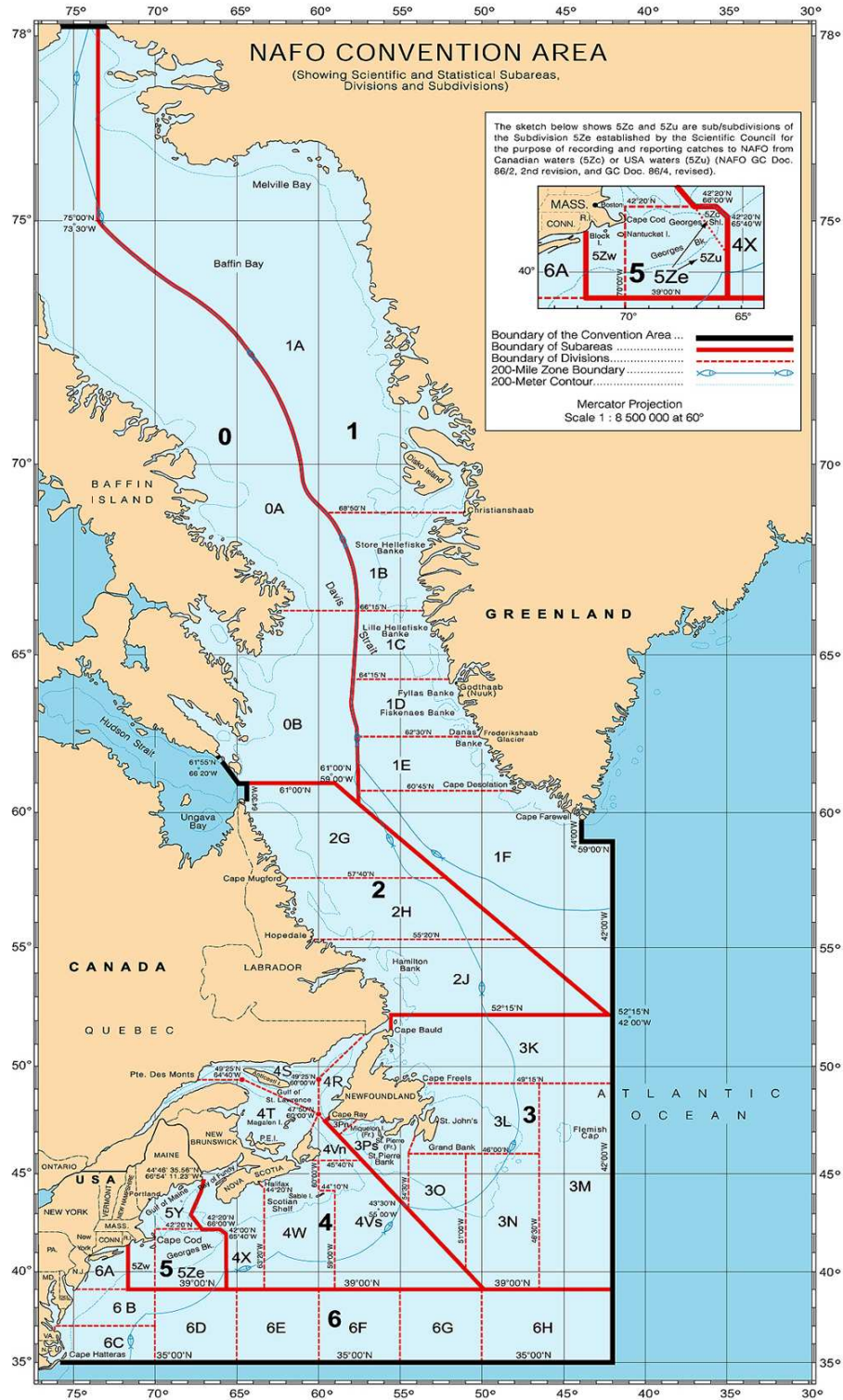


Figure 5.1: The Northwest Atlantic Fisheries Organisation (NAFO) area. This project centers on divisions 2J, 3K, 3L, and 3Ps.

et al. 1997) and consumption of cod by marine predators has been recognised as a major source of cod mortality (DFO 2003a), harp seals are seen by some as one likely agent that may be preventing cod stock recovery (Pemberton *et al.* (1994), DFO (2003a), Bundy (2001)). Also, at a time when most fish stocks are depressed, the harp seal population is actually growing (Shelton *et al.* 1995), and harvesting policies are in place to maintain it at current numbers (DFO 2003b). Scientists have therefore been asked to assess the impact of seal predation on fish stocks (see e. g. McLaren *et al.* (2001)) and to evaluate whether culling the seal population would be beneficial to the fishery (Yodzis 2001).

A generalist predator with a hyperbolic functional response could exacerbate pressure through overfishing by maintaining its attack rate despite diminishing prey abundance (see section 2.5.2). A generalist predator with a sigmoidal response, however, would refrain from consuming prey at very low prey abundances and thus help preserve a prey population that has dropped to population numbers close to extinction (see section 2.5.2). However, it appears that cod has not gone totally extinct despite the overexploitation (Lilly *et al.* 2003). Thus, through quantification of harp seal predation on fish stocks (cod in particular) and through identification of the form of functional response of this predation, it may be possible to determine the harp seals' role in the ongoing depression of cod stocks.

With this multi-species functional response (MSFR) project the aim was not to determine the cause of the cod stock failure (see e. g. McLaren *et al.* (2001) for a summary of possible causes). Scientists recognise that the assessments of cod stocks in the 1980s may have been misguided and over-confident (Alverson 1987). Nowadays, following the tenets of the precautionary approach (see section 3.1), greater emphasis is placed on capturing the uncertainty inherent in any management advice about future cod stock sizes (Lilly *et al.* 2003), and uncertainty in input parameters translates through the assessment model to give margins of uncertainty around the management predictions. With harp seals being a large and numerous marine mammal that feeds in part on cod, the uncertainty associated with estimates of cod consumption by harp seals (Stenson *et al.* (1997), Hammill and Stenson (2000), Stenson and Perry (2001)) is a major determinant of the high uncertainty around estimates of cod stock biomass lost to predation (Shelton *et al.* 1995).

Lawson *et al.* (1998) show that harp seals express different diet choices, replacing arctic cod (*Boreogadus saida*) in their nearshore diet with capelin (*Mallotus villosus*) in offshore areas, which manifests in different selectivities for these focal prey in inshore and offshore waters (Lawson *et al.* 1998). Selectivities by themselves, however, are insufficient to determine whether a generalist predator has a stabilising or destabilising effect on its prey (see section 2.10), but knowledge of the functional response allows the derivation of selectivities for given prey abundances. However, so far no analysis has been undertaken to estimate how an individual harp

seal's consumption of its different prey species relates to the abundances it encounters, although considerable unexplained variation has been recognised between different groups of seals (inshore and offshore: Stenson *et al.* (1995), regional and seasonal: Lawson and Stenson (1997), inter-annual: Stenson and Perry (2001)). An MSFR model could improve current estimates of cod consumption by harp seals by using prey abundances as explanatory variables and capturing the uncertainty in harp seal diet due to variation between individual seals.

According to the requirements of the fish stock assessment models, the quantity of interest from this analysis is the proportion of cod in the harp seal diet (see Hammill and Stenson (2000)). Absolute quantities of biomass consumed by the whole harp seal population are not required, because absolute prey consumption estimates are based on considerations of energy requirements and enter the stock assessment models separately (see Shelton *et al.* (1995) or Stenson *et al.* (1997), for example).

5.2 Harp seal stomach contents data

Seal diets are often estimated from the remains of prey (usually hard parts such as otoliths) found in seal stomachs or faeces (McLaren *et al.* 2001). Seal stomachs from the waters off Labrador and Newfoundland have been collected by DFO scientists since 1981 (Stenson *et al.* 1997). To my knowledge, this is the most comprehensive data-set available to inform a model of the harp seal diet, and results from analyses of this data-set have been used routinely to estimate the amounts of fish prey in the harp seal diet (e. g. DFO (2003a), Lilly *et al.* (2003), Stansbury *et al.* (1998), Wheeler *et al.* (2001)). However, these analyses have so far been limited to calculations of the total consumption of a particular prey, depending on area; the consumption of individual seals and its variation have never been studied in detail (Lawson *et al.* 1993).

5.2.1 Data collection

Harp seals were obtained as by-catch in gill-nets or trawls, or they were shot during directed research trips (Lawson and Stenson 1997) or by contract hunters in the near-shore regions (Lawson *et al.* 1998). The stomach contents provide information about the composition of a harp seal's diet during the last hours of its life. The number and size of prey items can be reconstructed by identifying and measuring hard parts. The proportion of each prey species in the harp seal's diet is estimated by reconstructing the wet weights of the prey ingested using either undigested remains or species-specific weight/otolith regressions. For each seal caught, the capture date and location (DFO "commercial fishery statistical unit area", see Figure 5.2), age and sex are recorded together with the wet weights (by species) of the reconstructed stomach

contents. For details of the sampling process, in particular the identification of prey species from otoliths and the estimation of the prey item's pre-digestion biomass, see Lawson *et al.* (1995) or Stenson *et al.* (1997).

The sampling effort of these consumption data is not allocated evenly throughout space. Of the 7152 seal stomachs collected 1981–2001, 6704 (94%) are from seals caught in inshore areas (defined as those commercial fishery statistical unit areas bordering on Labrador or Newfoundland). But harp seals appear to be spending most of their foraging time offshore (Stenson and Sjare 1997), where they are difficult to shoot (Lawson and Stenson 1997). Therefore, diets of offshore seals are underrepresented in the stomach samples. The most intensively covered NAFO divisions are 2J (1087 seal stomachs, i. e. 15%), 3K (3859 or 54%), and 3L (693 or 10%), with the remaining stomachs coming from 2G, 2H, 3N, 3O, 3P, and 4R.

In terms of temporal provenance of the seals, there is a pronounced lack of data during the summer months (July to October, only 154 stomachs or 2%), because harp seals spend most of these months feeding in arctic waters to the north of the study area. For November to February there are about 1,000 stomach samples each month (November 13%, December 16%, January 14%, February 14%). March to June have slightly fewer samples (March 11%, April 10%, May 12%, June 6%).

It seems that, after the start of the seal stomach collections in autumn 1981, there were no further collections made until winter 1985, from which year onwards there are more than 250 samples each year. If we define a “year” to run from September to August, there appear to be peaks of sampling intensity in the years 1986-87, 1992-93 and 1999-2000.

5.2.2 Qualitative description of stomach contents

Harp seals prefer feeding on fish prey of lengths around 5–25 cm (8–22 cm Lawson *et al.* (1998), 2–30 cm Lawson and Stenson (1997)), and they are unlikely to eat prey larger than 50 cm (Lawson and Stenson 1997). Their main prey is arctic cod (*Boreogadus saida*), which they complement in their diet with capelin (*Mallotus villosus*), sand lance (*Ammodytes* sp.) and, during summer, Atlantic herring (*Clupea harengus*) (see e. g. Lawson *et al.* (1993)). Harp seals are also known to eat Atlantic cod (*Gadus morhua*), sculpins (*Cottidae*) and shrimp (mainly *Pandalus*) as well as other vertebrate and invertebrate prey (Hammill and Stenson (2000), Lawson *et al.* (1993)).

The composition of the harp seal diet appears to differ between offshore and inshore areas (Stenson *et al.* (1995), Lawson and Stenson (1997), Lawson *et al.* (1998)) as well as by latitude

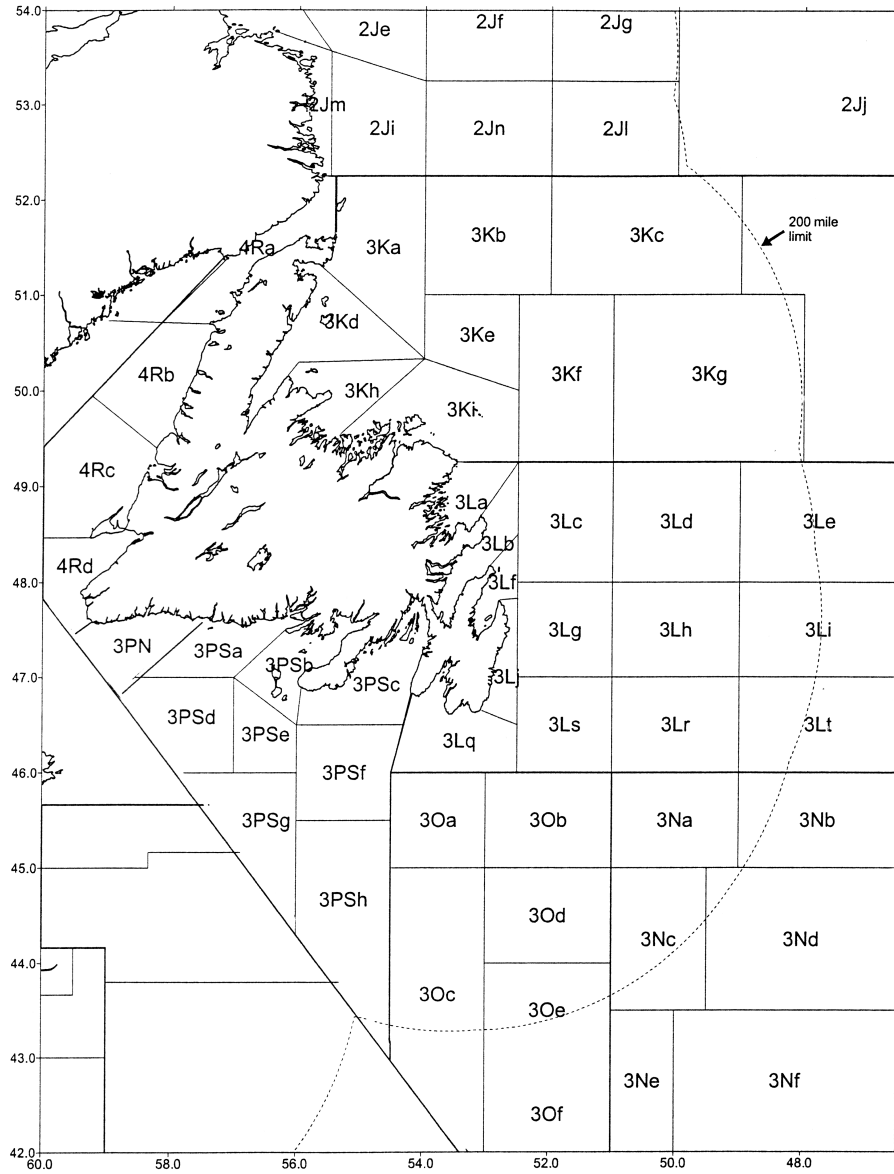


Figure 5.2: DFO “commercial fishery statistical unit areas” in the Northwest Atlantic (illustrated here for NAFO divisions 2J, 3KLNOP and 4R).

(Lawson *et al.* 1993). Also, seal stomach samples collected from commercial vessels trawling for cod had mostly cod in their stomachs (Lawson and Stenson 1997). It is not clear whether diet differs between harp seal pups and adults, or between male and female harp seals (Garry Stenson, *pers. comm.*).

Empty harp seal stomachs are often found, which may relate to seal behaviour (Lawson *et al.* 1993) or digestion (Lindstrøm *et al.* 1998). Because of the high number of empty stomachs in their data, Lindstrøm *et al.* (1998) analysed the content of entire intestines. In this analysis empty stomachs were ignored because they give no information on proportions of prey in the total diet and because intestine contents were not recorded in the data-set.

5.3 Sources of prey abundance data

Besides consumption data, any functional response model also requires information on the relevant prey abundances. To determine what abundance data-sets are available, I spent July and August 2003 at the Department of Fisheries and Oceans Canada, Newfoundland and Labrador branch, in St. John's, Newfoundland. Scientists working at DFO St. John's inform the Canadian government on the state of the Newfoundland fish stocks and are the natural point of contact regarding fish abundances in the Northwest Atlantic. Because surveys of marine abundance are costly and lengthy affairs and because the data on seal diet had already been collected before this project was conceived, I need to use already existing survey data rather than designing my own abundance survey.

5.3.1 Criteria for inclusion

Many surveys are carried out at DFO to assess the abundances of various fish species, but they differ in design and aims. For fitting the harp seal MSFR, abundance data were required to fulfill the following requirements.

1. The survey data must be multi-species, i. e. the surveys must collect abundance information on all required species at once. This ensures comparability of abundances across species. Regarding the harp seal data, it is important that the abundance survey can detect prey smaller than 50 cm, because harp seals eat prey of this size. However, most commercial fisheries target larger fish, and not all abundance surveys collect and retain data on smaller fish.
2. The abundance survey should give data for several years, as this will ensure coverage of different levels of abundance. If there are “good” and “bad” years in terms of the abundances of

some species, the consumption records of these years can be put in perspective to improve the definition of the functional response. However, all abundances must be measured in exactly the same way in each year to ensure comparability across years. Ideally, abundance data should be available for the years 1981 and 1985–2001, which is the extent of the collected stomach data.

3. The abundance survey should also cover the whole study region and provide abundances on a geographical scale that matches the distribution of the harp seal sample. Therefore, the ideal abundance survey would cover the regions 2H, 2J, 3K, 3L, and 3P, as well as the eastern part of the Strait of Belle Isle (part of 4R adjacent to Newfoundland). Its spatial resolution should allow us to associate distinct abundance measurements with each “commercial fishery statistical unit area”, or at least with the inshore and offshore components of each NAFO division. Ideally the survey should provide information on how prey abundances change in each of these areas throughout the year but, because abundance surveys are rarely carried out more frequently than annually, it is unlikely that this ideal level of synchronicity with the diet data can be achieved.

Note that different abundance surveys can be combined to augment the total geographical coverage only if the survey protocols are identical and result in abundance estimates that are commensurate. For example, it is unclear whether measuring twice as much herring “abundance” in an acoustic survey corresponds to the same proportional change as a measure of twice as much herring “abundance” in a bottom-trawl. Also, properties of the measurement error and detectability of certain species (e. g. bottom-dwelling fish or small prey) may differ between the two surveys. A similar argument applies to geographical coverage: we can only augment the survey area by combining results for two areas if both areas were surveyed according to the same survey specifications.

While I was at DFO St. John’s, I identified two sources of prey abundance data for fitting the harp seal MSFR: the annual 2J3KL bottom-trawl (e. g. Lilly *et al.* (2003)) and the 1992–94 pelagic 0-group surveys (Dalley and Anderson 1997).

5.3.2 2J3KL bottom-trawl survey

The 2J3KL bottom-trawl survey is the first choice for data on fish abundances, both because it is a long-running, regular survey with a wide geographical coverage and because it is explicitly multi-species in its design (Brodie 1996). DFO began this survey in the 1970s to inform the stock assessment models for various commercial fish stocks. The original design has been refined to improve the quality of data gathered (Lilly *et al.* 2003).

The survey consists of autumn and spring research vessel trawls. The autumn surveys have

been carried out in NAFO divisions 2J, 3K and 3L since 1977, 1978 and 1981 respectively (Lilly *et al.* 2003). The spring surveys have been carried out in NAFO division 3L during the years 1971–1982 and 1985–present (Lilly *et al.* 2003).

The surveys follow a stratified random design. The study area is partitioned into strata according to depth, and within each stratum a number of locations, called “sets”, are fished for a standardised tow duration. All catches are recorded. Sets are located randomly within strata, with the number of sets per stratum proportional to stratum area (Lilly *et al.* 2003). In some years, other designs were tried in an attempt to minimise variances (Lilly *et al.* 2003), for example an “adaptive design” in 1989 and 1990, or the allocation of extra sets based on the previous year’s observed variance (1991–1994). However, these methods were found to introduce a bias, and the original stratified random design was maintained, with a provision for allocating at least two sets per stratum, from 1995 onwards (Lilly *et al.* 2003).

In 1995 the committee overseeing the annual DFO bottom trawl decided to extend the survey area by additional strata, both inshore of the standard survey area in divisions 3K and 3L (up to a minimum depth of 50 m) and offshore up to a depth of 1500 m (Lilly *et al.* 2003), because these areas had been recognised as important for the accurate assessment of cod stocks. The additional inshore strata were surveyed in 1996–1998 and 2000–2002.

Until summer 1995, the vessels conducting the survey were fitted with Engel 145 Hi-rise trawling gear, but this gear is not appropriate for detecting the abundances of small fish (George Lilly, *pers. comm.*). From autumn 1995 onwards, therefore, the Campelen 1800 shrimp trawl with rockhopper footgear was used. During 1995 and 1996, both gears were deployed simultaneously, with the aim of deriving species-specific multipliers to convert Engel catches to Campelen-equivalents. However, for fish of lengths smaller than 50 cm it was impossible to determine adequate conversion factors, mainly because the Engel gear often caught no fish of a particular size, so the corresponding Campelen catch could not be obtained by multiplication (George Lilly, *pers. comm.*). Therefore the catch records of this bottom-trawl do not constitute one continuous time-series, rather the Engel-trawls before summer 1995 and the Campelen-trawls from summer 1995 onwards must be seen as two separate data-sets.

For each set of DFO records, the latitude and longitude, date, and total weight caught by species are available, together with ancillary information about the depth, bottom sediment type, weather, etc., at each trawl location. DFO also recorded the size distribution for some species at each set, but this information is not available in an accessible form (George Lilly, *pers. comm.*).

Scientists at DFO use the catch observations from these bottom-trawl surveys to inform the

stock assessment of various commercial species, most importantly cod. For the stock assessment model of cod, for example, all data on abundance are pooled for a whole NAFO subarea (e. g. 3L), and the age distribution of cod in that area is estimated from the size distribution data observed at several sets within that subarea (Peter Shelton, *pers. comm.*). The estimates of the strength of the various year-classes of cod for this area are combined with past estimates and other information on cod stocks from sentinel surveys, acoustic surveys in specific areas, tagging studies and other evidence (Lilly *et al.* 2003). The stock assessment model then gives an overall estimate of the size of current cod stocks which is used in determining the maximum sustainable yield (MSY).

One drawback of using the bottom-trawl data is the high degree of uncertainty associated with measurements of fish abundance in bottom-trawl sampling. The observed measurements have a log-normal distribution around the true value (Hjellvik *et al.* 2002), with a standard error of as high as 50% of the mean on the log-scale (Gunderson 1993). Although the true magnitude of the measurement error is unknown for the 2J3KL bottom-trawl, an error of 10% or greater has been confirmed by DFO stock assessment scientists (George Lilly, *pers. comm.*). Some of this measurement uncertainty is probably due to diel variations of prey that are not accounted for in survey design or analysis (Hjellvik *et al.* (2002), Benoît and Swain (2003)). Also, because it takes a few weeks to complete the bottom-trawl of the whole study area (fall surveys in 2J3KL since 1977: mean start date 25 October, mean end date 11 December) and there is high variation in the timing of the survey (start date range 2 October–9 November, end date range 8 December–21 January), we can expect some additional uncertainty in local abundance estimates to arise simply from this lack of synopticity (George Lilly, *pers. comm.*).

For NAFO subdivision 3Ps, south of Newfoundland, which is not included in the 2J3KL bottom-trawl survey, annual spring surveys using the same methodology and fishing gear have been conducted since 1972, and these complement the spring bottom-trawl data-sets in 3L (Stansbury *et al.* 1998).

This DFO bottom-trawl dataset is the preferred source of abundance data because it has a good spatial coverage (covering most of 2J3KL in winter and 3LPs in spring) and is carried out annually. Restricted to the data collected since autumn 1995, i. e. those using the Campelen gear, the bottom-trawl provides abundance estimates for many fish species, including small ones. This specificity for small fish is essential for ensuring reasonable overlap with the harp seal diet data. The bottom-trawl strata have been extended into the inshore areas since 1995, and this improves the spatial matching with the harp seal diet samples, many of which were taken inshore.

5.3.3 Dalley-Anderson bottom-trawl survey

From 1992 to 1994, Dalley and Anderson carried out a survey of the winter distribution of juvenile fish in near- and offshore areas northeast of Newfoundland (Dalley and Anderson 1997). The survey area covered some parts of 3KL, and it extended from near-shore shallow waters within the bays (minimum depth around 60 m) towards the shelf edge. This survey followed a line-transect design, using the Campelen 1800 modified shrimp trawl gear with 36 cm rockhopper footgear, which is suitable for detecting small fish. Although the aim of this survey was the detection of juvenile cod, all other species were also recorded.

This survey also fulfills the three requirements listed above, and I included results from this survey in my analysis because many seals sampled in 1992–94 are from the survey area. This survey was carried out for three winters only, so the temporal extent is limited, but the abundance records are truly multi-species and adequately cover some of the NAFO divisions of interest.

5.3.4 Other surveys

One other survey methodology that is widely used are acoustic surveys, e. g. for capelin (Fran Mowbray, *pers. comm.*) and herring (Wheeler *et al.* 2001). In an acoustic survey, fish are not caught by a net and counted but, instead, the size and density of schools of fish is measured using echolocation gear.

Sentinel surveys (for example DFO (2003a)) have also been used by DFO in recent years. In these surveys, local fishermen, fishing enthusiasts or other members of the local community are asked to report fishing activity and fishing success, and these observational data are used to obtain an index of abundance of the fish species in question (see Lilly *et al.* (1998)). Sentinel surveys generate extensive data from inshore regions, but sampling effort is usually not controlled for (Dawn Maddock-Parsons, *pers. comm.*). Also, when different catch methods are used in the same survey (such as gillnet and longline), the results are often incommensurate (Dawn Maddock-Parsons, *pers. comm.*).

Acoustic and sentinel surveys can provide time-series data on localised abundance of the species in question, and they are used in some stock assessment models. However, all of the surveys I found were single-species, so they could not be used in my analysis.

I explored the possibility of combining single-species surveys from several sources to make up a multi-species dataset, with each single-species survey informing only the abundances of that one species. However, there is, for example, no statistical relationship between the abundances

of capelin estimated by the annual DFO bottom-trawl and by acoustic surveys (Fran Mowbray, *pers. comm.*). This may be due to the completely different methodology of these surveys or a lack of temporal synchronicity. Because it is not clear how results from different survey design could be combined, even when the target species is the same in both cases, I abandoned the idea of creating a multi-species data-set by merging several single-species surveys.

Finally, there are estimates of the abundances of commercial species and also their size-class distributions in the published stock assessments. However, these are only available for some areas (see Table 1 in Anderson *et al.* (2001) for a list), and it is impossible to obtain estimates at a geographical resolution smaller than NAFO divisions. Also, many of the prey species of the harp seal are of no commercial interest, so their stocks are not assessed. As a result, this approach was also not pursued any further.

5.3.5 Catchability

For each abundance survey, its efficiency at detecting prey of a particular type can be summarised by a coefficient known as “catchability”. This denotes the proportion of prey caught out of the number of prey present in the search path. An equivalent interpretation of “catchability” is as a scaling parameter that relates true abundance to the measures of abundance observed in a given survey. It is known that catchabilities vary among survey design and fish species (Benoît and Swain 2003). Catchabilities can also vary through time, both inter- as well as intra-annually. However, the scientists at DFO who are in charge of estimating abundances from the annual bottom-trawl survey tried to find constants to represent the catchabilities of the results before and after the gear change in 1995 (see section 5.3.2 above). Because these constant catchabilities were to be applied to all catches made with the Engel gear from 1977 to 1995, i.e. because experts on the DFO bottom-trawl did not emphasise the question whether catchabilities in this survey vary with time, I assume that catchabilities are constant through time.

Different catchabilities need to be accounted for in stock assessments, and a lot of effort has been devoted to estimating their values. However, the exact values of these catchabilities were not needed for this analysis, as long as they are known to be non-zero, because the MSFR model can compensate for this (see section 5.6.4 below). We can extend the concept of catchabilities to say that single-species surveys have a catchability of zero for all but the target species.

5.4 Choices of scales and units

After identifying the sources of both consumption and abundance data, it was necessary to match up the two data-sets. The aim was to model an individual harp seal’s functional response, so a set of abundances had to be associated with each consumption record. However, the abundances were not measured synchronously with the seal stomach collection, so geographical and temporal resolutions to associate these two data-sets had to be determined. Furthermore, there were sometimes differences in the set of species that were recorded in the consumption and abundance data-sets. The resolution in the identification of species also varied between the two data-sets, and a common way of grouping species had to be decided.

5.4.1 Geographical scale

On the geographical scale, the abundance data (from either the 2J3KL or the Dalley–Anderson bottom-trawl) has the highest spatial resolution. For each trawl set, the exact latitudes and longitudes are recorded. For the consumption data, however, the provenance of each sample is known only up to the DFO “commercial fishery statistical unit area” (see Figure 5.2). In order to match individual seals with abundances, therefore, the smallest spatial unit is the “statistical unit area”.

Accordingly, the prey abundance estimates had to be extrapolated to the relevant statistical unit area and these were then applied to all the seal samples collected within that area.

Various methods exist for obtaining area estimates of fish abundance given measurements taken at a number of points. The most commonly used ones are averaging, and smoothing methods such as kriging (Cressie 1991), generalised linear mixed models (GLMM, Cooper *et al.* (2004)) or approaches that model zero and positive catches hierarchically (e. g. the δ -GLM method, Stefánsson (1996)). The advantage of smoothing and GLM models is that covariates, for example vessel effects (Cooper *et al.* 2004), can be included in the estimation process. These models also allow greater flexibility in defining the stochastic relationship between observed catches and underlying abundances. Averaging is a simpler and potentially less biased method.

I evaluated the use of depth as a covariate in some form of kriging. Depth information is available for every set location and in the form of maps for the whole study area. However, the locations of the bottom-trawl sets are spaced randomly and depth is accounted for through the stratification system. The set locations are therefore representative of the depth in each area. As there is no information relating seal foraging to depths within each area, equal weights can be applied to each abundance estimate when taking the average of the catch records, so kriging is unnecessary.

A second reason for not applying kriging is the high level of heterogeneity in abundances (George Lilly, *pers. comm.*). Fish densities appear to be dependent on localised oceanographic features, such as sediment type and depth gradients, and there is no reason to assume that, within the typical distance between two bottom-trawl sets (tens of kilometres, George Lilly, *pers. comm.*), any correlation would be detected.

5.4.2 Temporal scale

Regarding the temporal scale, the situation is the opposite of that for the spatial scale. The seal data has exact recordings of the date on which a seal was caught, whereas the abundance data-sets have less temporal detail. Trawl surveys are costly and time-consuming and are rarely carried out more than once a year. With the 2J3KL bottom-trawl data NAFO subarea 3L was covered twice a year (roughly in April-May and in November-December), and regions 2J, 3K and 3Ps were surveyed annually (between October and January, and in April/May, respectively).

As a result, a time-frame that is coarse enough to take into account the temporal sparsity of the abundance data had to be identified. A fine temporal scale, say that of days or weeks, will result in hardly any synchronous observations of seal consumption and fish abundance in the same area. At the other extreme, the coarsest possible temporal frame (calendar years or years beginning at some other biologically sensible date) would remove any information on variations in prey abundances within a year. It was necessary to trade off the applicability of abundances measured only once or twice a year, with the number of consumption data that are matched with abundance data.

The approach chosen in this project recognises that changes in fish abundance follow seasonal patterns (due to annual occurrence of reproductive and migratory events in fish populations). Accordingly, it makes sense to assume that local fish abundances remain relatively constant within certain seasons, which are defined according to the absence of reproductive or migratory events. Defining these seasons was done for each fish species, because each has its own reproductive cycles and migratory patterns. However, a detailed and accurate description of the life-histories of each fish species is not required because of the low temporal resolution of the abundance data.

While I was at DFO St. John's, I interviewed 15 fish scientists to determine what is known about the changes of fish abundance for each species. Following these discussions fish species were grouped into three classes: bottom-dwelling, migratory, and "others". Bottom-dwelling species include fish such as flounders, halibut and other sedentary species. The important migratory species were capelin, herring and the gadoids, which tend to move from their overwintering

grounds to spawning grounds and then to feeding places before returning to the overwintering grounds at the end of the year. “Other” species such as eelpout and shanny did not feature strongly in harp seal diets and detailed information on their biology was not required.

There appear to be at most three “seasons” during which migratory fish abundances may be considered relatively constant: overwintering season, spawning season and summer feeding season. Outside these seasons, fish move in masses between areas. Capelin are thought to arrive at their spawning locations in early April and spawn there towards late May (or, recently, in early June), whereas Atlantic cod are believed to “follow” the capelin to their spawning grounds and usually spawn in May (O’Driscoll *et al.* 2000). For those migratory species that are important in the harp seal diet, I defined the overwintering season as extending through the months October to March, the spawning season as the months April and May, and the summer feeding season as the months June to September. The bottom-dwelling and other species do not undergo any important movements in these months.

Thus, it appears that the prey species relevant to this project move little between October and mid-March. Accordingly, it was decided that the abundances measured by the autumn bottom-trawl between October and January could be taken to apply for all dates from October through to the end of March. Grouping the months October to March into “winter” is also consistent with the approach taken by Stenson *et al.* (1997). Most (70%) of the harp seals were caught during October to March, when fish abundances can be assumed to be relatively constant.

Furthermore, it seems reasonable to assume that the abundances recorded by the spring survey during April and May may be applied to all dates during April and May in regions 3L and 3Ps, for which there are data. This assumption does not generalise to the whole of the study area. For instance, a lot of fish movement occurs in the Strait of Belle Isle (NAFO division 4R) in April and May (Johanne Gauthier, *pers. comm.*). However, in terms of this project, which only looks at regions 3L and 3Ps in spring, our assumption of nearly-constant prey abundances during April and May appears to be valid.

5.4.3 Species

Another “scale” that has to be chosen to allow the relation between consumption and abundance to be estimated concerns the matching of prey items, as recorded in the consumption data-set, to the corresponding fish abundances, as measured by the abundance data. If both the abundance survey and the harp seal targeted the same fish species and if these were recorded in identical ways in both data-sets, the prey groups to choose would be obvious. But the two data-sets differ in this regard.

Foremost, harp seals are known to prefer certain prey species over others, and the abundance surveys catch and record abundances for many species that harp seals would not eat (anglemouths, barracudinas, butterflyfish, grenadiers, skates, wolf eels, etc., Dave McKinnon, *pers. comm.*). I excluded these species from the final abundance data-set, to make sure that they did not artificially inflate the abundances of “other fish” when I related these to the harp seal consumption records.

Secondly, some fish are only recorded in the consumption data-set to family or genus level (e. g. *Pleuronectidae*), because the species could not be identified from the otolith. However, the abundance survey invariably identifies prey to the species level. Additionally, the identification by species introduces a lot more detail than required, and it would be impossible to fit a multi-species functional response to hundreds of species that occur very rarely.

For these three reasons I decided to define groups of prey (cf. Lindstrøm *et al.* (1998)), each comprising several species that form “functional groups”. The aim was to distinguish individual fish species that are commercially important (American plaice, Atlantic cod, Atlantic halibut, Atlantic herring, Atlantic mackerel, Greenland halibut, haddock, hake, lumpfish, *Pandanus*, pollock, redfish, salmon, winter flounder, witch flounder, yellowtail flounder, smooth flounder) or that constitute a high proportion of the harp seal’s diet (i. e. capelin, arctic cod, amphipod, euphausiid, mysid, rock cod, sand lance, sculpin, shrimp, smelt and squid; see Lawson and Stenson (1997) and Lawson *et al.* (1993)) from these that are of very little importance or of no interest commercially (“other fish”, “other invertebrate”, “non-food”). Finally, prey groups for “unidentified gadoid”, “unidentified gadus” and “unidentified *Pleuronectidae*”, which correspond to records in the diet data that could not be identified to species level but which are nevertheless interesting commercially, were retained at this stage. A method for distinguishing the component species that make up each of these groups is given in section 5.5.

Tables 5.1 and 5.2 show the 33 groups that were investigated as separate components of a multi-species functional response and list those component species that are most prevalent within each prey group. In the functional response model it was only possible to include those prey groups for which matching abundance and consumption data were available. In particular, “Redfish”, “Salmon” and “Smelt” were excluded because no abundance data were available, “Yellowtail Flounder” and “Smooth Flounder” were excluded because no consumption data were available, “Lumpfish” was excluded because all of the consumption recorded for this species lies outside the region that is covered by any of the abundance data-sets, and “Non-food” was discarded from any analyses.

Ideally, it would be useful to distinguish size classes of some species. For fish of commercial importance, any preference of the harp seal for a particular size-class of this prey and the way

Prey group	Main component species in diet data
American Plaice	American Plaice <i>Hippoglossoides platessoides</i> (27.34 kg, 100%)
Amphipod	<i>Hyperiid</i> (18.5 kg, 97%), <i>Gammaridea</i> (380 g, 2%)
Arctic Cod	Arctic Cod <i>Boreogadus saida</i> (1947 kg, 100%)
Atlantic Cod	Atlantic Cod <i>Gadus morhua</i> (1059 kg, 100%)
Atlantic Halibut	Atlantic Halibut <i>Hippoglossus hippoglossus</i> (469 g, 100%)
Atlantic Herring	Atlantic Herring <i>Clupea harengus</i> (527 kg, 100%)
Atlantic Mackerel	Atlantic Mackerel <i>Scomber scombrus</i> (1.85 kg, 100%)
Capelin	Capelin <i>Mallotus villosus</i> (559 kg, 100%)
Euphausiid	<i>Thyssanoessa</i> (27.9 kg, 55%), <i>Euphausiacea</i> (22.1 kg, 43%)
Greenland Halibut	Greenland Halibut <i>Reinhardtius hippoglossoides</i> (29.4 kg, 100%)
Haddock	Haddock <i>Melanogrammus aeglefinus</i> (925 g, 100%)
Hake	White Hake <i>Urophycis tenuis</i> (1.90 kg, 72%), Silver Hake <i>Merluccius bilinearis</i> (741 g, 28%)
Lumpfish	Common Lumpfish <i>Cyclopterus lumpus</i> (760 g, 100%)
Mysid	<i>Mysidae</i> (11.9 kg, 100%)
Other fish	Eelpouts <i>Zoarcidae</i> (93.1 kg, 46%), Seasnails <i>Liparidae</i> (92.4 kg, 46%), Scaled Lancetfish <i>Notolepis Rissoi Kroyeri</i> (3.86 kg, 2%), Pricklebacks <i>Stichaeidae</i> sp. (2.46 kg, 1%), Fourline Snakeblenny <i>Eumesogrammus praecisus</i> (2.00 kg, 1%), Daubed Shanny <i>Lumpenus maculatus</i> (1.41 kg, 1%)
Other invertebrate	Snow Crab <i>Chionoecetes opilio</i> (943 g, 48%), unidentified invertebrate (314 g, 16%), Mussels <i>Mytilidae</i> (261 g, 13%), <i>Crustacea</i> (87 g, 4%)
Pandalus	<i>Pandalus montagui</i> (33.4 kg, 48%), <i>Pandalus borealis</i> (13.1 kg, 22%), unidentified <i>Pandalus</i> (13.7 kg, 23%)
Pollock	Pollock <i>Pollachius virens</i> (8.31 kg, 100%)
Redfish	Redfish <i>Sebastes</i> (65.28 kg, 100%)
Rock Cod	Rock Cod <i>Gadus ogac</i> (143 kg, 100%)
Salmon	Atlantic Salmon <i>Salmo salar</i> (629 g, 53%), unidentified <i>Salmonidae</i> (564 g, 47%)
Sand Lance	Sand Lance <i>Ammodytidae</i> (146 kg, 100%)
Sculpin	Shorthorn Sculpin <i>Myoxocephalus scorpius</i> (158 kg, 91%), unidentified Sculpin <i>Cottidae</i> (11 kg, 6%), Arctic Deepsea Sculpin <i>Cottunculus microps</i> (1,49 kg, 1%)
Shrimp	<i>Natantia</i> (14.5 kg, 52%), <i>Eualus macilentus</i> (4.67 kg 17%), <i>Pasiphaea</i> (1.58 kg, 6%), <i>Argis dentata</i> (1.18 kg, 4%), <i>Hippolytidae</i> (960 g, 3%), <i>Eualus gaimardii</i> (928 g, 3%)
Smelt	Smelt <i>Osmerus mordax</i> (6.39 kg, 100%)
Squid	<i>Teuthoidea</i> (20.9 kg, 97%), <i>Gonatus</i> (247 g, 1%)
Unidentified Flatfish	Righteye Flounders <i>Pleuronectidae</i> (64.9 kg, 100%)
Unidentified Gadoid	<i>Gadidae</i> (15.7 kg, 100%)
Unidentified Gadus	<i>Gadus</i> (64.1 kg, 100%)
Winter Flounder	Winter Flounder <i>Pseudopleuronectes americanus</i> (12.0 kg, 100%)
Witch Flounder	Witch Flounder <i>Glyptocephalus cynoglossus</i> (8.56 kg, 100%)

Table 5.1: **Prey groups in diet data.** The above table lists the prey groups in the consumption data, together with the individual species making up 1% or more of the total biomass in each group. The Latin names are from the classification in Akenhead and LeGrow (1981) and Lilly (1982), which was used to record the data-sets.

Prey group	Component species in 2J3KL abundance data
American Plaice	American Plaice <i>Hippoglossoides platessoides</i> (80.3 t, 100%)
Amphipod	<i>Amphipoda</i> sp. (910 g, 100%)
Arctic Cod	Arctic Cod <i>Boreogadus saida</i> (12.3 t, 100%)
Atlantic Cod	Atlantic Cod <i>Gadus morhua</i> (63.1 t, 100%)
Atlantic Halibut	Atlantic Halibut <i>Hippoglossus hippoglossus</i> (1.19 t, 100%)
Atlantic Herring	Atlantic Herring <i>Clupea harengus</i> (1.17 t, 100%)
Atlantic Mackerel	Atlantic Mackerel <i>Scomber scombrus</i> (2.3 kg, 100%)
Capelin	Capelin <i>Mallotus villosus</i> (37.4 t, 100%)
Euphausiid	<i>Euphausiacea</i> (342 kg, 99%)
Greenland Halibut	Greenland Halibut <i>Reinhardtius hippoglossoides</i> (90.8 t, 100%)
Haddock	Haddock <i>Melanogrammus aeglefinus</i> (9.47 t, 100%)
Hake	White Hake <i>Urophycis tenuis</i> (10.0 t, 86%), Silver Hake <i>Merluccius bilinearis</i> (1.60 t, 14%)
Lumpfish	Common Lumpfish <i>Cyclopterus lumpus</i> (6.89 t, 100%)
Mysid	<i>Mysidacea</i> (2.51 kg, 75%), unidentified <i>Mysidae</i> (580 g, 17%), <i>Gnathophausia</i> (250 g, 7%)
Non-food	Deepwater Redfish <i>Sebastes mentella</i> (254 t, 80%), Longfin Hake <i>Urophycis chesleri</i> (10.0 t, 3%), Black Dogfish <i>Centroscyllium fabricii</i> (9.35 t, 3%), Roundnose Grenadier <i>Coryphaenoides rupestris</i> (8.18 t, 3%), Longnose Eel <i>Synaphobranchus kaupi</i> (6.36 t, 2%)
Other fish	Thorny Skate <i>Raja radiata</i> (49.7 t, 52%), Roughhead Grenadier <i>Macrourus berglax</i> (13.1 t, 14%), Eelpouts <i>Lycodes</i> (8.58 t, 9%), Common Grenadier <i>Nezumia bairdi</i> (6.72 t, 7%), Blue Hake <i>Antimora rostrata</i> (6.37 t, 7%), Atlantic Argentine <i>Argentina silus</i> (2.66 t, 3%), Northern Alligatorfish <i>Agonus decagonus</i> (2.25 t, 2%)
Other invertebrate	Unidentified invertebrate (61.7 t, 40%), Snow Crab <i>Chionoecetes opilio</i> (38.1 t, 24%), Sponges <i>Porifera</i> (28.4 t, 18%), Sea Cucumbers <i>Holothuroidea</i> (8.08 t, 5%), <i>Scyphozoa</i> (6.95 t, 4%), Sea Anemone <i>Actinaria</i> (5.11 t, 3%)
Pandalus	<i>Pandalus borealis</i> (29.2 t, 86%), <i>Pandalus montagui</i> (3.42 t, 10%), unidentified <i>Pandalus</i> (1.2 t, 40%)
Pollock	Pollock <i>Pollachius virens</i> (1.45 t, 100%)
Rock Cod	Rock Cod <i>Gadus ogac</i> (11.6 kg, 100%)
Sand Lance	Offshore Sand Lance <i>Ammodytes dubius</i> (44.2 t, 99%)
Sculpin	Mailed Sculpin <i>Triglops murrayi</i> (5.80 t, 42%), Shorthorn Sculpin <i>Myoxocephalus scorpius</i> (2.96 t, 21%), Longhorn Sculpin <i>Myoxocephalus octodecemspinosus</i> (2.25 t, 16%), Sea Raven <i>Hemitripterus americanus</i> (1.78 t, 13%), Hookear Sculpin <i>Arctediellus</i> (528 kg, 4%)
Shrimp	unidentified <i>Natantia</i> (146 t, 99%)
Smooth Flounder	Smooth Flounder <i>Liopsetta putnami</i> (2.1 kg, 100%)
Squid	<i>Illex illecebrosus</i> (243 kg, 34%), <i>Cephalopoda</i> (216 kg, 30%), <i>Gonatus fabricii</i> (114 kg, 16%), unidentified <i>Illex</i> (74.8 kg, 10%), <i>Rossinae</i> (27.1 kg, 4%), unidentified <i>Gonatus</i> (21.5 kg, 3%),
Unidentified Flatfish	unidentified <i>Pleuronectiformes</i> (20 g, 100%)
Unidentified Gadoid	<i>Gadidae</i> (190 g, 95%), <i>Gadiformes</i> (10 g, 5%)
Winter Flounder	Winter Flounder <i>Pseudopleuronectes americanus</i> (20 kg, 100%)
Witch Flounder	Witch Flounder <i>Glyptocephalus cynoglossus</i> (9.90 t, 100%)
Yellowtail Flounder	Yellowtail Flounder <i>Limanda ferruginea</i> (87.9 t, 100%)

Table 5.2: **Prey groups in abundance data.** The above table lists the prey groups occurring between winter 1995 and spring 2002 in catch details from those areas of the 2J3KL bottom-trawl for which diet data is available, together with the individual species making up 2% or more of the total recorded biomass in each group.

in which other size classes or species influence its functional response to this size class would be valuable in improving the stock assessment models for that species. However, I was unable to find any suitable abundance data that would allow abundances to be assigned to individual size-classes of a species.

5.5 The final data-sets

Out of the 7152 seal stomachs in the 1981–2001 diet data-set, 1514 (21%) can be matched with abundances from the 2J3KL bottom-trawl data-set, and the Dalley-Anderson data-set gives abundance matches for another 423 seals (6%). It is impossible to determine whether the selection process outlined above has resulted in a bias in terms of the functional response of all 7152 seals because no abundance data were available for the remaining seals to assess their functional response. However, to give an intuitive idea of whether the diet of all 7152 seals is different from those matched by the two abundance surveys, Table 5.3 lists the two most prevalent prey items in the seal’s diet by month, for each of the three sets of seal stomachs.

It appears that, as far as the most prevalent prey in the diet is concerned, using the Dalley-Anderson data does not introduce any selection bias: Arctic cod is the dominant prey for each month October to March, just as in the full data-set. However, a lot of variation in diet is lost, this is evident in the high proportions of the dominant prey in each month of the Dalley-Anderson data-set. The 2J3KL data-set paints a less clear picture: Only in January and February do the dominant and second prey types agree with those in the full data-set, and it is difficult to see to what extent the diets are similar between the full set and the 2J3KL subset of stomach samples. However, the 2J3KL data-set captures the variability in the seals’ diet much better than the Dalley-Anderson data-set.

In some cases (in particular the genera *Gadus* and *Pleuronectidae*) the consumption data do not provide the resolution required. For example, in the analysis of stomach contents, sometimes the otoliths of rock cod and Atlantic cod are indistinguishable. However, in such cases the same stomach will often also contain otoliths that can be recognised as being either rock cod or Atlantic cod. In these cases the unidentifiable remains were assigned to the constituent species in proportion to their recorded occurrence. When the stomach contained only partially identified prey and no prey of the constituent groups, the split was carried out according to the proportions of these constituent species found in seal stomachs caught in the same area and season. In the 2J3KL data-set, this meant reassigning around 13 kg of unidentified *Gadus* to rock cod (55%) and Atlantic cod (45%). Likewise, around 14 kg of unidentified *Pleuronectidae* were assigned to American plaice (44%), winter flounder (38%), Greenland halibut (17%) and witch flounder (1%).

Month	All seals	2J3KL	Dalley-Anderson
Sep	Capelin 37%, Rock Cod 22%	—	—
Oct	Arctic Cod 36%, Capelin 29%	Capelin 42%, Atlantic Herring 25%	Arctic Cod 91%, Capelin 9%
Nov	Arctic Cod 23%, Sculpin 21%	Sculpin 20%, Sand Lance 17%	Arctic Cod 91%, Capelin 9%
Dec	Arctic Cod 24%, Atlantic Herring 18%	Rock Cod 17%, Atlantic Cod 15%	Arctic Cod 54%, Atlantic Herring 26%
Jan	Arctic Cod 47%, Atlantic Cod 22%	Arctic Cod 26%, Atlantic Cod 25%	Arctic Cod 53%, Capelin 15%
Feb	Arctic Cod 47%, Atlantic Cod 32%	Arctic Cod 36%, Atlantic Cod 29%	Arctic Cod 79%, Capelin 8%
Mar	Arctic Cod 49%, Atlantic Cod 15%	Atlantic Cod 35%, Capelin 22%	Arctic Cod 44%, Atlantic Herring 27%
Apr	Arctic Cod 21%, Capelin 18%	Atlantic Cod 37%, Witch Flounder 33%	—
May	Capelin 24%, Arctic Cod 18%	Sand Lance 40%, Atlantic Herring 23%	—
Jun	Capelin 36%, Atlantic Herring 16%	—	—
Jul	Capelin 63%, Sand Lance 26%	—	—
Aug	Atlantic Cod 52%, Sand Lance 18%	—	—

Table 5.3: **Prey group prevalence by month.** For each month, the two prey groups that make up most of the prey consumption recorded in each data-set are shown. For comparison, the column “All seals” shows the two prey groups that dominate the prey consumption in the whole seal stomach data-set.

Also, some consumption records were matched with abundance records that indicate that particular prey species was absent at that location and year, resulting in a logical impasse (see section 5.6.5 below). In particular, this affected 100% of the consumption records for amphipod (10.7 kg of biomass consumed), Atlantic halibut (470 g), Atlantic mackerel (570 g), euphausiid (15 kg), mysid (4.5 kg), winter flounder (8.5 kg), redfish (600 g), and smelt (700 g). These consumptions cannot therefore be explained by the MSFR. Zero-matched consumption occurs to a lesser extent in 86% of the rock cod data (representing 85 kg of biomass consumed), hake (60% or 320 g) and Atlantic herring (21% or 46 kg), indicating a mismatch between the locations that are included in the abundance trawls and the seal stomach data-base. Hence, functional responses cannot be estimated for these species.

In summary, the following prey groups are included in the model: “American Plaice”, “Arctic Cod”, “Atlantic Cod”, “Atlantic Herring”, “Capelin”, “Greenland Halibut”, “Haddock”, “Hake”, “Other fish”, “Other invertebrate”, “Pandalus”, “Pollock”, “Rock Cod”, “Sand Lance”, “Sculpin”, “Shrimp”, “Squid”, and “Witch Flounder”.

5.6 Model and extensions

5.6.1 Modelling assumptions

In attempting to model the harp seal consumption and abundance data I made a number of assumptions (cf. Lindstrøm *et al.* (1998)):

1. The data represent a random sample of all seals.
2. The prey abundance estimates are relevant.
3. The diet composition estimates are relevant.
4. Any subset of the seal sample expresses the same functional response relationship as the full set.

If the overall diet of harp seals could be estimated, the consumption data-set would probably fail assumption (1) because off-shore foraging is underrepresented (Stenson and Perry 2001). However, by assuming (4) that, as far as the functional response is concerned, the chosen data-set is unbiased, we assume that both inshore and offshore seals exhibit the same functional response and the underrepresentation of offshore seals in the sample is no longer a problem. If we were to estimate the total seal diet from our functional response fit, we could then adjust

for the underrepresentation of offshore seals by adjusting the weightings on the predicted diets of seals exposed to inshore or offshore prey abundances.

5.6.2 Basic model

To model the harp seal consumption records, a model that follows closely the rationale of Chapter 2 was used. The amount $F_{j,k}$ of prey group j consumed by an individual seal k is predicted to have mean $\mu_{j,k}$, which depends on all n prey abundances N_{j,A_k,T_k} , $j = 1 \dots n$, that seal k encounters in area A_k in time period T_k .

It is reasonable to assume that seals have a non-linear functional response (Mori and Boyd 2004). Different foraging methods, depending on prey type, have been observed in harbour seals (*Phoca vitulina*, see Bowen *et al.* (2002)), suggesting that the shape parameter m must be allowed to vary with prey type. Assuming a sigmoidal functional response to at least some prey types j (i. e. $m_j > 1$) can approximate “threshold feeding” behaviour that has been observed in marine predators at the top of the food chain (e. g. Lindstrøm and Haug (2001)).

Because consumption is a Poisson process of constituent predation events, I expect consumption $F_{j,k}$ to have a Poisson error distribution with given mean $\mu_{j,k}$ (and equal variance). However, in the case of the harp seal the consumption data are recorded in terms of biomass, which is a continuous variable. Therefore the consumption error was modelled using the continuous analogue of a Poisson distribution, i. e. a gamma distribution with equal mean and variance:

$$F_{j,k} \sim \text{Gamma}(\text{shape} = \mu_{j,k}^2, \text{scale} = \frac{1}{\mu_{j,k}}). \quad (5.1)$$

To predict the mean $\mu_{j,k}$, I use the functional response model described in section 2.7,

$$\mu_{j,k} = \frac{a_j N_{j,A_k,T_k}^{m_j}}{1 + \sum_r a_r t_r N_{r,A_k,T_k}^{m_r}}, \quad (5.2)$$

with r summing over the 18 prey groups (see section 5.5). With three parameters per species, fitting this model requires fitting over 60 parameters, many of which may be correlated. Although each data-set contains many observations, fitting such a complicated model may still be a tall order, especially when the data-set is high in variability that cannot be explained by the functional response alone.

5.6.3 Consumption error

Even a cursory glance at the consumption data reveals very high over-dispersion. These additional errors enter the consumption data from such sources as sampling and measurement error, individual variation, corrections applied to account for the seal's digestive process, etc. To model this over-dispersion, I decided to represent the consumption error not by a gamma distribution with variance equal to mean, but rather by a gamma distribution with variance proportional to the mean, introducing a proportionality parameter v_j specific to each prey group j . The extended model

$$F_{j,k} \sim \text{Gamma} \left(\text{shape} = \frac{\mu_{j,k}^2}{v_j}, \text{scale} = \frac{v_j}{\mu_{j,k}} \right) \quad (5.3)$$

has mean $\mu_{j,k}$ and variance $v_j \mu_{j,k}$.

5.6.4 Abundance error

The abundance estimates N_{j,A_k,T_k} are not error-free. In fact, the errors inherent in abundance estimates from an individual bottom-trawl set are probably rather large (see section 5.3.2 above). However, modelling these errors explicitly requires many additional parameters – one for every single abundance datum. This additional computational effort is probably unwarranted for the following two reasons. The abundance estimates are usually averages of abundance measurements taken from several sets within one area and season, so some of the measurement errors cancel out. Also, the consumption error model allows for a lot of deviation from the predicted means, and adding an abundance error model with many additional parameters would probably make it difficult to distinguish signal from noise in the final fit. For those reasons, abundance was assumed to be known exactly.

If catchabilities (see section 5.3.5) differ between species, due to the different efficiencies of the bottom-trawl gear at catching particular prey, the parameters a_j in equation (5.2) will reflect this. For example, if catchability β_j for species j was $\beta_j = 0.3$, rather than the ideal catchability of $\beta_j = 1$, then instead of observing the value a'_j , the model fit would give $a_j = a'_j \beta_j^{m_j}$. Hence it is not necessary to know the true values for catchability, as long as one constant species-specific catchability β_j applies to all records of abundance of species j throughout the whole data-set. This was ensured by requiring that the survey methodology remained unchanged.

5.6.5 Problems with zeroes

The basic model outlined above has singularities as far as zeroes in the data are concerned. If a consumption datum $F_{j,k} = 0$ (and the corresponding mean $\mu_{j,k} \neq 0$), the gamma distribution (both 5.1 and 5.3) assigns a probability of 0 to that consumption datum. If a consumption $F_{j,k} > 0$ but the corresponding mean $\mu_{j,k} = 0$, again both gamma distributions result in a probability of exactly 0. Because the model's total likelihood is a product of probabilities (priors and data), a single probability of 0 renders the whole model impossible to fit.

The first situation, of having a consumption of exactly 0, occurs quite frequently because the average number of prey species contained in a seal stomach is around 2.5 (Lawson *et al.* 1993), but the model contains $n = 18$ prey groups (see section 5.5), so most consumptions will be 0. Hierarchical methods, such as the δ -GLM method (Stefánsson 1996), have been developed to address this problem. The present model was extended as follows, to predict the probability $z_{j,k}$ of a consumption being exactly 0 and, conditional on positive consumption, the functional response model was used to predict how likely the observed consumption value was. That is,

$$F_{j,k} \sim \text{Bernoulli}(1 - z_{j,k}) \quad \text{for } F_{j,k} = 0, \quad (5.4)$$

$$F_{j,k} \sim \text{Gamma}(\text{shape} = \frac{\mu_{j,k}^2}{v_j}, \text{scale} = \frac{v_j}{\mu_{j,k}}) \quad \text{for } F_{j,k} > 0. \quad (5.5)$$

In the simplest case, those “zero-probabilities” were set to be species-specific constants, i. e. $z_{j,k} = z_j$ to be estimated.

The second situation, of having an abundance of exactly 0 but positive consumption, cannot be remedied without introducing an abundance error model. If, as above, it is assumed that abundances are known exactly, a seal cannot be eating a prey j at a location where that prey is known to be absent. However, for reasons mentioned above an abundance error model was not added to the model. Instead, these positive consumptions happening at 0 abundances were ignored.

5.6.6 Probability equations for basic model

The model defined by equations (5.2), (5.4) and (5.5) can be fitted easily within a Bayesian modelling framework. From Bayes' theorem (see section 3.3.1) we have

$$p_{\text{post}}(\text{parameters}|\text{data}) \propto p_{\text{prior}}(\text{parameters}) \times p(\text{data}|\text{parameters}). \quad (5.6)$$

In this study, the data are the abundances N_{j,A_k,T_k} and the consumptions $F_{j,k}$, while the parameters are a_j , m_j , t_j , v_j and z_j .

Focussing first on the likelihood of observing the data given the parameters, we can write

$$p(\text{data}|\text{parameters}) = p(F_{j,k}|N_{j,A_k,T_k}, a_j, m_j, t_j, v_j, z_j) \quad (5.7)$$

because in our model the abundances N_{j,A_k,T_k} together with the model parameters predict the distribution of the consumptions $F_{j,k}$. Equations (5.4) and (5.5) mean that conditioning on N_{j,A_k,T_k} together with the parameters a_j , m_j , t_j , v_j and z_j is equivalent to conditioning with $\mu_{j,k}$, v_j and z_j , and we have, for each consumption datum $F_{j,k}$, writing $\alpha_{j,k} = \frac{\mu_{j,k}^2}{v_j}$, and dropping the subscripts for ease of reading

$$p(F|\mu, v, z) = \begin{cases} z & \text{if } F = 0 \\ \frac{v^\alpha}{\mu^\alpha \Gamma(\alpha)} F^{\alpha-1} e^{-\frac{vF}{\mu}} (1-z) & \text{if } F > 0 \end{cases} \quad (5.8)$$

If we specify a beta prior for the parameters z_j , the posterior for these parameters can be found analytically. For the remaining parameters, numerical algorithms are required to evaluate their posterior distributions (see section 5.7).

5.6.7 Extensions

The basic model above is the simplest model used, but it does not fit the data at all well (see section 5.8). To allow the model more flexibility, the following extensions were added. Each of these gives additional degrees of freedom to the model and should improve model fit.

1. Having recognised the problem of abundances that are assumed to be exactly zero (see section 5.6.5 above), all occurrences of $N_{A_k,T_k,j} = 0$ were replaced with $N_{A_k,T_k,j} = \delta$, for a small positive constant $\delta > 0$. Through this approximation of 0 by δ , the predictions made for the consumption at “zero” abundances will be equivalent to those made for “very low” abundances. This reasonable approximation makes those data-points with zero abundance relevant to the functional response model itself, and eliminates the need for modelling the zero-probabilities $z_{j,k}$ explicitly.
2. One property of the harp seal consumption data-set ignored so far is “stomach fullness”. It is known that harp seals do not eat constantly, and there are times during which they fast. Accordingly, some of the seals sampled have stomachs that are empty or half-empty, rather than full. The basic model above assumes that stomach fullness is a result of the abundances

that the seals encounters. The seal’s total consumption is then predicted as the sum of these consumptions per species. This assumption seems entirely reasonable and, with the aim of predicting the composition of the harp seal diet, preferable. However, it is possible that it distorts the actual amounts of consumption by ignoring the fact that some of the seals sampled will have eaten less because of factors other than prey abundance. To explore whether this consideration may be important in fitting the consumption model, a “stomach fullness” factor f_k was added for each individual seal k . The mean consumption of prey j by seal k is now predicted not by $\mu_{j,k}$, but by $f_k\mu_{j,k}$. Because “stomach fullness” corresponds to the time a seal spends actively foraging, and seals that forage less are expected to have emptier stomachs, f_k can be considered as measuring the hours of seal foraging that have given rise to the observed stomach contents. A priori, this quantity is around $3h$, according to the time-scale on which the digestive processes operate (Garry Stenson, *pers. comm.*).

3. Another shortcoming of the model, which can be remedied relatively easily, is that the abundances or consumptions of some species may be missing from the data-set. For example, seals may be eating some prey that digest so quickly that they do not show up in the consumption data, and these prey may be present in quantities that the abundance survey does not detect. To take this into account, an additional constant $\omega_{A_k, T_k} \geq 0$ was added, to represent the amount of relevant prey abundances that are missing from the records for location A_k at time T_k . Through the limiting role of the denominator, the modified model now accounts for lower observed consumption for some prey species due to the unknown presence of other relevant prey. In summary, equation (5.2) is replaced with

$$\mu_{j,k} = \frac{a_j N_{j,A_k, T_k}^{m_j}}{1 + \omega_{A_k, T_k} + \sum_r a_r t_r N_{r,A_k, T_k}^{m_r}}. \quad (5.9)$$

4. The probabilities $z_{j,k}$ of observing a zero consumption of a particular prey could be prey-specific constants (as in section 5.6.5 above) or they could depend on the corresponding abundances. To introduce a dependence between the predicted consumption $\mu_{j,k}$ and the probability $z_{j,k}$ of observing zero consumption, recall that originally I was going to use an over-dispersed Poisson model to predict consumption. Hence, an alternative definition for $z_{j,k}$ is the probability $z_{j,k} = p(F'_{j,k} = 0)$, where

$$F'_{j,k} \sim \text{NegBin}(\text{mean} = \mu_{j,k}, \text{var} = v_j \mu_{j,k}). \quad (5.10)$$

5. Finally, flexibility was introduced into the model fitting by allowing the parameters m to take any values $m > 0$ (instead of $m \geq 1$ in the basic model). Values of $m < 1$ may not seem very realistic biologically, as they represent lower attack rates at higher prey abundance (see

section 2.4.4). But note that the present model assumes that prey encounter rate is the product of prey abundance and attack rate. When prey encounter rate is not a linear function of prey density, a slower than expected increase in prey encounter rate (Travis and Palmer (2005) and Ruxton (2005)) can be confounded in the present model with an attack rate that apparently decreases at high prey densities. Exploratory model fitting attempts indicated that values for $m < 1$ resulted in higher posterior likelihoods.

5.6.8 Filtering

I also explored whether the model fit could be improved by modifying some of the assumptions that went into creating the final abundance and consumption data-sets.

6. In section 5.4.3 species of primary interest were selected. Other species were modelled as a functional group, without distinguishing between them. Finally, a decision was made about which species should be considered as part of the “other” group, and which could be ignored completely. This is an arbitrary choice from the point of view of the seal. Ideally, each prey species should be modelled separately, but there is a trade-off between level of detail and the amount of data required to fit the model, which can have negative impacts on the generalisability of results. To explore this trade-off, more of the comparatively uninteresting species were merged into the “other” group or ignored altogether. For example, a “minimum realistic” set of prey groupings includes only 4 of the original 33 groups, i. e. capelin, arctic cod, Atlantic herring (being the major seal preys) and Atlantic cod (being the main species of commercial relevance).

7. I also wanted to explore whether the harp seal’s multi-species functional response is constant through time or if it changes from season to season or from year to year. With this aim, the data for “spring” (April and May) and the data for “winter” (October to March) were analysed separately. I also attempted to fit just the data of 1995–1998, and 1999–2001, to see if the functional response may have been different for those two periods. Any differences between the posteriors for these two year-sets, or any unusual properties of the fit (bimodal posterior distributions, for example) would indicate that, indeed, the functional response is not constant. I also attempted to fit the functional response model to inshore seal samples, or offshore samples only.

8. Going in the opposite direction, it may be that the level of detail of many years and many areas is not warranted given the quality of the data. I attempted to merge more data by combining several years into one time-period, or by working at the larger geographic scale of NAFO divisions. This approach reduced the variability of the abundance data, with the result of having fewer different abundance data-points, but with each of these being related to more

consumption data than before. Thus the model will capture the variability in the consumption data without attempting to relate it to possibly spurious differences between abundances, which may arise from the inexact measurement of abundances.

5.6.9 Reductionist view: Single-species functional responses

I also attempted to fit single-species functional responses to each prey species, ignoring the interaction terms with the abundances of other species. This simplification defeats the purpose of providing a multi-species functional response, but it is interesting from a methodological point of view to describe how different the functional responses obtained in this way are from the multi-species functional responses.

5.7 Priors, model fitting and verification

All models were coded in Compaq Fortran using IMSL libraries for statistical calculations. The models were fitted using a random-walk Metropolis–Hastings algorithm to update individual parameters (t_j, v_j) or parameter blocks $(a_j$ and m_j as a pair) within a Markov chain Monte Carlo framework (see section 3.4.1).

Priors for all model parameters were chosen to be as uninformative as possible. For parameters m_j , constrained to be at least 1, I chose a gamma prior with mean 2 and variance 0.9. Parameters z_j were assigned an uninformative Beta(1,1) distribution. For all other parameters, I tried various gamma priors with large variances as well as uniform priors with sufficiently large upper limits (and lower limit 0).

To verify the accuracy of the Fortran code, I also coded the basic model in WinBUGS (Spiegelhalter *et al.* 2004). A successful recovery of true parameter values for a hypothetical data-set with 4 prey groups, for which true parameter values were known, indicated that both the WinBUGS program and the Fortran program were free of coding errors.

5.8 Results

The main tool to assess goodness-of-fit of the functional response models is the Q–Q plot, which verifies the quantiles of individual data-points under their predicted distributions against the expected distribution of data-points according to the distributional assumptions made. Additionally, the Gelman-Rubin convergence statistic (Brooks and Gelman 1998) was checked

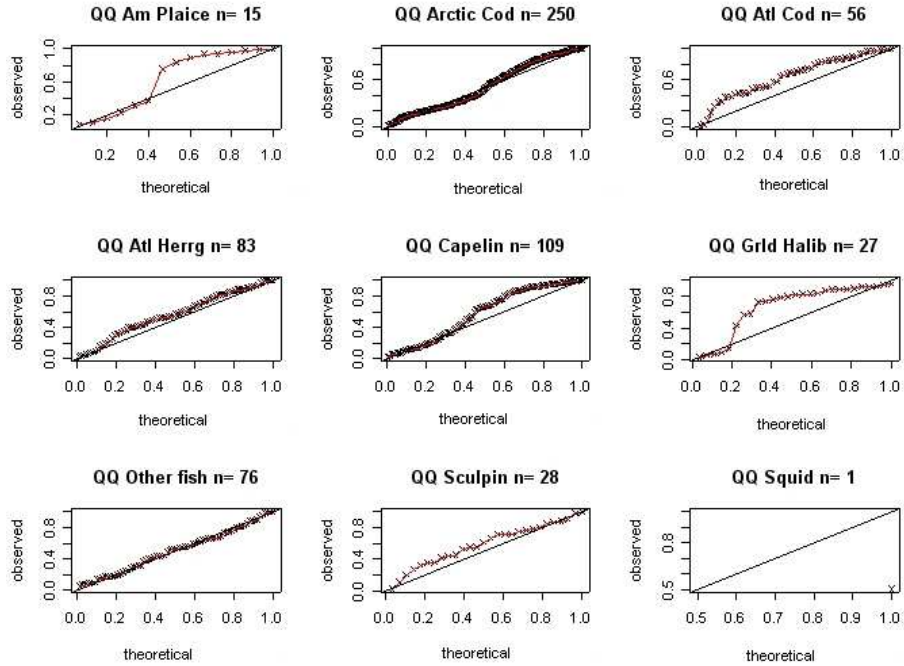


Figure 5.3: **Q-Q plots showing bad model fit.** A Q-Q plot shows the fitted quantiles of each datum against the quantiles expected from a theoretical distribution. The plots above illustrate an unacceptably bad “fit” for the non-zero consumptions in the Dalley-Anderson data-set, by species group. Ideally, the points should lie close to the diagonal line, but for most species groups there are clear divergences from the line. Also, in the only case where the Q-Q plot would suggest a good fit (“Other fish”), an inspection of the parameter values of this spurious fit reveals that the model predicts nearly the same mean consumption regardless of prey abundance, i. e. it does not explain anything.

visually.

All model fits failed on these criteria. In most of the models and extensions described above, lack of fit became apparent immediately during the numerical simulation: regardless of the starting values chosen, some parameters appeared to be “fleeing” to very high ($\gg 10^{20}$) or infinitesimally small ($\sim 10^{-20}$) values, which indicated that the model could not fit the data adequately. Even when it seemed as if convergence had been established around unlikely extreme parameter values, the Q-Q plot showed that the model did not fit the data at all (see Figure 5.3 for an example).

In the functional response models considered here, spurious parameter convergence usually occurred in the parameters a or t . I often observed $a \rightarrow \infty$, which implies that consumption $F \rightarrow 1/t$, i. e. constant regardless of observed abundances. Alternatively $t \rightarrow 0$, which together with values of $m \sim 1$ implies a consumption rate $F \sim aN$ that increases linearly without limit.

If these pathological “convergence” properties occur for many different sets of starting values, this indicates that the model at hand is unable to detect any signal in the data.

In particular, with model extension (5) above, when $m < 1$ is allowed, the model fitting algorithm attempts to force all parameters m to take values as close to 0 as possible. But, when $m = 0$, all terms N^m in the model become constants, and the predicted consumptions are no longer related to abundances. Model extension (5) thus provides the strongest indication that, in the present datasets, abundances have no bearing on consumptions and that a constant predictor of consumptions would be more appropriate.

The functional response model did not detect any relationship between abundance data and observed data on consumption by harp seals. This negative result applies both to the data-set using the 2J3KL bottom-trawl abundances and also to the data-set using the Dalley–Anderson abundance survey. Additionally, none of the model extensions, data filtering, or combinations of these resulted in a model with any explanatory power for the data-sets at hand. This is strong evidence that in fact there is no functional response relationship evident in the harp seal data, even with the very general models of functional response defined above.

5.9 Discussion

5.9.1 Validity of the results

A number of different paths can be taken to interpret these results, depending on the amount of confidence placed in the adequacy of the data collected. If the data are, in principle, suitable for predicting the harp seal’s functional response, then we have to conclude that abundance and consumption are unrelated. If, on the other hand, we have reservations about accepting the data-sets used in this analysis as suitable for this project, we can blame the lack of fit on data quality. Following the second route would render this whole functional response model-fitting inconclusive, whereas following the first path gives strong evidence that, at the local level, seal consumption patterns show no relation to the observed abundances.

To investigate which of these two hypotheses is more appropriate, I generated artificial data. The artificial data-sets were designed to be similar to the Dalley-Anderson data-set. In the artificial data-sets, 4 prey species (the minimum number of species identified in extension (6) above) were modelled, and I assumed that there were abundance and consumption data from 3 years (at low, medium and high abundances, respectively). The number of seal stomachs analysed in the artificial data-set, and their provenance was taken to be equal, seal by seal, to the seal stomachs that match the actual Dalley-Anderson abundance data-set. To represent an

abundance measurement error similar to what might reasonably be expected from a bottom-trawl, all abundances were perturbed using a normal distribution (truncated at 0), with a variance of 10% around their mean.

For those artificial data-sets, I was able to fit the basic functional response model successfully. For the 16 parameters (a , m , t , v for each of 4 species), the predicted 90% credibility intervals contained the true value on average for 14 parameters, which is close to 90% of 16 as expected. The artificial data-sets show conclusively that it is possible to fit the multi-species functional response model with an amount of data comparable to that which was available in the Dalley-Anderson data-set.

Still, the actual Dalley-Anderson data-set does not result in any model fit, and neither does the 2J3KL bottom-trawl data-set, which provides even more data. It seems reasonable to conclude that it is not the demands for amount of data that may have led to the negative result, but rather the nature of the data itself. Plotting the consumption data against abundance gives a further visual indication that supports the conclusion of no relationship between the abundance and consumption data. Although it is impossible to visualise these plots for a multi-species data-set when only 3 dimensions are available for plotting, we would expect to see at least some kind of trend when plotting the single-species data. However, for none of the species does the single-species plots show any pattern that would resemble a functional response. In Figure 5.4 one can neither recognise satiation of the harp seal at high prey densities nor any shape of the functional response. The examples shown in Figure 5.4 are representative of all prey species, and for most prey species there are even fewer data available than for the example species illustrated.

It is for these reasons that I trust in the negative results of this multi-species functional response analysis. Using the best data available and a very general model, I conclude that there is no evidence for a functional response relationship in this harp seal data-set. In my view, it would be foolish to reject this conclusion and blame it on inadequate data.

5.9.2 Possible reasons for the lack of fit for the functional response model

I perceive three major reasons for the lack of relationship between the observed local prey abundances and the consumptions observed through the stomachs of killed seals. Two of these are methodological. The data collection, both on prey abundances and on prey consumptions, may be insufficient because “prey pockets”, i. e. small areas of high local prey abundances, are unlikely to be detected reliably. Also, the high degree of spatio-temporal mismatch, resulting in part from the low spatio-temporal resolution of the abundance data, make it unlikely that a sufficient relevance of prey abundances to prey consumptions has been achieved. A third

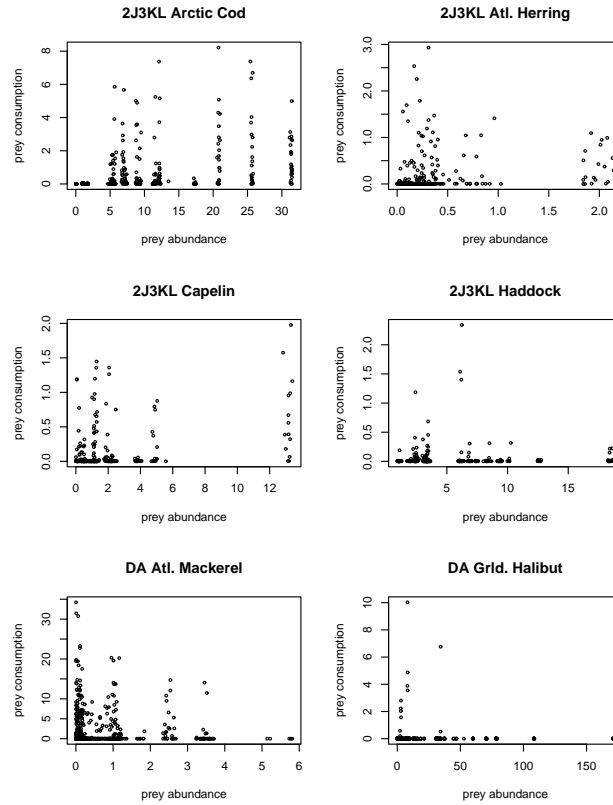


Figure 5.4: **Example plots of single-species consumption records against corresponding abundance data.** These plots show harp seal consumption data (in $100g$) (each dot corresponds to one seal stomach) against the corresponding abundance estimate (in $10kg/set$) that matches the seal's capture location and time. Each of these plots shows the abundance and consumption data for a single species only. The nature of these data informs the multi-species functional response fit, in particular the maximum consumption at predator satiation and the shape of the predator's functional response curve. (2J3KL refers to data from the 2J3KL bottom-trawl data-set, DA indicates data from the Dalley-Anderson data-set.)

reason that may have contributed substantially to the observed lack of relationship is theoretical. Because seals are active predators that seek out areas of prey densities suitable for foraging, all the seals included in this study were foraging at self-selected prey abundances, but a study of the functional response requires coverage of a wide range of low and high prey abundances. I explain these and other reasons in more detail below.

5.9.2.1 Possible reasons relating to data requirements Lawson *et al.* (1998) found that previous studies had been equivocal about the factors that influence prey choice in harp seals. It is possible that the abundances that are measured by humans through bottom-trawls have little bearing on the abundances as they are actually encountered by the seals, especially for seals caught inshore (George Lilly, John Wheeler, *pers. comm.*). For example, seals may be foraging in remote locations (Bowen *et al.* 2002) that are not covered in the bottom-trawl because of poor accessibility (rocky bottoms, steep underwater contours, shallow depth etc.), which suggests a spatial mismatch between abundances and consumptions. Juvenile cod utilise shallow near-shore waters (depth 4–7 m) that are untrawlable (minimum depth of bottom-trawl is around 50 m), prompting Dalley and Anderson (1995) to call for a study of juvenile utilisation of trawlable versus untrawlable areas. Similarly, the assumption of equal abundance throughout a whole statistical unit area is a very sweeping generalisation of fish distributions, so bottom-trawl abundance estimates may not come from relevant geographical locations (violating assumption 2 in section 5.6.1 above). Also, harp seals are mobile predators, thus consumption observed in one location may be the result of prey abundances in a different location. Including a mechanistic model of predator movement would in theory help lessen this mismatch, but the geographical resolution of the consumption data-set is much coarser than the relevant movement range of the harp seal during the hours preceding its collection (see section 5.2.1), so a movement model cannot be informed by the data-sets available in this study. However, these factors may have resulted in a lack of relationship between the observed abundances and consumptions.

The identifications on temporal and species scale may also have contributed to mismatch. For example, seals may be perceiving their prey field not according to species, as assumed in this study, but rather according to length of prey. In that case, our prey groups should have been something like “1-year old small pelagic fish (cod, capelin etc.)”, “adult cod and other fishes > 50cm” and so on. Likewise, a mismatch may have occurred on the temporal scale, in that fish abundances may actually be very different between February and March, although we assumed that they were not (see e. g. Zhu (2003), who successfully uses abundance data collected monthly).

Another problem with this multi-species functional response project is the requirement of covering as many combinations of low and high abundances as possible. Even the 2J3KL data-set

with its temporal extent of 7 years probably does not represent sufficiently different points in the many-dimensional field of possible prey abundances, because fish stocks were severely depressed in most areas for all those years. The contrast between low and high abundances required to detect the properties of the multi-species functional response may simply be lacking.

5.9.2.2 Possible theoretical reasons The above reasons are all methodological. In principle, a more exhaustive collection of data would overcome them. For example, prey abundance data could be collected synchronously with harp seal stomachs, as has been done for minke whales (Lindstrøm and Haug 2001). However, a more likely limiting factor in this analysis is the interaction of seals with local prey abundances through behaviour other than strict “foraging”. For example, seals relocate throughout the year, and during their foraging bouts they tend to spend more time foraging in areas of high prey abundances (Mori and Boyd 2004). Therefore, seals that are caught with food in their stomachs may be expected to have been exposed to “self-selected” abundances that, in themselves, no longer have any bearing on the amount of consumption. This caveat regarding the functional response model fitting is not methodological, because even a more accurate or more detailed data collection on abundance and consumption will not remedy this problem. Rather, if harp seal movement is related to foraging, as it undoubtedly is, an adequate model for the functional response must include a component to model this aggregative response of individual harp seals. Without it, the functional response will appear to be unrelated to abundance estimates (as I did find in this analysis), because the harp seal has conditioned the relevant local prey abundances by its movement. A model of both harp seal functional response and movement, which combines prey abundance data on a small geographical scale with data on seal consumption as well as seal movement, may overcome this limitation.

Another problem with fitting the functional response of a predator is that there may always be other factors that are relevant to the question but not considered. For example, in many higher predators, competition between predators (or sometimes facilitation through group predation) influences prey consumption, so that predator density as well as prey density must be included in the functional response model. However, predator interference of this kind still results in consumption data from which a functional response shape should be obvious, unlike what we have found here. Instead, it may be other, possibly unknown or haphazard, factors that influence prey consumption in this study. I imagine, for example, that the weather or the roughness of the seas will affect harp seal predation, but these variables are not included in our model (see section 2.2.2).

5.9.2.3 Possible methodological reasons Another reason that may have contributed to the observed lack of relationship between abundances and consumptions is measurement and observation error in the prey abundances, which the present model does not account for (see section 5.6.4). It may be possible and computationally feasible to extend the present model and add a component to take account of measurement error in the abundances, but given the low spatial and temporal resolution in the abundance data-sets, I doubt that an explicit model for the measurement error will be able to distinguish the magnitude of measurement error from the variability in the underlying prey abundances that are relevant to prey consumption.

Finally, modelling foraging behaviour might have to take into account caloric density of prey species that varies with season and location (Markussen and Oritsland 1991).

5.10 Further research

Foraging success of a marine predator may be unrelated to high local abundances of profitable prey (Grémillet *et al.* 2004). To determine conclusively whether local abundances of prey are relevant predictors for the harp seal diet, I join Lawson *et al.* (1998) in requesting that local prey abundances be measured at the same time as stomach samples are collected. Bottom-trawl surveys may not be the most applicable method of surveying prey abundance in this case, because in offshore areas they are very costly and imprecise and in inshore areas they do not reach the shallow, rocky areas where harp seals may be foraging. Alternative approaches for collecting indices of prey abundance exist, for example by fitting video-recording equipment to a seal (Bowen *et al.* 2002).

An alternative approach would be to look at harp seal predation on a grander scale. If the year is taken to be the smallest temporal resolution and looking at harp seal consumption on a correspondingly large geographical scale, harp seal movement is effectively factored out from the functional response. In this case, measuring harp seal consumption may present a challenge, because the method of stomach sampling is fatal to the seal and cannot give an estimate of individual annual consumption. However, other methods of sampling the seal diet are being developed (see e. g. the analysis of fatty acids in blubber samples, mentioned in Lawson and Stenson (1997)). Alternatively, it is possible to infer the consumption of generalist predators indirectly in an ecosystem model of biomass flow, if sufficient detail is known about the biomasses of all preys and other predators (Koen-Alonso and Yodzis 2005).

Finally, I want to advise scientists to analyse harp seal foraging by modelling a functional response, rather than through the calculation of selectivities. An estimate of the selectivity of a particular prey by a generalist predator says nothing about the absolute amounts of prey con-

sumption (see section 2.10) or the resulting prey mortalities. However, when studying predation by a generalist predator, especially in an ecosystem context, estimates of absolute amounts are essential and nothing is gained by knowing only the selectivities. Furthermore, it can be difficult to estimate the selectivities of a generalist predator that switches between different prey, because then selectivities are not necessarily constant (see section 2.4.1). This may be one of the reasons why the well-planned study by Lindstrøm *et al.* (1998) produced inconclusive results.

5.11 Literature cited

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6 Conclusions

6.1 Summary of the previous chapters

In Chapter 2 I give an introduction to the theory of functional responses as a way of quantifying the relationship between prey abundance and prey consumption. The functional response equation can be incorporated directly into mathematical models of predator-prey dynamics. The form of the functional response provides information on these dynamics that is not available in other formulations, such as preferences and switching coefficients. Chapter 3 explains the value of Bayesian methods and shows how they can be especially valuable for modelling functional responses. Chapters 4 and 5 describe applications of this approach to examples involving the interaction between a generalist predator (the hen harrier and the harp seal) and commercially important prey species.

In the hen harrier example I showed that it is necessary to model the multi-species functional response of this predator. The use of single-species functional responses to describe this system is likely to lead to misguided management decisions because these functions are unable to describe the full dynamic complexities of the system. In the harp seal example I did not find any indication for a functional response at all, despite having modelled it very carefully. What are the differences between these two ecological contexts responsible for the good model fit in the hen harrier example, but no model fit at all in the harp seal example?

Certainly hen harrier predation is easier to observe than harp seal predation, because the harp seal is a marine predator. The easier accessibility of the hen harrier with a view to data collection may have been the decisive factor in ensuring that the data-set adequately represented the relationship between prey abundance and consumption. However, even with the hen harrier, the data-set was very limited, with only 43 data-points. The harp seal data-set, on the other hand, contains hundreds of data-points, so the amount of data available for fitting a functional response is clearly not the cause for obtaining a fit in the one example and not in the other.

The distinction may be due to our understanding of the foraging behaviour of each predator. Individual hen harriers can be observed hunting and capturing prey, so amounts of their consumption and the species composition of their diet can be observed precisely. But all evidence on harp seal predation is indirect – the harp seals in this study were never observed while hunting and capturing prey. Instead, we have to rely on an analysis of the prey remains recovered from the stomachs of dead animals. This collection method also results in higher uncertainty due to individual variation, because every individual is only observed once when their stomach is sampled after death. All these complications mean that variation in prey choice can only be

inferred, but not observed directly.

The greater problem in fitting the harp seal functional response, however, may well be the lack of specificity in the abundance data. In this analysis approximate abundances of prey had to be used for a whole area at once (DFO “statistical unit areas”, cf. Figure 5.2), and this area is certainly larger than the area covered by a harp seal in the few hours of foraging before it is killed and its stomach sampled. Thus, the abundances may not really apply to the seals sampled, whose consumption may relate much more closely to local abundances. But with the cost and high effort that goes into sampling prey abundances in the sea (bottom-trawl surveys, acoustic surveys etc.) it is unlikely that these localised abundances will ever be measured exhaustively.

I think that the distinction between the harp seal and the hen harrier examples should be made on a level of scale. The hen harrier data uses the geographical unit of one “moor”, which is an area roughly equivalent to the foraging range of birds at their nesting location. The crucial difference from the harp seal example is that the hen harriers, having chosen a particular nesting location, are bound to stay there during the period of data collection. The harp seals, however, are observed more or less randomly throughout space, whether they are actively foraging or not, because the study design does not ensure that seals are caught only at those locations that provide prey at abundances suitable for seal foraging. Hence the foraging that we observe in the hen harrier data-set is all conditional on having found adequate prey abundance for foraging, whereas there is no such conditioning on adequate prey abundances in the harp seal project. Instead, the harp seals are free to move around, which changes the prey abundances that they are exposed to.

6.2 Functional response and questions of scale and scope

I suggest that there is, in fact, no unique concept of a “functional response”, because this definition is confounded on local and temporal scales. The choice of the spatial and temporal scale of the functional response model (\mathbf{F}) determines, to some extent, the scope of mechanisms that have to be incorporated in the model: predation *per se* (\mathbf{P}), movement (\mathbf{M}) and reproduction/death (\mathbf{R}). When studying a predator locally and over a short time-scale, the effects that its movement have on the relationship between numbers of prey encountered and prey consumed is determined by its instantaneous functional response, independent of movement (“behavioural functional response”: $\mathbf{F} = f(\mathbf{P})$), because movement does not occur on these small scales. This is the scope of the hen harrier functional response study. However, when the geographical or temporal scale are larger and the predator can move into areas of locally high abundance or exploit changes in abundance through time by timing its predation behaviour, the functional response no longer involves simply choosing among the available prey. It also involves choosing to move into areas of

different abundance if required (“population functional response”: $\mathbf{F} = g(\mathbf{P} + \mathbf{M})$). In this case the functional response includes some aspects of the aggregative response—at least in the way that Turchin (2003) defines it. Certainly this is why Gascoigne and Lipcius (2004) use identical functional forms for the two responses in their analysis. However, now it becomes difficult to say what exactly we should take as the corresponding abundances: the “average” abundance for an area of heterogeneous abundance does not apply to any individual predator because it moves within the area, but an abundance for a sub-area only applies to some individuals, i. e. those that move into that sub-area to forage. This difficulty applies to the harp seal data-set, because the abundances are estimated both on large time-scales (several months) and for large areas (DFO “statistical unit areas”), whereas the harp seal consumption data is obtained from small time-scales (the time it takes for a harp seal to completely digest a meal, i. e. hours) and small areas (the area where it foraged for this meal). There is therefore a mismatch between the scale on which consumption and prey abundance are measured: The consumption data would be suitable for fitting the instantaneous functional response, but the abundance data only allows us to fit the combination of directed movement and functional response.

I see a third context of “functional response” with a scope wider than the two discussed above. This “community functional response” is measured on even larger temporal and spatial scales, which encompass the whole predator population (“community functional response”: $\mathbf{F} = h(\mathbf{P} + \mathbf{M} + \mathbf{R})$). This combines predation and all processes that may affect the distribution of predators in space, including movement but also those changes to predator numbers that occur on smaller temporal and spatial resolution, such as predator migration or accidental deaths. For predators where reproduction or other biological processes repeat every year, this functional response operates with an annual resolution and describes the biomass redistribution between species throughout a year, given the population sizes at the beginning of the year. But predators may die or migrate within the long time-scale of the community functional response, which makes it impossible to identify an exact number of predators that share this functional response. And because both prey distribution and predator diets are likely to vary throughout a year but none of these changes are modelled explicitly in the large-scale context of this “functional response”, this “functional response” thus has to be thought of as an “empirical” functional response that models biomass flows at the level of whole populations. A functional response model in this context is simply a function that relates removals of prey by an average individual predator to total abundance of prey, rather than a mechanistic description of the predation process.

Table 6.1 summarises these three contexts and their implications on functional response models.

Clearly the community functional response will be different from the individual, instantaneous behavioural functional response, because it includes movement and uses population averages to represent other processes such as variations in prey abundances and predator diets within a year.

	Behavioural ecology	Population ecology	Community ecology
Scale	small geographical scale, short timescale	medium geographical scale, medium timescale	large geographical scale, long timescale
Processes	P : predation	P + M : predation, predator aggregation	P + M + R : predation, predator movement, short-term changes to predator numbers
Unit of predation	individual predator	individual predator	fraction of an annual population average
Functional response theory	shapes: types I, II, III etc.	unclear	unclear
Data requirements	prey abundances, prey consumption for individual predators	prey abundances, prey consumption for individual predators, predator movement	average prey abundances and prey consumption for predator population
Examples	functional response experiments	unknown	e. g. Koen-Alonso and Yodzis (2005)
Possible management uses	limited to stationary predators	predator relocation	population-based, e. g. fish stocks

Table 6.1: **Classification of functional response by context.** This table summarises the three contexts of functional response introduced in section 6.2.

By modelling a population-average functional response, the community functional response also differs from the population functional response, which is based on a fixed number of individual predators. Behavioural and population functional responses are also different, because the behavioural functional response models predation only but the population functional response includes aggregative movement.

By distinguishing these three contexts of functional response, it becomes much easier to choose a context for the functional response that is appropriate for addressing a given management question. If the abundance of a predator species is related throughout its life-cycle to prey species abundances (through trophic links), then both functional response itself (**P**) as well as movement (**M**) and reproductive processes (**R**) need to be taken into account. In a modelling framework, prey consumption may best be represented by implementing a community functional response to model these overall effects of predation during one reproductive cycle. Alternatively, a model consisting of component models of behavioural predation, predator and prey movement could be fitted, but this requires much more data because smaller geographical and temporal resolutions are used to fit these component models at the level of individual predators. If, however, the interaction between the two species is limited to a particular season or location, the trophic interaction must be modelled through an appropriate behavioural or population functional response, and changes in abundance throughout the rest of the year must be explained

by other models. If the aggregative response is an important component of the system, it would be wrong to use a behavioural functional response model to represent the trophic interaction and thereby ignore the aggregative response. A better choice would be either to model predation and aggregation jointly in a population functional response model or to combine a behavioural predation model and an explicit model of the aggregative response. However, it may be difficult to collect all the relevant data to fit a behavioural functional response in that case, because predators self-select the prey abundances that make foraging profitable, implying that they do not meet at many different combinations of predator and prey abundances. Indeed, Levin (1992) argues that the observation of patterns in ecology depends intricately on the scale at which data are observed, and that the scale on which the processes responsible for the emergence of these patterns operate is typically not the scale on which the patterns are observed. Both a full understanding of a predator's behaviour and the implications of its predation for the ecosystem can thus only be gleaned exhaustively by studying the ecosystem on different scales at once.

Koen-Alonso and Yodzis (2005) describe a model of time-series data on marine populations that includes a component model for the functional response. Because no data were available to fit the functional response, the functional response was estimated indirectly by fitting the whole model to data on population sizes. In terms of the categories suggested here, such a functional response belongs to the community functional responses because it operates at the population level and no data on individual predators are used. In contrast, experiments on individual predators, such as feeding experiments or most of the functional response experiments mentioned in Chapter 2 study individual predators that are exposed to fixed abundances, i. e. they provide data on behavioural functional responses. Because of the different meanings of "functional response" in these two contexts, one should not expect the two approaches to give similar estimates of the functional response. In particular, models of predator and prey movement throughout a year are required to link the behavioural functional response of an individual predator to the population functional response of an average predator.

While behavioural functional response data are required for a better understanding of predator biology, population and community functional responses represent predation as it actually occurs in natural contexts (by an individual predator that has moved to a location suitable for predation in the case of a population functional response, or by a whole population in a community functional response). The population functional response is amenable to management problems in which the aim is to relocate predators or prey: by aiming at prey abundances that optimise predation with regard to human aims (e. g. low predation mortality for a rare or harvested prey species), we can expect the predator to change its prey consumption as predicted. Using a behavioural functional response model only, however, might not give the desired results, because the predator might relocate instead, thus applying its behavioural response to different prey

abundances and thereby foiling the management plans.

From a fisheries management point of view it is probably the community functional response that is relevant, because the management of human interventions in fisheries concerns not so much the location of fish stocks but rather their total size. However, for conservation interests, the context of functional response required is determined by the type of interaction between the species of interest. If, as in the hen harrier example, the management conflict only manifests itself during a particular season (here the grouse breeding season) or a small area, the prey densities that individual predators are exposed to can be assumed to be constant, and the functional response that determines the nature of this interaction belongs to the behavioural context. If predator movement is important within the scope of the management model but prey densities cannot be estimated on the small resolution that influences predator movement, predation can be modelled within the population context. Because the population functional response combines both the behavioural, instantaneous functional response and the predator's aggregative response, a detailed understanding of the aggregative response itself is not required. A population functional response model may thus be useful in managing a predator whose aggregative behaviour is not well documented.

Finally, the theory of functional response shapes (see section 2.3) belongs within the context of behavioural ecology. All theoretical arguments to explain how the different shapes of type I, II or III functional responses could arise are based on individual predators. In section 2.4.3 I mentioned how the averaging of individual predators can result in type III functional responses at the population level. While this may sound as an argument to support the existence of type III community functional responses, the reasoning for this is unclear, because the community functional response not only requires an averaging over individual predators, but also over changes in prey densities that occur on shorter time-scales. Because of the non-constant nature of prey densities in nature, but the assumption of approximate constancy throughout a year in the context of the community functional response, arguments that suggest particular shapes for the behavioural functional response may not apply to community functional responses. I suggest that further research is required into unifying the behavioural and community approaches in ecology (see Levin (1992)). In particular, knowledge is currently limited of both the mechanisms that link individual predators' behavioural functional responses with the average community functional response, and of the properties of community functional responses, which need not be similar in shape to behavioural functional responses. Given the use of community functional responses in stock assessment models, these applications of community ecology make research into the properties of such functional responses even more important.

6.3 Literature cited

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Appendix: The functional response of generalist predators and its implications for the monitoring of marine ecosystems

I am a co-author on the following paper, which is in press. The correct reference for it is

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