Temperature-Mediated Shifts in the Foraging Behaviour of the Eurasian Otter, *Lutra lutra* L.

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CANDIDATES DECLARATION

I declare that the work recorded in this is entirely my own unless otherwise stated. No part of this work has been submitted for any other degree.

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ABSTRACT

Environmental variables will influence the behaviour of an animal by changing its state, and a relationship exists between such variables and the animal's behaviour. Aquatic animals are particularly under the influence of the medium in which they forage, and changes in this may have profound effects on the behaviour

Recent studies have demonstrated that the metabolic costs of foraging in the Eurasian otter (*Lutra lutra*) are increased substantially by depressed water temperature. Otters are common around the west coast of Scotland, and yet they are frequently exposed to low water temperatures. This project examined the foraging behaviour of otters at the Taynish peninsula, Mid-Argyll, Scotland, and the effect of low water temperatures on otters and their prey, by observing the behaviour of otters at a range of water temperatures around.

A regime of stationary fish trapping was initiated over 15 months to examine seasonal and spatial fluctuations in the abundance of the prey species. While the limitations of this method of assessing prey populations are discussed, it was clear that there were profound differences in the prey composition of the three habitats studied and that these changed seasonally. An examination of the accuracy of faecal analysis as a means of quantifying the diet of otters, was carried out. From this, potentially more accurate methods of assessing diet were suggested. The diet of the otters around the study site, as determined by observations and analysis of the faeces, demonstrated that the otters were selective of their prey at certain times of year, corresponding with those times of high prey abundance, but at times of poor prey abundance such selectivity was reduced.

Foraging site use by the otters was examined in the context of temperature mediated fluctuations in prey biomass, as determined from the trapping. While the overall use of the habitats matched that with the highest biomass, temporal variations in this did not correspond with variations in biomass. Potential explanations for this are discussed. Changes in the activity levels and escape responses of some of the otter prey species were examined experimentally, and were found to have a significant positive relationship with water temperature. However, the actual capture times of these species, as determined from direct observations of the otters feeding, did not change with water temperature. This may have been caused by longer search times in colder water, or be due to the fact that otters forage for their prey when it is in the inactive component of its activity cycle. From this it was hypothesised that the otters would change the timing of their foraging in cold water, as it would no longer be dependent on the behaviour of their prey. This was tested by direct observation, and while no relationship was observed at any time of year with the tide, the observed relationship between foraging activity and time of day was altered in the winter.

The relationship between the parameters of dive behaviour and water temperature was investigated. There was no strong relationship with any of them, however following recent studies in the literature, it was hypothesised that the metabolic costs of foraging would largely be met after the foraging bout was completed. A mathematical model was constructed to describe the relative amount of on land recovery time needed after a foraging bout at different water temperatures. This predicted that more time would be spent on land in lower water temperatures, and these predictions were upheld by observations from the wild. It was also apparent that the otters made greater use of deeper water during warmer water temperatures. This phenomenon was investigated by cost benefit analysis. Fish trapping revealed that there were better prey in deeper water and the success rate of dives was also higher. Conversely, dive times were longer in deeper water, and the prey, though of better quality were associated with longer handling times. Furthermore the rate of heat loss from the otter pelt was determined experimentally to be greater in deeper water. These data were combined in the form of an optimality model, which confirmed the results of observations that the otter only foraged in deeper water when the temperature of the water was relatively high.

In conclusion it was found that the foraging behaviour of the otter was influenced by water temperature in the following ways:

1. The temporal pattern of foraging changes in the winter
2. Post-foraging recovery times on land are increased in colder water temperatures
3. Otters are restricted in their use of depth in colder water

These results have demonstrated that the foraging behaviour of the otter cannot simply be viewed in terms of handling costs and prey energetic value, rather the complex influences of environmental variables on the otters physiological state, and the complex relationship this has with its behaviour, must be considered.

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Chapter 2. Seasonal and spatial fluctuations in the prey species of the Eurasian otter

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CHAPTER 1.

INTRODUCTION

CHAPTER 1

INTRODUCTION

The science of ethology has provided us with accurate methods for describing and analysing animal behaviour, and the theoretical framework to understand and predict the response of an animal to a particular situation (Huntingford 1984). In particular, ethology is concerned with explanations of behaviour in both causal and functional terms. This does not however mean that it cannot have positive applications outwith its theoretical realms, since an understanding of an animal's behaviour will be of value in all situations where there is an interaction between humans and animals (Monaghan 1984). Such understanding, for example, can be critical in situations where an animal population is threatened, in order to implement constructive conservation policies to protect it (Macdonald, 1995). Of particular importance to conservation is a comprehension of the manner in which an animal interacts with its environment, particularly with reference to foraging behaviour (Clemmons and Buchholz 1997).

Of all the aspects of behaviour, the finding and consumption of food is of paramount importance to virtually all animals. It will influence subsequent aspects of their behaviour and ecology by determining their ability to carry out further activity, breeding and growth. As such it has created the basis for much of the taxonomic diversity evident in present biological systems and is one of the driving forces of adaptive radiation (Hughes 1993). In common with other behaviours, foraging can be studied by the application of economic principles, and two key papers that were published in 1966 can be seen as the beginning of the principles of what is now known as optimal foraging theory. Both the work of MacArthur and Pianka (1966) and Emlen (1966) predicted that natural selection would mould foraging behaviour whereby an animal would promote its fitness by maximising its net rate of energy gain. In order to understand this process the behaviour can be viewed as having costs, for example travel time and predation risk, and benefits, for example the energetic gains of different food types.

Such aspects of foraging are of particular interest in the context of diving predators, animals that forage underwater, but that must come to the surface to breathe. Selection pressure has acted upon these animals to produce a range of anatomical and physiological adaptations to cope with the difficulties that are faced by foraging in an aquatic medium. This medium creates a range of constraints, particularly with regard to respiration, pressure and heat loss. The effects these have been studied both *in vivo* (for example de Leeuw 1996) and by modelling (for example Carbone *et al.* 1996). Historically the study of such diving behaviour was initiated by Dewar (1924) who described the diving of birds via direct observations, followed by Scholander (1940) who attempted to define the respiratory adaptations of divers experimentally by forced submersion. Such involuntary diving could not, in retrospect, provide accurate physiological data, but it did provide valuable insight into some aspects of the animals means of coping with the respiratory stresses of diving. The real breakthrough in our understanding of the adaptations to diving came with the advent in the 1960s and

1970s of recording devices and transmitters that could be attached to or implanted in the divers, (for example Kooyman 1973, Le Boeuf *et al.* 1988). These allowed, for the first time, detailed studies to be made of both the behavioural and physiological demands and adaptations of diving predators.

Mathematical models, which attempted to describe diving behaviour and physiology, have added greatly to our understanding of the underlying mechanisms behind aquatic predation. A major prototype in this field came from the insight of Kramer (1988) that the marginal value theorem, one of the commonest optimality models, could be applied to divers. Kramer (1988) modelled the optimal allocation of time within the dive cycle, that is travel time, from and back to the surface, foraging time, and inter-dive recovery time for divers and his approach was further refined by Houston and Carbone (1992). Subsequently numerous models based around the dive cycle have been produced, with perhaps more models than empirical evidence to support them, examining all the physiological and behavioural aspects of diving. While such models have concentrated on the dive cycle, it has been demonstrated that all the metabolic costs of diving are not met during the diving bout, but are met subsequent to it during recovery periods, (de Leeuw 1996). This work demonstrated the need for reliable field data to be obtained describing the aspects of diving defined mathematically elsewhere. Furthermore a degree of stochasticity must be incorporated into such models to allow for variation in the costs and benefits that may be caused by environmental influences, such as water temperature, on the animals state (Houston 1993).

There are a number of difficulties in attempting to study aquatic predators in their natural habitat. For example, much of their foraging behaviour occurs underwater, and they are often too far from the shore for direct observations to be made. To some extent many such difficulties have been overcome by the use of radio-telemetry (Macdonald and Amlaner 1980). Not only can a reasonably accurate location for an animal be given, but certain aspects of their foraging behaviour can be measured, for example the length of dives can be recorded since the signal may not transmit underwater. This has successfully been used to monitor the feeding behaviour of common guillemots, *Uria aalge*, in years of fluctuating habitat quality, (Monaghan *et al.* 1994). Radio-telemetry does however also pose problems. Only a limited number of animals can be tracked at any one time, thereby reducing the sample size, and the attachment of the transmitter may cause behavioural or physiological problems that invalidate the data, (see for example review for penguins and other seabirds, Wilson *et al.* 1997). Implantation of the transmitter can reduce some of these problems, however the necessity of invasive surgery creates a number of new problems, and the range of the transmitter may also be reduced (Kuelche 1982). Many of these problems could be overcome by the study of an animal that not only forages close to the periphery of the water to allow direct observation to be made, but that also feeds on the surface, so that prey can be identified. One such animal is the Eurasian otter, *Lutra lutra*.

Although described as "vulnerable" in the current IUCN Red Data Book (IUCN 1988), the Eurasian otter is the most widely distributed of the 13 species of Lutrinae from the family Mustelidae, and the only one that occurs in Europe. It also occurs in

Africa and Asia. Of the other 13 species, two are found in North America, *L. canadensis*, the river otter, and *Enhydra lutris*, the sea otter, in South America there four, the sea cat, *L. felina*, the giant otter, *Pteronura brasiliensis,* the southern river otter *L. provovax* and the neotropical otter *L. longicandis*. Four species are found in Africa, *L. lutra, L. maculicollis,* the spotted-necked otter, *Aonyx capensis,* the Cape clawless otter, and *Aonyx congica,* about which virtually nothing is known. Finally, five are found in Asia, *L. lutra, Enhydra lutris,* the small clawed otter, *Aonyx* cinera the smooth coated otter, *L. perspicillata,* and the rather inelegantly named hairy nosed otter, *L. sumatrana,* (Kruuk 1995)

In many ways the Eurasian otter is ideally suited to the study of behavioural adaptations to aquatic foraging. It is large enough to allow observations to be made, it feeds close to the shore, it always eats its prey on the surface (as confirmed by all observers, see review in Kruuk 1995), so its prey can be identified, and it feeds on bottom-living prey (for example Watt 1995), so the depth it is diving to can be judged. They feed successfully in both freshwater and the sea, and generally in the sea they feed during the day so it is possible to make direct observations of them from concealed viewpoints along the coast, (Kruuk and Hewson 1978). From these observations many of the basic parameters of diving can be described, such as dive time, surface time, and success and depth of dive.

Most of these behaviours were first coherently described and evaluated by Hans Kruuk and his team at the Institute of Terrestrial Ecology in Banchory (see review in Kruuk 1995). His first published account of otters made basic descriptions on the otters feeding in the sea of the west coast of Scotland (Kruuk and Hewson 1978), and his ideas developed to include examinations of the organisation and densities of otters (for example Kruuk and Moorhouse 1991), food and foraging behaviour (for example Kruuk and Moorhouse 1990), and the energetics of foraging (for example Kruuk and Carss 1996). These studies have demonstrated that while the otter is a successful predator, it is not highly adapted for the semi-aquatic mode of life, and foraging in the aquatic environment is highly costly to it. It is particularly costly, as demonstrated by metabolic studies by Kruuk *et al.* 1994, with respect to the loss of body heat to the surrounding water, where there is a sharp increase in the metabolic costs of foraging with decreasing water temperatures. All otters do not have the physical adaptations to reduce heat loss normally associated with aquatic animals, such as a layer of blubber (for example, Irving and Hart 1957) or an ability to restrict the flow of blood to peripheral organs (see for example Harrison and Kooyman 1971), relying instead on their dense fur (Tarasoff 1974). There are inner and outer layers of hair in the otters pelt, and air is trapped between them during submersion creating an insulating barrier against heat loss, similar to the air layer between the feathers of many diving birds (Wilson and Wilson 1996). The function of this air layer can be relatively easily compromised, for example by salt crystals (Kruuk and Balharry 1990) or pollution (Costa and Kooyman 1982), and so requires constant grooming and maintenance (Nolet and Kruuk, 1989). However the pelt, while providing the only insulation an otter has against heat loss, is a relatively poor insulator when compared with blubber (Tarasoff 1974). Therefore the loss of heat is a major cost to foraging otters, as demonstrated metabolically by Kruuk *et al.* (1994) and these costs will have to be met in some way, particularly for animals foraging in cold water. Potential solutions to this have been modelled, for example Kruuk and Carss (1997), created a model which demonstrated that the amount of time that the otter required to spend foraging in each 24 hour period increased with depressed water temperatures. However there have been no field studies to examine how the otter copes with foraging in low water temperatures.

Therefore this study set out to examine how some of the physiological demands of being an aquatic predator, particularly those related to heat loss, are met by behavioural responses by otters during foraging. To do so, a series of basic habitat parameters were examined to determine if any effects on foraging were related to increased costs in cold water, or were secondary effects due to changes in prey or habitat. Then we were able to examine the foraging behaviour of the otters in different circumstances to determine the functional significance of any changes seen.

In chapter 2, I examine seasonal fluctuations in the numbers and distribution of the main prey species of the otter. Chapter 3 attempts to refine the description of an otter's diet by spraint analysis through the use of feeding trials on captive otters. This methodology, in conjunction with direct observation, is used in chapter 4 to describe seasonal and spatial variations in the diet of otters around the study site. Chapter 5 examines seasonal changes in habitat use by otters, particularly in relation to fluctuations in prey biomass and water temperature. In chapter 6 describes an experimental study of the effects of water temperature on the behaviour of prey species, and otter foraging behaviour is examined in this context in chapter 7. Chapter 8, with the assistance of a basic mathematical model, attempts to describe how the increased metabolic demands of foraging in cold water described by Kruuk *et al.* (1994) are met by behavioural change, and one particular aspect of this, the use of depth is investigated in chapter 9. Finally in chapter 10 all of these ideas are brought together to describe some of the behavioural responses to the physiological demands of foraging in cold water, and to describe the potential usefulness of such information in the context of the conservation of this vulnerable species.

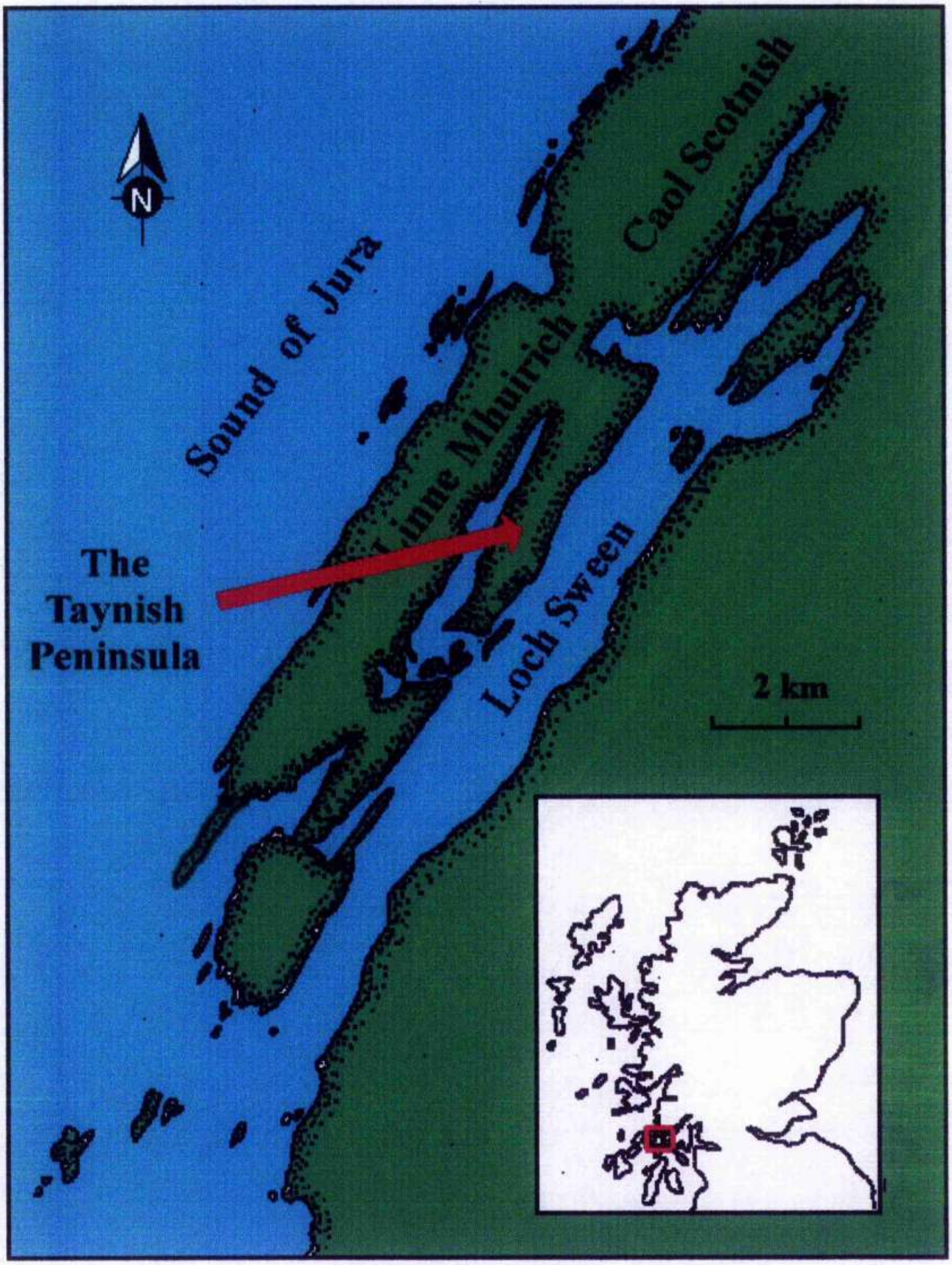


Figure 1.1. The Taynish Peninsula

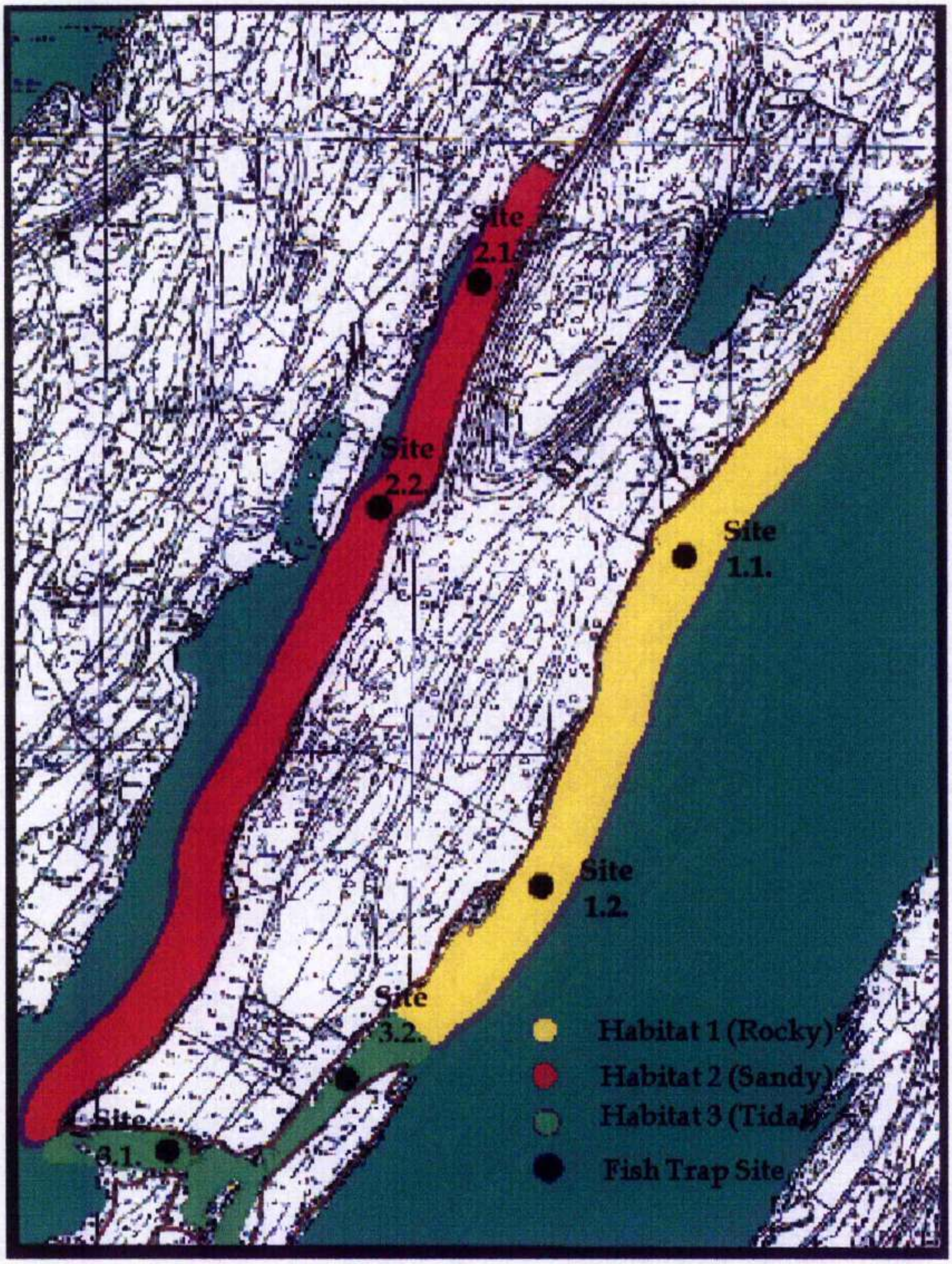


Figure 2.1. The Location of Trap Sites around the Taynish Peninsula

CHAPTER 2

SEASONAL AND SPATIAL FLUCTUATIONS IN THE PREY SPECIES OF THE EURASIAN OTTER

CHAPTER 2

2.1. INTRODUCTION

Foraging patterns of any predator will to a large extent be determined by the patterns of distribution of its prey. Therefore, in order to understand the functional significance of the foraging behaviour of an animal, it is necessary to examine the temporal and spatial patterns of the distribution of their prey species.

While Eurasian otters, (*Lutra lutra*) forage in both marine and freshwater habitats, the greatest concentrations of their numbers are found in marine environments, due to a number of factors including prey concentration, pollution and disturbance (Kruuk 1995). In the British Isles, the most important of these include the Shetland islands, the Hebrides and the west coasts of Scotland and Ireland (Green and Green, 1988). This concentration in the west coasts in likely to be due to some extent to poorer drainage and therefore a higher availability of fresh water in which to bathe, (Kruuk and Balharry, 1990). In the marine environment, otters feed largely on bottom dwelling fish and crustacea within the inter-tidal and sub-tidal zones (Kruuk, 1996). Variations in the population levels of these species, both seasonal and spatial, will directly affect the local populations of otters.

There have been several studies on the diet of otters feeding on marine prey, (e.g. Mason & MacDonald 1980, Kruuk & Moorhouse 1990, Watt 1995, Beja 1997). All suggest that otters feed on locally abundant species, and where there is an abundance of prey, such as in Shetland, the otters will choose the most energetically profitable (Kruuk & Moorhouse, 1990, Watt, 1991). The majority of these prey items are bottom dwelling, such as eelpout (*Zoarces viviparous*), butterfish (*Pholis gunnellus*), 5-bearded rockling (*Ciliata mustela*), bullrout (*Myoxocephalus scorpius*), eel (*Anguilla anguilla*), as well as a limited amount of crustaceans, especially shore and edible crabs (*Cancer maenas* and *Cancerus paganelus*). The proportion of crustaceans in the diet is likely to be related to the age and experience of the otter (Watt, 1993). Other, free-swimming species may become seasonally important, for example gadoids such as cod (*Gadus morhua*), and pollack (*Pollachius pollachius*), increase the proportion of time they spend in shallow waters in the winter, and at this time become important prey species to the otter (Watt, 1995, and see chapter 5). Goldsinny, rock cook and corkwing wrasse (*Ctenolabrus rupensis, Centrolabrus exoletus,* and *Crenilabrus melops*) retreat into crevices at night and in the winter (Sayer *et al*, 1994), when they become available to foraging otters. At this study site, the Taynish peninsula, the otters followed the pattern of other west coast studies (e.g. Watt, 1995, Mason and Macdonald, 1980), feeding predominantly on butterfish, gadoids, and eels. However unlike other areas, rock and black gobies (*Gobius pagannellus* and *G. niger*) and goldsinny, rockcook and corkwing wrasse, are also important in their diet (see chapter 5).

In a number of studies (Kruuk *et al* 1988, Heggberget 1993, Beja 1995, and Watt 1995), fish traps have been used to monitor the populations of the prey species of the otters. These are funnel traps that rely on the prey species' tendency to seek out cervices, rather than baiting, to attract the fish (Kruuk *et al* 1988). A sampling method such as this, which relies on the prey species behaviour, will carry a certain amount of bias, making inter-specific comparisons of abundance based solely on catches unreliable. Kruuk *et al* (1988) suggested hand searches of the infra-littoral zone to obtain correct numbers of prey and using these figures to calculate correction factors, which can then be applied to the catches from traps. The implicit assumption here is that the population of fish at low tide (when the hand sampling is carried out) is the same as at other tide states, when the fish are caught. While this may be true for certain prey species, especially the eelpout, which was the most important component of the otters diet in Shetland where Kruuk's study was carried out (Kruuk and Moorhouse 1990) there is little evidence to either support or contradict this assumption for other prey species. Indeed the eelpout is of little importance in otter diet at Loch Sween where the present study was carried out (see chapter 5). Beja (1995) supplemented his data from fish trapping in Portugal by sampling via hand netting and angling. His results showed profound differences in the species composition and numbers obtained by different sampling methods (*Ibid.*) and suggested that none of the methods he used in fact gave an accurate representation of the overall composition of the fish population.

All of the above limitations apply only to making inter specific comparisons of prey abundance. They do not apply when making intra - specific comparisons, such as differences between the abundance of the same fish species in different sites. Fish trapping can, in fact, provide us with valuable information on the relative populations of species in different habitats, and the inherent implications of this to otters foraging in these habitats, as well as information on seasonal variations of different species.

For this study, we intended to answer the following specific questions:

1. What species of demersal fish are present within the foraging range of the otters at Loch Sween?
2. How does the abundance of these species vary between the different habitats present within this range?
3. Do the levels of these species vary seasonally?
4. What implications does this have for habitat use by the otters foraging at this site?

2.2. STUDY AREA AND METHODS

The study was carried out around the Taynish peninsula, Loch Sween, Mid-Argyll, Scotland (figure 1.1), between June 1995 and August 1996. This site offered a range of marine habitats, all of which were utilised by foraging otters, (see chapter 5). For the purposes of this study, the peninsula was subdivided into three discreet study habitats, as defined by physical and ecological features, and each of these was further divided into two, with regard to the location of the fish traps as defined by more subtle features, (see fig.2.1.). The two sites within each habitat were chosen to show two different aspects of this habitat. This gave a total number of six trap sites. They were as follows

HABITAT 1.

Loch Sween. A fairly sheltered range of steep bedrock cliffs, separated by ledges of broken rock.

Site 1.1. A bay of broken rock and mud, with a shallow gradient. The infralittoral zone is dominated by Lithothamnia and *Laminaria saccherina,* as well as *L. hyperborea, L. digitatta* and *Corallina officinalis*

Site 1.2. Steep bedrock cliffs, dominated by Lithothamnia and *Trailliella* along with *Corallina officinalis, Chondrus crispus, Plocamium cartilagineum, Chylocladia verticillata* and *Laminaria saccherina.*

HABITAT 2.

Linnhe Mhuirich. An enclosed shallow body of water, with a muddy bottom, and some cobble and pebble shores.

Site 2.1. A slope of broken rock, pebbles and cobbles, descending down to muddy sediment. Dominated by Lithothamnia and *Pomatoceros triqueter.*

Site 2.2. A shallow muddy slope dominated by a dense bed of *Zostera marina.*

HABITAT 3.

Linnhe Mhuirich rapids. Shallow tidal rapids with extensive beds of maerl and massive sponge colonies.

Site 3.1. Narrow tidal channel, composed of boulders and bedrock, with patches of cobbles and pebbles and maerl gravel. The boulders and bedrock have growths of Lithothamia as well as *Laminaria hyperborea* and *L. saccherina.* In the deeper section there is also extensive growths of the sponges, *Halidrys siliquosa* and *Amphilectus fucorum.*

Site 3.2. The deepest cross-section of the tidal rapids with a dense canopy of *Laminaria saccherina* and *L. hyperborea.* Boulders are characterised by Lithothamnia, while pebbles are dominated by encrusting calcareous and non-calcareous algae, along with *Escharoides coccinea* and *Pomatoceros triqueter.*

Two fish traps were put out at each of these sites, 10m apart, at a depth of 1 - 2m, for five consecutive 24 hr periods each month, throughout the study. The traps were double funnelled creels, (see figure 2.2.), similar to those used by Kruuk *et al* (1988), Heggberget (1993), and Watt (1995). They were 80 cm long, with a 27 cm diameter, covered with plastic 7 mm mesh and weighted with a large stone tied inside the second compartment. They were unbaited, to prevent them from filling with shore crabs, relying instead on the fishes' tendency to seek out crevices (Kruuk, 1995) during the night and low tide. Traps were emptied daily at low tide, and all prey was identified, measured and weighed.

Biomass was calculated as the total weight of the animal contents of the traps and this was done both including and omitting any crabs found. The 15 months trapping was subdivided into seasons thus,

Summer : June, July and August

Autumn : September, October and November

Winter : December, January and February

Spring : March, April and May

Catches for each species were expressed as "catch per trap night", that is, the mean no. of fish caught per trap, per night, for all traps in a particular habitat or season. Catches, and overall biomass, at different sites and in different seasons, were analysed, using SPSS 7. statistical package, and a Shannon-Weiner function of species diversity was calculated for each study site, (Krebs, 1987)

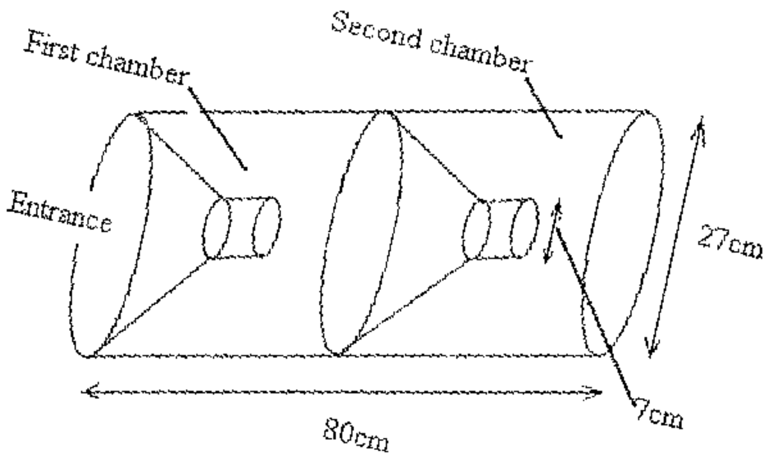


Figure 2.2. A double funnelled fishtrap

2.3. RESULTS

2.3.1. Total catches

The total catches, with all sites combined, over the 15 months of the study are shown in table 2.1. Of the fish caught, the most abundant species were the black and rock gobies, the 15 spined stickleback, eels, corkwing and goldsinny wrasse, and the gadoids: pollack, saithe and cod. Shore crabs were also caught in very high numbers.

Eel	55
Butterfish	8
Rock goby	134
Black goby	212
Sand goby	76
2-spot goby	21
Unid. goby	21
Shore rockling	1
5-bearded rockling	14
Bullrout	7
Long-spined sea scorpion	12
3-spined stickleback	35
15-spined stickleback	106
Goldsinny wrasse	83
Corkwing wrasse	70
Rockcook wrasse	5
Pollack	56
Saithe	37
Cod	48
Pipefish	2
Shanny	1
Flatfish	1
Montague's sea snail	8
Clingfish	15
Trout	2
Edible crab	4
Shore crab	851
Velvet crab	1
Squat lobster	2

Table 2.1. Total catches over the whole trapping regime

2.3.2. Habitat effects

Catches of each of the main species were compared between the paired sites, within the three habitats, via a Wilcoxon's matched pairs test, with data paired via month of collection and corrected for inaccuracy caused by the large numbers of repeated tests by a Dunn - Sidak sequential Bonferroni. None of the species showed a significant difference between any of the pairs. These pairs were therefore aggregated, into the three habitat types for further analysis. These habitats will be subsequently referred to as "Rocky", (habitat 1), "Sandy", (habitat 2), and "Tidal", (habitat 3).

Catches of the main prey items of the otters were examined for variation in total catch of each species, at the different habitats, via a Kruskall - Wallis one - way ANOVA. This was done for each season. Due to the large numbers of repeated tests, the probabilities obtained were corrected by a Dunn - Sidak sequential Bonferroni, (see Table 2.2). Where a species did not show a significant difference between sites the data from all the habitats was aggregated for subsequent analysis.

	Summer	Autumn	Winter	Spring
Eel	NS	NS	†	†
Butterfish	NS	†	†	NS
Rock goby	**	**	†	NS
Black goby	**	**	†	NS
5-bearded rockling	†	†	NS	NS
15 spine stickleback	NS	NS	NS	NS
Goldsinny wrasse	NS	†	†	†
Corkwing wrasse	**	NS	†	†
Pollack	**	NS	NS	†
Saithe	†	NS	*	†
Cod	NS	NS	NS	†
Shore crab	NS	NS	NS	**

Kruskal-Wallis 1 way ANOVA, corrected by Dunn - Sidak sequential Bonferroni method to , * = $p < 0.05$; ** = $p < 0.01$; † = too small a sample

Table 2.2. Results of statistical comparison of catches of the different fish species at different sites, in each season

A number of species were common in certain habitats, (figures 2.3. –2.16.). Rock gobies were caught significantly more at habitat 1, the rocky shores. Black gobies were caught in significantly larger numbers at habitat 2, the sandy bottomed sites. Saithe, corkwing wrasse and shore crabs were caught in significantly larger numbers at habitat 3, the tidal rapids. Finally pollack showed a significant preference for the rocky and tidal habitats over the sandy habitat.

2.3.3. Seasonal effects

To eliminate the possibility that any seasonal variation is caused by changes in fish behaviour driven by fluctuations in water temperature, following Kruuk *et al* (1988) we assumed that such behavioural change would be common throughout all the fish species, therefore their behaviour would change together if such temperature mediated variation in catch existed. This somewhat strong assumption is tested to some extent in chapter 6. Therefore, we calculated Kendall's Coefficient of Concordance for the most common species of fish, and this demonstrated that the catches did not fluctuate together, ($W = 0.36$, $\chi^2 = 14.57$, $p = 0.15$). We therefore concluded that temperature was not a major influence on the seasonality of catches.

In order to examine seasonal effects on the catches the fish were split into two groups. Those species that had shown no significant differences between catches in different habitats, that is eels, butterfish, five–bearded rockling, 15–spine stickleback, goldsinny wrasse and cod, were analysed with the habitats grouped together, table 2.3.

Where there had been significant differences between habitats, that is with rock and black gobies, corkwing wrasse, pollack, saithe and shore crabs, the data were analysed separately for each habitat, to determine whether there were any seasonal effects, table 2.4. All these catches were compared using Kruskal - Wallis one - way ANOVA, and corrected by Dunn - Sidak sequential Bonferroni.

	Summer	Autumn	Winter	Spring	sig
Eel	.12 ± .023	.06 ± .014	.00	.03 ± .012	***
Butterfish	.01 ± .006	.00 ± .000	.00	.02 ± .011	NS
5-beard rockling	.01 ± .005	.01 ± .007	.03 ± .014	.02 ± .011	NS
15-spine stickleback	.13 ± .011	.35 ± .032	.40 ± .044	.23 ± .034	***
Goldsinny wrasse	.21 ± .030	.03 ± .012	.00	.02 ± .010	***
Cod	.09 ± .028	.06 ± .017	.04 ± .020	.00 ± .000	**

Kruskal-Wallis 1 way ANOVA: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 2.3. Results of the statistical comparison of catches of the prey species between seasons, with sites grouped together. Given are the catches expressed as mean catch per trap night, and the statistical significance of the ANOVA comparing the seasons.

HABITAT	1				2				3					sig.	
SEASON	Su	Au	Wi	Sp	Su	Au	Wi	Sp	Su	Au	Wi	Sp	1	2	3
Rock goby	.65 ± .08	.35 ± .08	.00	.05 ± .03	.11 ± .04	.02 ± .01	.00	.00	.11 ± .03	.13 ± .06	.00	.00	**	NS	NS
Black goby	.04 ± .02	.00	.00	.07 ± .04	.79 ± .13	.49 ± .13	.05 ± .03	.31 ± .13	.36 ± .07	.05 ± .03	.02 ± .02	.17 ± .05	NS	**	**
Corkwing wrasse	.04 ± .02	.03 ± .02	.03 ±.02	.02 ± .01	.13 ± .04	.03 ± .02	.00	.00	.26 ± .06	.17 ± .07	.00	.03 ± .02	NS	NS	**
Pollack	.09 ± .04	.22 ± .08	.10 ±.04	.03 ± .02	.00	.02 ± .01	.00	.00	.13 ± .03	.13 ± .05	.00	.00	NS	†	NS
Saithe	.00	.10 ± .05	.02 ±.01	.03 ± .02	.00	.12 ± .05	.00	.00	.01 ± .01	.20 ± .06	.14 ± .05	.00	NS	**	**
Shore crab	.99 ± .19	1.4 ± .29	.20 ±.06	.23 ± .08	.72 ± .11	2.4 ± .65	.21 ± .06	.14 ± .05	1.79 ± .50	.84 ± .17	.86 ± .33	1.0 ± .18	**	**	NS

Kruskal-Wallis 1 way ANOVA, corrected by Dunn - Sidak sequential Bonferroni method to: * = $p < 0.05$; ** = $p < 0.01$; † = too small a sample for analysis

Table 2.4. Results of the comparison of catches of the prey species between seasons, at separate habitats. Given are the catches expressed as catch per trap night with standard errors, and the statistical significance of the ANOVA comparing the seasons.

Most of the species show the highest catches in the late summer and early autumn, (see graphs 2.16 – 2.28.), with rock and black gobies, eels, goldsinny and corkwing wrasse, cod and shore crabs doing so significantly. The exceptions to this are the saithe, rockling and 15 - spine stickleback, which peak significantly in the winter.

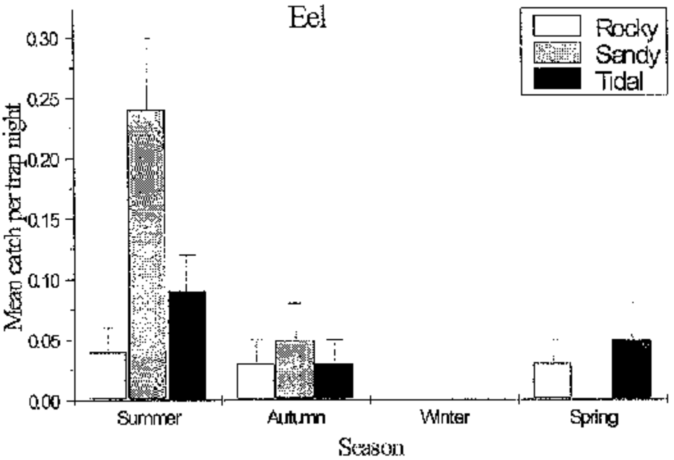


Figure 2.3. The mean catch of eels per trap, per night, with standard errors, in different seasons and different habitats

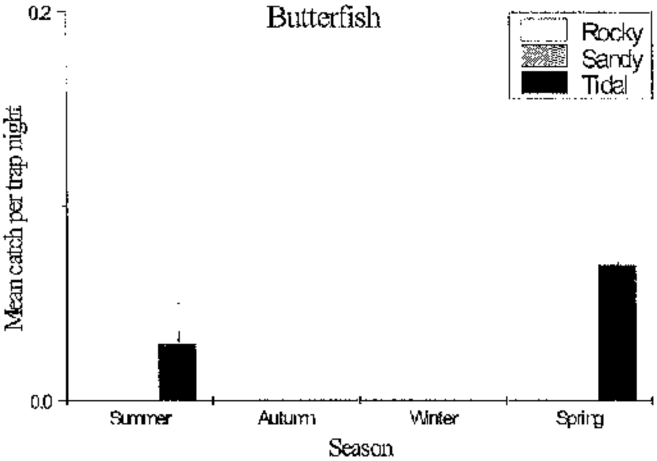


Figure 2.4. The mean catch of butterfish per trap, per night, with standard errors, in different seasons and different habitats.

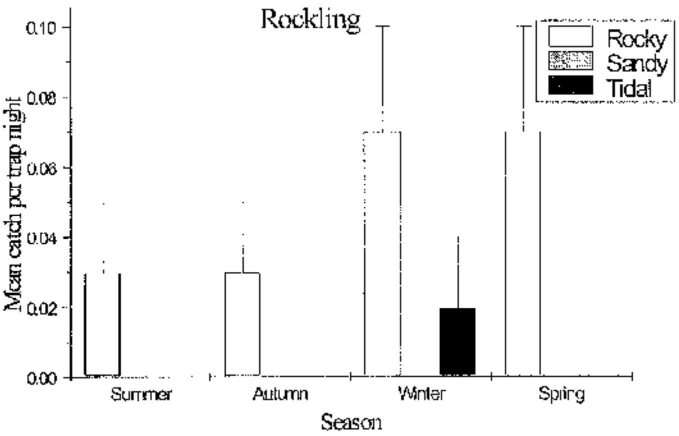


Figure 2.5. The mean catch of five-bearded rockling per trap, per night, with standard errors, in different seasons and different habitats

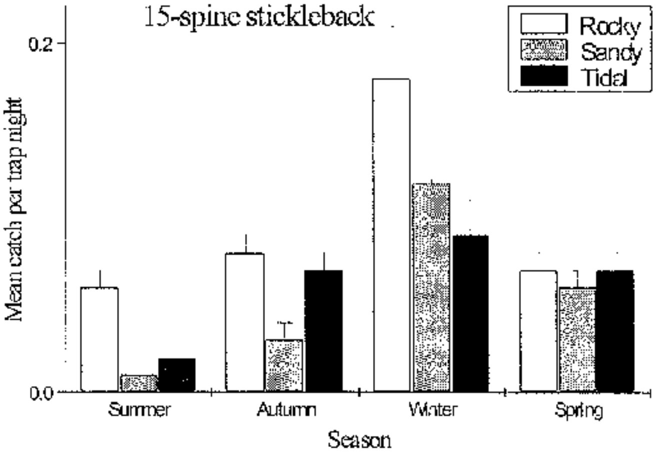


Figure 2.6. The mean catch of 15-spine sticklebacks per trap, per night, with standard errors, in different seasons and different habitats

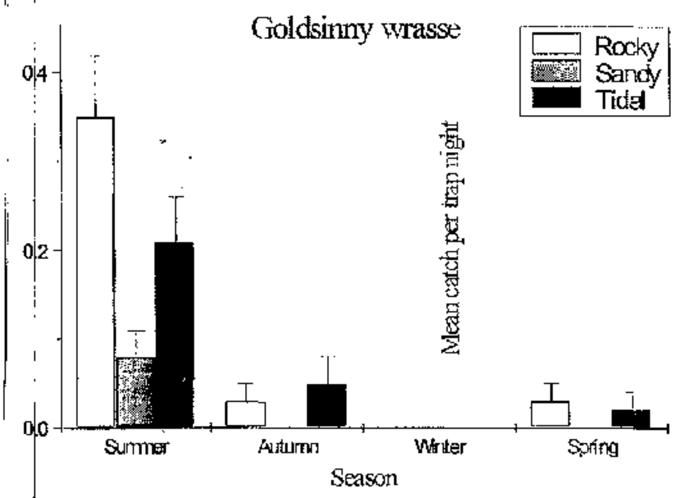


Figure 2.7. The mean catch of goldsinny wrasse per trap, per night, with standard errors, in different seasons and different habitats

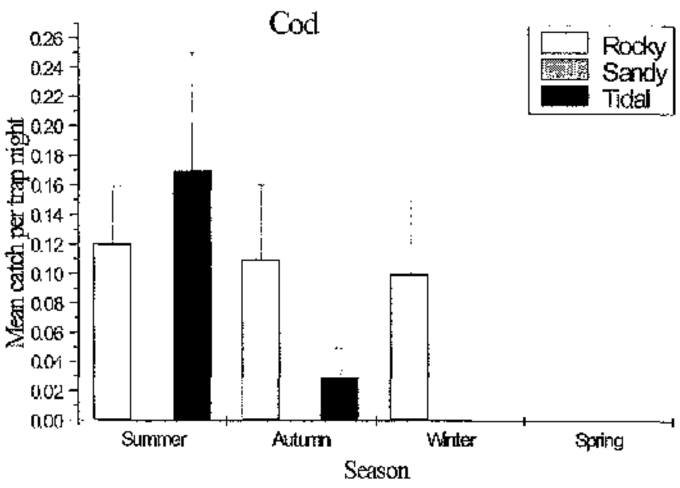


Figure 2.8. The mean catch of cod per trap, per night, with standard errors, in different seasons and different habitats

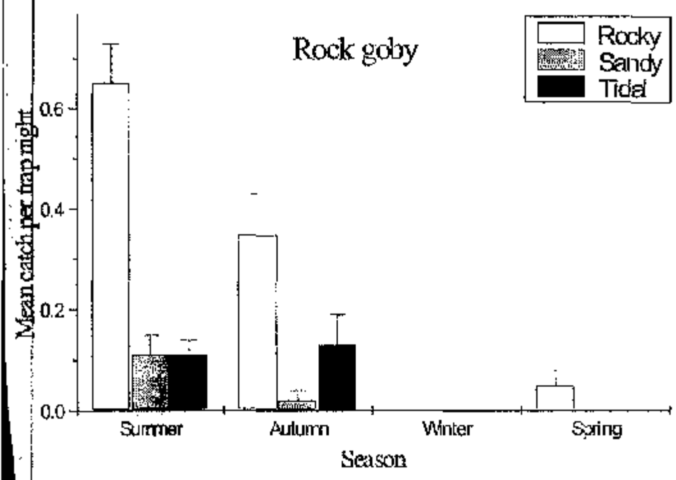


Figure 2.9. The mean catch of rock gobies per trap, per night, with standard errors, in different seasons and different habitats

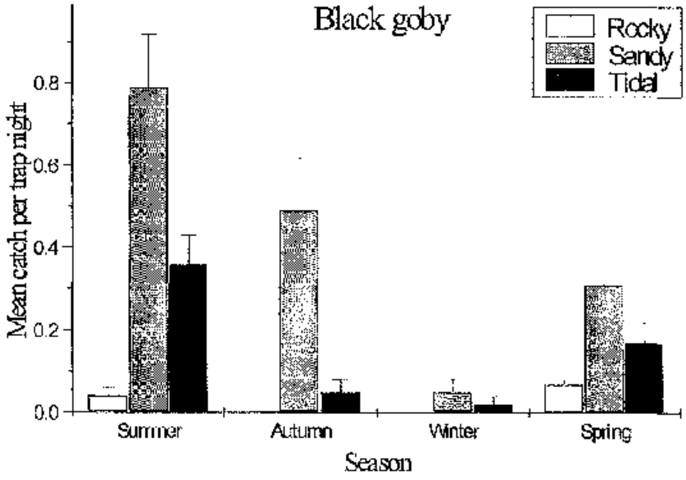
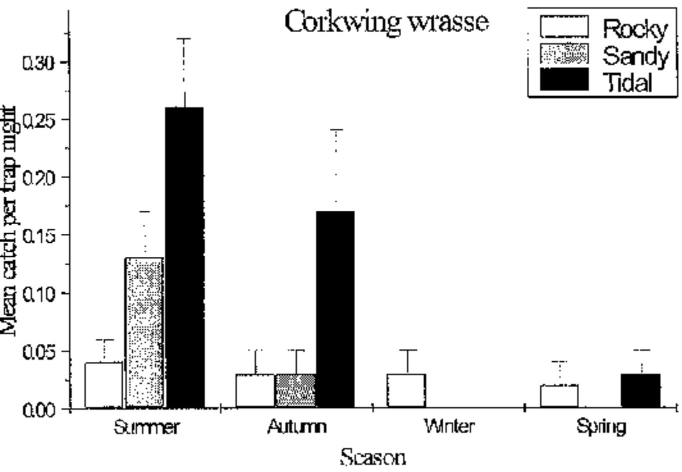


Figure 2.10. The mean catch of black gobies per trap, per night, with standard errors, in different seasons and different habitats



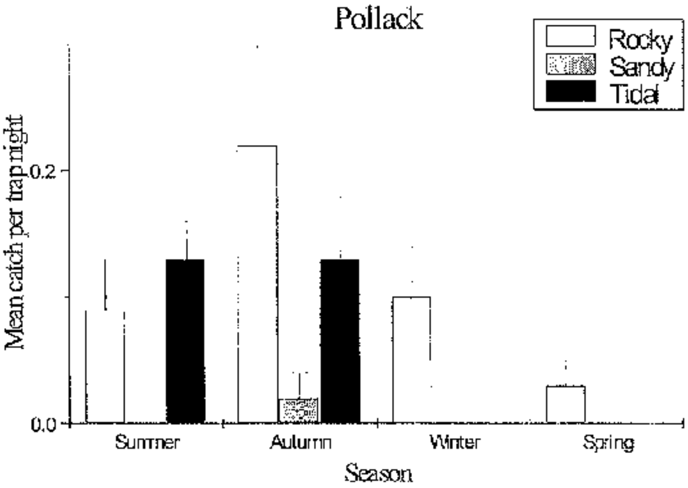
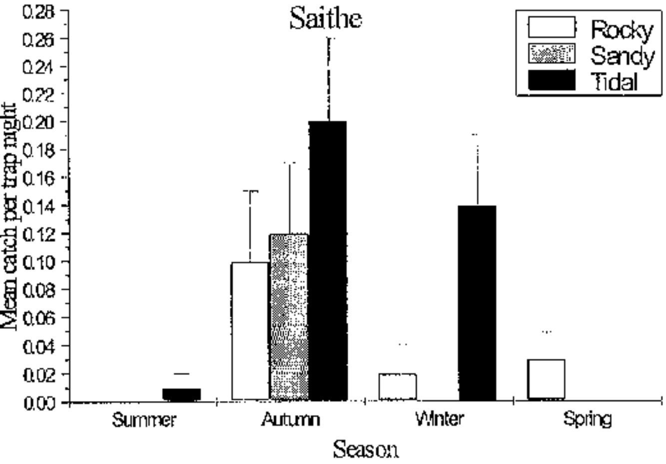


Figure 2.11. The mean catch of corkwing wrasse per trap, per night, with standard errors, in different seasons and different habitats

Figure 2.12. The mean catch of pollack per trap, per night, with standard errors, in different seasons and different habitats



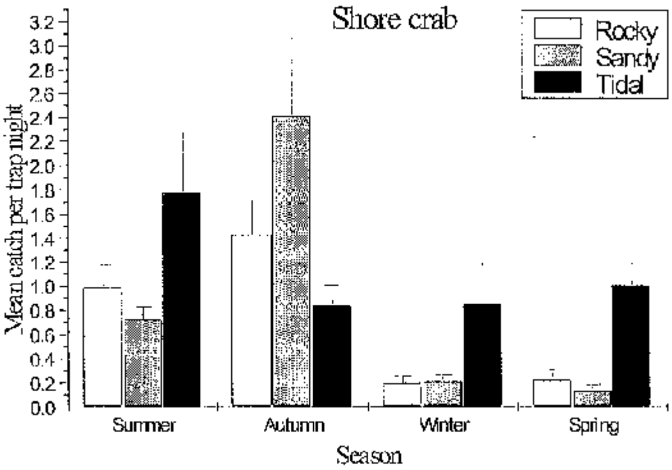


Figure 2.13. The mean catch of saithe per trap, per night, with standard errors, in different seasons and different habitats

Figure 2.14. The mean catch of shore crabs per trap, per night, with standard errors, in different seasons and different habitats

2.3.4. Biomass

The biomass of the catches at each site, and season were calculated. This was done both including crabs, and also excluding them, since a large proportion of their body mass is made up of the shell, the main bulk of which is not eaten by otters, as shown in table 2.5. This was then analysed via a 2 - way ANOVA to examine any differences between the biomass of catches between seasons and between habitats

		1				2				3				sig.	
	Su	Au	Wi	Sp	Su	Au	Wi	Sp	Su	Au	Wi	Sp	site	seas	int.
Mean biomass with crabs, per night	264 ± 54	322 ± 58	119 ± 18	110 ± 19	296 ± 51	592 ± 152	45 ± 17	66 ± 22	547± 127	254± 50	185 ± 56	252 ± 44	NS	***	*
Mean biomass without crabs, per night	80 ± 10	92 ± 17	83 ± 15	63 ± 12	82 ± 12	72 ± 14	7 ± 2	20 ± 8	116± 20	100± 23	36 ± 9	36 ± 8	*	***	NS

2 way ANOVA, * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 2.5. Results of the statistical comparisons of mean biomass of prey catches between seasons and habitats. Given are the mean biomasses per trap night, with standard errors shown, and the statistical significance of the 2-way ANOVA for both factors and the interactive term ("int.").

The results show that when the crabs are included, figure 2.15, there are no significant differences between the biomass of the catches at different habitats, but there is a significant difference between the seasons. There is also a significant interaction between habitat and season. However when the crabs are not included in biomass, figure 2.16, there is still a highly significant seasonal effect, and there are significant differences between habitats. There is no longer a significant interaction between habitat and season when crabs are removed from the calculation.

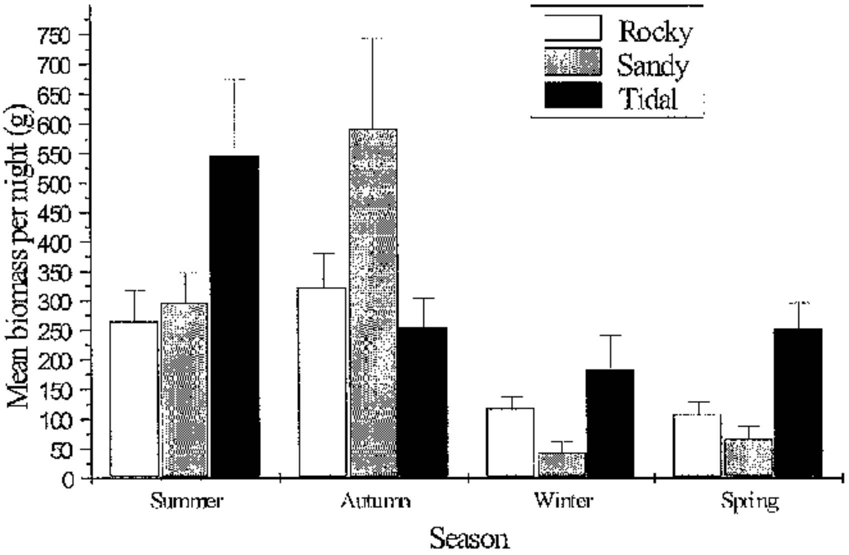


Figure 2.15. The mean biomass in grams, with standard errors, caught per trap per night, in different seasons and in different habitat, with crustaceans included.

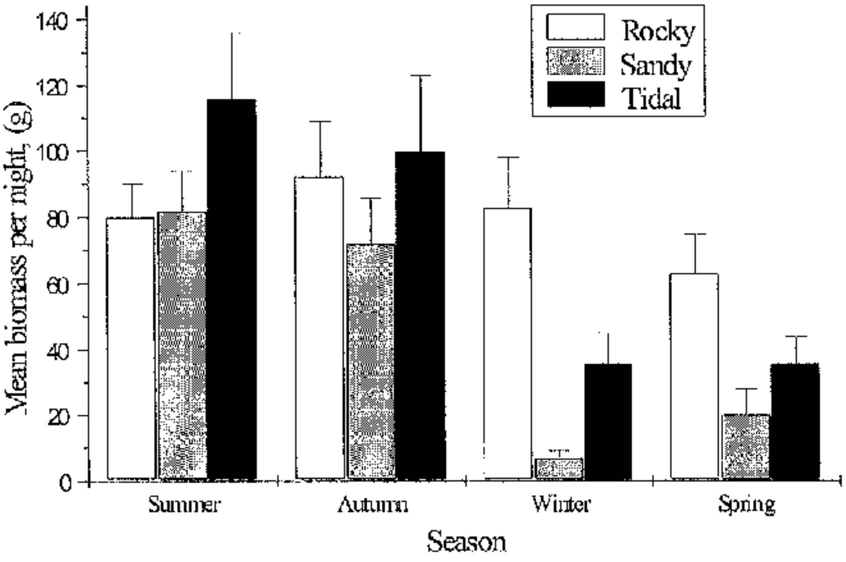


Figure 2.16. The mean biomass in grams, with standard errors, caught per trap per night, in different seasons and in different habitats, with crustaceans excluded.

2.3.4. Shannon - Weiner Function

Finally a Shannon Weiner function was calculated for each study site, using the data number of species, and number of each species collected. This function is a measure of the species diversity of a habitat, and is represented by a calculated number between 0 and 1. The higher the species diversity, the closer the calculated function is to one. The results of this are shown in table 2.6. All of the sites have a similar value, except site 3.2., within the tidal rapids.:

Site	Shannon – Weiner function
1.1. (rocky)	0.44
1.2. (rocky)	0.56
2.1. (sandy)	0.62
2.2. (sandy)	0.52
3.1. (tidal)	0.83
3.2. (tidal)	0.44

Table 2.6. The results of a Shannon - Weiner function of species diversity of different trap sites. The higher the value, the greater the species diversity

2.4. DISCUSSION

Throughout this experiment there has been one underlying assumption, that the catch in these traps is a reasonable representation of local prey species' availability to foraging otters. There are a number of considerations to bear in mind here,

1. Since the traps rely on the fish behaviour, it is not possible to infer inter-specific information from the data, since different fish species will respond differently to the traps. The traps may therefore give a biased view of the suite of prey species available to the otter since it is strongly influenced by the species catchability rather their availability to the otter.

2. When comparing catches from different times of year, it must be borne in mind that, variations in water temperature will have an effect on the prey's activity levels and consequently may affect their catchability. To examine this possibility we applied Kendal's coefficient of concordance to the data, in the form of species abundance for each season. We assumed that if there were a temperature effect that it would apply more or less equally to all species and therefore cause them to fluctuate together. The result we obtained showed that the species did not fluctuate together at all, thereby suggesting that factors other than temperature have influenced prey abundance. Some caution is necessary, however. This result shows that there are stronger effects occurring, but it remains likely that there will be some temperature-related effect.

Bearing these limitations of the methodology in mind, it still is possible to infer useful information about fish populations and behaviour from trapping, and to examine such information in the context of otter foraging behaviour.

The range of fish present in the study area, as shown in table 1.1, can be compared with those at other study sites, Shetland, in Scotland, (Kruuk *et al.* 1988), Mull, in Scotland, (Watt 1995), Norway, (Heggberget 1993) and Portugal, (Beja 1995). In comparison with these sites, the most noticeable trend in Loch Sween is the abundance of Black and Rock gobies, *Gobius niger* and *G. paganellus,* and the wrasse, Goldsinny, Corkwing and Rockcook. These are very different to the amounts at the other Scottish sites, Shetland and Mull. These species are not listed as being found in Shetland so this is expected. There are far fewer butterfish than at either Shetland or Mull, though they are an important food source at Loch Sween, (see chapter 5). The success with which butterfish are trapped seems to be variable. Only Watt (1995) caught large numbers in similar traps, and while they were caught in Shetland and Norway, actual numbers were low. A similar trapping regime in Orkney, as part of a study of the prey of the black guillemot, *Cepphus grylle,* also had little success in catching butterfish (Sawyer, *pers. comm.*). Gibson *et al,* (1993), compared catches from two methods of fish sampling, trawling and seine nets. Seine nets are similar in method of capture to funnel traps. The seine nets were almost totally ineffective at catching butterfish, which were found to be present in large numbers in trawl samples. Therefore, in terms of this species only, stationary trapping is not useful, and the results of previous similar studies must be viewed with a degree of caution.

Differences between Shetland and Loch Sween would be expected to some extent, but the fairly large differences between Mull and Loch Sween are unexpected. These areas are close to each other and are broadly similar habitats. It is unclear whether this is a measure of a difference in the habitats or of the inaccuracy of the trapping. The fact that both trappings were carried out over long periods suggests the former explanation is correct.

2.4.1. Differences Between Habitats

2.4.1.1. Small changes in habitat:

The lack of difference in local habitats i.e. between sites 1 and 2, 3 and 4, and 5 and 6, is not surprising. These sites are close together and only have small differences in their habitat composition. This similarity in the species composition of adjacent sites suggests a degree of reliability in the trapping method, since such similarities would be predicted from habitat descriptions. However there were differences in the species diversity index we calculated for these sites. Unfortunately there is no rigorous statistical method to compare these figures so we cannot accurately estimate the extent of these differences

2.4.1.2. Differences between the three habitats

(i) Species with a significant difference

Rock Goby (figure 2.9.): These fish are typical of rocky sub and inter-tidal habitats, Wheeler, (1969), described them as wholly dependent on rocky shores, and they were found in the largest numbers at habitat 1, which conforms to this description. Few were caught at habitat 2, as would be expected from this soft bottomed, sheltered site, and catches in habitat 3 lay somewhere between the other two.

Black Goby (figure 2.10.): Catches of this species were almost a negative image of those of rock gobies. It is found in inshore, sandy or muddy bottomed conditions, and is frequently associated with *Zostera* beds, (Wheeler, 1969), hence its abundance at habitat 2. Virtually none were found at habitat 1 and a fairly large number were found at habitat 3, where there are both soft and hard substrates.

Corkwing wrasse (figure 2.11.): This species is generally associated with algal beds on rocky shores, though it can be found in areas of softer substrate provided there is dense vegetation cover, (Sayer and Treasurer, 1996). Habitats 1 and 2 show little differences between them, and the main difference is the larger catch at habitat 3. This would suggest that it is not the substrate, but the density of vegetation, or the actual surface area of vegetation and/or the substrate, that is the controlling factor.

Pollack (figure 2.12.): While often an inshore mid-water species, the pollack can also be bottom dwelling, especially in rocky areas, (Wheeler, 1969), where they use kelp forests as cover, (Sarno *et al*, 1994). These are commonest in this study in those areas where there are extensive kelp forests, that is habitats 1 and 3, with very few found in habitat 2. While there is some vegetation cover here, pollack in the wild have been observed showing a preference for dense algal habitat over sparse habitat, (Sarno *et al*, 1994), and all vegetation cover in habitat 2 is thin.

Saithe (figure 2.13): In contrast to pollack, to which they are closely related, saithe forage more extensively, and cover wider areas, though they return to algal beds at night, (Sarno *et al*, 1994). They are most common in this study at habitat 3, where there is a high surface area of algal for foraging though it is likely that saithe are caught overnight when they are going into cover. The fast currents in habitat 3, which may discourage more territorial species, would not be a problem to the wider ranging saithe.

(ii) species with no significant differences.

Eel (figure 2.3.): While there is no significant difference between the sites, habitat 2 has a distinct peak in eel numbers in the summer. These eels are concentrated in the eel grass beds present at this area. It is not clear whether the eels use the eel grass beds for shelter or as a foraging site. Eels will however gather in brackish water prior to their oceanic migration in the autumn, (Wheeler, 1969)

Butterfish (figure 2.4.): There was a very small sample size for butterfish, (n = 8), and it is likely that this is what caused the lack of significance since all the catches were at habitat 3. Otters were frequently seen taking butterfish from habitat 1, (see chapter 5), however none were caught at this area. This may be a function of the difficulties in trapping butterfish, or it may be that there is indeed a higher concentration of this species at habitat 3, attracted by the greater surface area of algal cover.

5-bearded rockling (figure 2.5.): Again the small sample size, (n = 14), makes it difficult to obtain any significant result, but there are very visible trends. The large majority of the catch was at habitat 1, and the rest at habitat 3. This is as expected from a species that prefers rocky shores, (Wheeler, 1969), but that is more dependant on the substrate for cover than algal beds, (*Ibid.*).

15-spine stickleback (figure 2.6.): There was a large sample size for this species so it is likely that this non–significant result is not artifactual, and due to the wide ranging habits of this species. It is known to be tolerant of arrange of salinities, and is found in most marine habitats with a degree of algal cover, (Wheeler, 1969). It is known to be associated with *Zostera* beds as well as rocky areas, (*Ibid.*).

Goldsinny wrasse (figure 2.7.): There was no significant result for this species, and there was a large sample size. There does however seem to be a marked preference for rocky areas, habitat 1 and 3, as would be expected from the literature, (Sayer and Treasurer, 1996). In contrast to this there are fairly high numbers also caught in the soft bottomed habitat 2, suggesting that the species' habitat preference is not as defined as previously thought, both Wheeler, (1969), and Sayer and Treasurer, (1996), claiming that they are rarely found above sandy substrates.

Cod (figure 2.8.): There is a pattern of preference for the rockier, more algal covered shores in cod, but they do occur at all habitats. They are known to utilise a range of habitats up to the shore line, and are known to move into shallow water at night to forage, (Burrows *et al.*, 1994), resting in deeper water during the day, so are inaccessible to the diurnally foraging otter. It is during the night that they will be therefore caught in the traps. This pattern of depth use by cod, at different times of day, changes in the winter, in that they will spend greater amounts of time in shallow water in the winter.

Shore crab (figure 2.15.): These crustaceans occur over a wide range of depth and substrates, (Ingle 1980), and can tolerate extremes of salinity, (Dries and Adelung 1982). This will therefore account for the wide distribution of the shore crab in this study, and similar wide patterns of distribution have been shown to occur elsewhere, (e.g. Mathieson and Berry (1997), caught large numbers of shore crabs throughout the Forth estuary).

2.4.2. Differences between seasons

2.4.2.1. Fish that show no habitat variation

Eel (figure 2.3): The Eel showed a highly significant variation in catch between the seasons, with a distinct peak in the summer and none at all caught in the winter. This may be related to a pre - migration gathering, or it may be related to an increase in catchability with higher water temperatures. Catchability in stationary traps and water temperature have been positively correlated in other *Anguilla* species, (Jellyman, 1991). This summer peak is particularly associated with the *Zostera* beds at habitat 2.

15-spine stickleback (figure 2.6): This species, in common with many inshore species, (Kruuk *et al*, 1988), shows a peak in numbers in the autumn. This will be partly associated with high water temperatures at this time, but the trend is a highly significant one and the young of the species are known to congregate in weed in the autumn, (Wheeler, 1969).

Goldsinny wrasse (figure 2.7): There is a clear peak in catches of the species in the summer, and this may be related to the importance of bivalve molluscs, particularly mussels, *Mytilus edulus*, during this period, (Sayer *et al*, 1996). During the colder months they retreat into crevices, (Sayer *et al*, 1994), and this is reflected in the low catches in the winter.

Cod (figure 2.8.): Cod also showed a summer peak, and this catch was predominantly yearlings, (*pers. obs.*) which have been described as congregating in shallow waters at this time, (Burrows *et al*, 1994.). Those caught in the winter were generally large adult and often were gravid individuals, (*pers. obs.*). These would have been caught at night as they come into algal beds to feed (Burrows *et al*, 1994.).

Butterfish (figure 2.4.): There was no significant variation in the seasonal catches in this species, but as before this will have been due to the small sample size, (n = 8). All the animals were caught in spring or summer. This trend has been noticed on other studies,(Kruuk *et al.* 1988, and Watt, 1995) and was attributed to an offshore migration in colder temperatures. However, Sayer *et al*, (1994), demonstrated that the fish had in fact remained inshore and retreated into crevices where they became quiescent. Many will still therefore be available to otters.

5-bearded rockling (figure 2.5.): Again the lack of significance may be an artefact of a low sample size. There is a peak in the winter, in the catch of this species and the species is spawning in algal beds at this time, (Wheeler, 1969).

2.4.2.2. Fish with habitat variation

Rock goby (figure 2.9.): This only shows a significant variation in habitat 1, and here we see a clear summer peak, possibly related to spawning, which occurs at this time, (Wheeler, 1969).

Black goby (figure 2.10.): These also have a summer peak, and are also summer spawners. Significant results are only seen at habitats 2 and 3, habitat 1 had a very small sample size, (n = 4).

Corkwing wrasse (figure 2.11.): Only significant at habitat 3, where a summer peak was shown. Corkwing are known to retreat into crevices in the winter and so this result may not be an indication of real population levels, but of the active population.

Pollack (figure 2.12.): While there is no significant seasonal variation, there is a slight trend for there to be a peak in autumn. They spawn in winter in deep water, (Wheeler, 1969), and this will account for this pattern.

Saithe (figure 2.13.): These show a significant summer peak in habitats 2 and 3, and this is when young fish first come inshore from the winter deep- water spawning, (Wheeler, 1969).

Shore crab (2.14.): Traditionally, shore crabs were thought to migrate offshore in the winter, (e.g. Dries and Abelung, 1982), but have been found by divers, (van dar Meeren, 1992), retreating into crevices and burying in sand during this period. This behaviour will account for the reduced trap success during the winter. It is not clear why the catches at habitat 3 do not show a significant difference.

2.4.3. Inter habitat variations in biomass

Biomass of the catch was calculated and using a two-way ANOVA, variation in site and season was examined. This analysis was carried out twice, once including crabs and once without. In the former case habitat was not a significant variable while the effect of season was. Seasonal fish abundance showed a peak occurring in summer and autumn, as would be expected from other studies, (e.g. Kruuk 1988). This suggests that season will have a strong effect on the foraging of the otter, and that there may be problems with food supply in the winter and spring. There is also a significant interaction between site and season, when crab mass in included in biomass calculations. At habitat 1 the peak in biomass occurs in the autumn and the lowest point is in the spring. By contrast the peak is in the summer in habitats 2 and 3, and the trough is in the winter.

When the crabs were excluded from the calculations of biomass there is still a highly significant seasonal effect, and there are significant differences between habitats. This suggests that crabs do not have habitat preferences and the other prey species do, and it is the large mass of the crabs that dilutes this effect when they are included in biomass calculations. There is no longer a significant interaction between habitat and season when crabs are removed from the calculation suggesting that it is crabs that drive this interaction rather than the fish species.

2.4.4. Species diversity

From the Shannon - Weiner index of species diversity calculated we see that all but one trap site have broadly equal values. Site 3.1., however, has a higher value. This site has a well-documented richness, (SNH Reports etc.), and the richness in vertebrates and crustaceans described here is mirrored in a exuberance of algae, porifera, cniderians and echinoderms. Observations have shown the rapids to be an important foraging site to the local otter community.

2.4.5. Relevance to the foraging of otters.

Comparison of the biomass between habitats showed that there were no significant differences between the sites in terms of available biomass. The sites were sufficiently similar for us to assume that the traps would work equally well, with the same limitations, at every location they were set. We can therefore conclude that the similarities in biomass and differences in species composition between sites were real.

While the catch biomass, with crabs excluded, varies between these habitats, any predator would make decisions on its patterns of usage of these habitats not only on available biomass, but also on the basis of ease of obtaining the prey. This will be influenced by a number of factors, such as prey behaviour, nutritional value and loading time, as well as habitat type, and these will be discussed in subsequent chapters.

Species composition also varies between habitats. There is a clear increase in abundance in habitats 1 and 2 among the majority of fish captured. Goldsinny wrasse, 5-bearded rockling, rock gobies and cod, are all found largely at habitat 1, while eels and black gobies dominate habitat 2. The habitat 1 species all prefer rocky coasts rich in algae, while habitat 2 species prefer a soft substrate. Habitat 3 lies in the middle both geographically and in terms of species make up, with species from both the other sites turning up in large numbers. In particular this seems to be a shared habitat for the rock and black gobies, which almost exclusively inhabit their preferred habitats of 1 and 2 respectively. There are also some species that prefer habitat 3, notably corkwing wrasse, saithe and butterfish. Habitat 3 has a variety of substrates, and also a large and varied topography, and this is shown in the variety of species found there and therefore in the diversity index of the site. This would therefore be expected to be an area of intense otter foraging.

The seasonal effect on the fish catches and the overall biomass are marked with a notable reduction in spring and summer. The possibility of this being due to a decrease in activity in colder water temperatures has been already mentioned. The seasonal fluctuations on the fish are not all the same. Species that peak in the summer are the gobies, the wrasse, eel and cod, whilst those peaking in the autumn are pollack saithe and 15-spine stickleback. In the winter the largest numbers of 5-bearded rockling are caught, and there is the highest numbers of butterfish in the spring. It is also not entirely clear whether lower temperature would have a negative effect or not on the catches, since a more active fish may be more likely to escape than a sluggish one.

However, in the case of some species that show a marked decline in the winter, particularly the wrasses, butterfish and gobies, the basic assumption of this work, that the catch in these traps reflects the availability to otters may not be met. This is due to the fact that these species do not migrate offshore in the colder months as was previously thought, but move into crevices and enter a state of quiescence, (Sayer *et al*, 1994). The effect of this on an otter foraging is not clear, and whether it has a negative or positive effect on the otters foraging is likely to depend on the substrate within which the crevices lie.

These interactions between site and season described may have profound effects on the foraging of otters. Where it is possible for an otter to choose between sites, this would be expected to follow a seasonal pattern, all other variables being equal, where the predator utilises most the areas with the greatest profitability, and that these choices would change with the seasonal variations. In the chapter 5 we will examine this prediction.

CHAPTER 3

FACTS FROM FAECES:

AN ASSESSEMENT OF THE ACCURACY OF SPRAINT ANALYSIS FOR QUANTIFYING THE DIET OF MARINE FEEDING OTTERS

CHAPTER 3

3.1. INTRODUCTION

Accurate assessment of the diet of any animal can be difficult, particularly when the animal cannot be clearly observed throughout the day. With carnivores, a frequently applied method is the analysis of the undigested prey remains found in the faeces (Ewer, 1973). This is possible due to the comparatively short length of the carnivore intestine. Many hard parts of the food remain partially, or totally, undigested, and can be found, and subsequently identified, in the faeces. Frequency of occurrence, that is the either the percentage of faeces that contain a particular prey item, or the number of occurrences of a particular item as a percentage of all recorded items, is the most commonly applied method of quantifying the results of such dietary analyses.

This method has been widely used to determine the diet of the Eurasian otter, *Lutra lutra* (see review in Mason and Macdonald 1986, and Kruuk 1995), and since Wise (1980) identification of prey species, of which fish make up the largest majority, (Kruuk, 1995) has been based around the use of vertebrae recovered from the spraints, (faeces), with several keys in existence (Webb 1980, Watson 1978, Conroy *et al*, 1992). The numbers of prey species identified in this way, have been quantified by frequency of occurrence, or variations upon it, (for example, Jenkins *et al* (1979) estimated the bulk of each prey type in the spraints), and while its accuracy has been debated it has rarely been tested. Elridge (1968) first stated that small prey items are over-represented and large prey items under-represented by frequency of occurrence, and carried out feeding trials to look for any inaccuracies. In his results he claimed that percentage occurrence "gave a reasonably true picture of the relative importance of the different food categories" (*Ibid.*), but presented no statistical evidence to support this. Rowe-Rowe (1977) stated that he had carried out trails on cape clawless otters, *Aonyx capensis*, showing that relative frequency of occurrence gave a true picture of the animals' diet. However no data in support of this were given. More detailed trials with the Eurasian otter were carried out with fresh water prey by Jacobsen and Hansen (1996) and these studies demonstrated a correlation between frequency of occurrence and the biomass of the actual diet. This correlation was, however, based on ranked data, and so suggested that while the rank order of prey biomass is correlated with the results of frequency of occurrence analysis, there was no evidence of a relationship between absolute values.

Carss and Parkinson (1996) have carried out the most detailed trials, again with fresh water prey species. These trials were the first to test the relationship between actual proportions of particular prey in the diet, both in terms of numbers and biomass, and the proportions obtained from spraint analysis. Their main conclusions were that:

1. Frequency of occurrence methods do not correctly reflect the true proportions of the components of the otters diet.
2. Rank orders of prey numbers and biomass can be accurately determined by spraint analysis.

This means effectively that any quantification of the amount of a prey item consumed is likely to be inaccurate, by potentially large margins. These trials were only for fresh water prey, and there have been no trials to determine the accuracy of spraint analysis where the otters are feeding in the sea. Carss and Parkinson (1996) suggested that the best way to overcome these inaccuracies would be by the use of "key bones" from the prey skeleton to calculate minimum number estimates of prey in the diet with appropriate regression equations applied to them in order to calculate the actual size of the prey.

Key bones are bones, which, unlike most vertebrae, exist in the prey as only a single bone, for example a pharangeal bone, or in pairs, for example the premaxillae. Such bones eliminate the errors created by frequency of occurrence methods by giving an accurate minimum number of prey eaten. Fish otoliths have been frequently used as key bones in diet estimation of birds and mammals, (Pierce *et al.*, 1991). Dellinger and Trillmich (1988) carried out feeding trials with Californian sea lions, *Zalophus californianus*, and South American fur seals, *Arctocephalus australis*, and demonstrated a highly significant correlation between diet composition and the proportion of otoliths recovered from scats. Otoliths, however, can break down in the carnivore gut faster than other bones, (Pierce *et al*, 1991), and are rarely found whole in otter spraints, (Wise, 1980, *pers. obs.*).

Examination of other key bones as an accurate method of determining an animals diet was used by Feltham and Marquis (1989) who developed a method of distinguishing the atlas vertebrae of brown trout, *Salmo trutta*, and Atlantic salmon, *S. salar*, and estimating the prey size from this. Because there is only a single atlas in each fish, the estimation of prey numbers is far more accurate, as demonstrated by Feltham (1990), analysing the stomach contents of red-breasted mergansers.

The use of regression equations, obtained by dissection of undigested prey species to calculate the size of prey items from bones found in faeces or stomachs has been applied to a number of animal species. Perhaps the commonest use is of fish otoliths to assess piscivorous bird and seal diets, (Pierce *et al*, 1991). The use of the caudal vertebrae of fish, as found in otter spraints, to determine the size of otter prey items has been applied since Wise, (1980). There are, however, problems with this methodology:

1. The size and shape of the bone are likely to change as they pass through the otters digestion system. This would make regressions obtained direct from dissection of fresh and undigested prey species inaccurate.
2. Regressions based on vertebrae give a mean value for all vertebrae. However within any fish, there is a large difference in vertebrae length from the anterior and posterior of the spine. This variation implies that no absolute relationship between bone size and prey size can be determined, and any such determined will be consistently inaccurate, (Carss and Elston, 1996).
3. For some very large prey such as lumpsuckers and dogfish, the otter will only eat part of the fish and so there may be no recoverable hard parts in the faeces.

The first problem can be eliminated by the use of post-digestive regression equations obtained from feeding trials, the second by the use of key bones to derive these equations rather than vertebrae. The third problem may only be solved by direct observation of the otter feeding, see chapter 4.

Such procedures, with the use of the salmonid atlas vertebrae, to determine the relative number and size of salmon and trout in the otter diet, were tested using feeding trials, by Carss and Elston (1996) and their results confirmed that this methodology eliminated the errors described above. There have been no such trials to determine suitable bones from marine prey species

In this study we set out to determine:

1. How accurate conventional methods of spraint analysis are for marine prey
2. Which key bones would be most suitable for use in spraint analysis of marine prey
3. Regressions equations, post digestion, for these bones to allow accurate estimation of prey size
4. Corrections factors for these key bones to calculate relative numbers of prey species

The study was carried out in association with the David Carss of the Institute of Terrestrial Ecology, Banchory, (see internal report for Scottish Natural Heritage, Carss and Nelson, 1996).

3.2. METHODS

3.2.1. Feeding trials

Four otters, two males and two females, were used to conduct nine separate feeding trials. They were kept in two 15 x 6 m enclosures, at the Institute of Terrestrial Ecology, Banchory, each with a 5 x 2 x 2 m swimming pool and a straw lined sleeping enclosure. One female otter was kept separately from the other otters because they were prone to attacking her. All spraints were removed from the enclosures before the trials began. A total of nine trials were carried out.

The otters were fed a trial meal at 10.00 h, consisting of marine fish, see table 2.1., and shore crabs. Any uneaten food was removed from the enclosures and re-weighed to exclude it from analysis. The guts of the only piscivorous fish in the trial were removed to avoid contamination with other fish that may have been in their stomachs. Spraint production and composition is affected by the activity of the otters after a meal (Carss *et al*, 1998). In order to most closely mimic the situation in the wild otter activity was increased by playing with the animals for 20 minutes in every hour, for six hours after the meal, with the otters diving, swimming and running during this period.

During the periods of play the enclosures were searched thoroughly and all spraints collected. If the spraints were together in a pile, their shape was integral enough to allow it to be gently separated from the others. There were two further searches the following day at 0930 and 1530. The spraints were soaked in a saturated solution of biological washing powder for approximately 48 hours at room temperature, and then rinsed, consecutively, through two sieves of 0.50mm and 0.25mm mesh. They were then dried at room temperature for 24 -48 hours before examination.

3.2.2. Assessment of the accuracy of spraint analysis

Spraints from trials 1 - 5, table 3.1., were analysed by both relative frequency, (the number of occurrences of a prey item as a percentage of all recorded items), and percentage frequency, (the percentage of spraints containing a particular prey item), on the basis of contents of undigested fish bones and crustacean chitin, and such items were identified by comparison with reference material. The results obtained were then compared with both the number of different prey items and the biomass of the different prey items, from the test meal.

Trial	**Species fed**	**Total mass (g)**
1	Butterfish, Bullrout, Corkwing, Stickleback, Shore crab	1134
2	Butterfish, Bullrout, Stickleback	604
3	Butterfish, Corkwing, Goby, Eelpout	183
4	Butterfish, Corkwing, Goby, Eelpout	122
5	Butterfish, Corkwing, Goby, Eelpout	93

Table 3.1. Total food fed to all four otters as part of the trials carried out to test the accuracy of frequency of occurrence methods of quantifying diet.

*3.2.3. **Key bones***

3.2.3.1. Assessing best key bone

Spraints from trials 1 - 5 were further examined and specific key bones, dentaries, premaxillae and articulars, were counted from the analysed spraints. Those that gave the closest indication of actual species numbers consumed were determined. Where the bones are paired in the prey skeleton, left and right bones were compared via fish size to bone size regressions obtained from dissected fish, to ensure that either could be used for size assessment. This was carried out for butterfish, 5-bearded rockling, 15-spine stickleback, and long-spined sea-scorpion.

3.2.3.2. Fish to bone size regressions

Further trials (see table 3.2.) were carried out, as above, with meals consisting of fewer numbers of each prey item to eliminate any overlap in possible size of recovered bones. The recovery rate of the key bones, from these tests were examined to determine whether there was a size bias in the proportion recovered, by separating each into size classes, and comparing the proportions recovered from each. They were further tested via logistic regression analysis, after Carss *et al*, (1998), where, counter intuitively, recovery rate was shown to decline with increasing fish size in a logistic curve.

These post-digestive recovered bones were measured and regressions were constructed of bone size to original fish size.

Species	**Trials used**	**Total no. of prey fed**
Butterfish	3,6,9	9
Bullrout	1,6,7	8
Wrasse	6,8	7

Table 3.2. The prey species fed to the four otters during feeding trials to determine equations for bone to fish size regressions.

3.2.3.3. Correction factors

For each species, the recovery rates of key bones from different trials were compared to test for a consistency of proportional recovery. Where this was found to be so, a correction factor with confidence limits was calculated to allow an accurate assessment of prey numbers to be calculated.

3.3. RESULTS

3.3.1. Accuracy of spraint analysis

Five trials were conducted using three of the otters, see table 3.1., to determine the overall accuracy of applying frequency of occurrence methods to spraint analysis. 141 prey items were consumed, weighing a total of 2170 g. Eighty-eight spraints were collected with identifiable hard parts present.

The data from all five trials were combined to test the results of quantification via frequency of occurrence against the actual diet. The percentage of each prey item fed to the otters was compared by the estimate obtained from the two different methods of frequency analysis, via a Spearman's rank correlation coefficient. Correlation analysis was used since there may have been a consistent error throughout analysis, for example analysis may have consistently underestimated the true proportions by 50%. For both methods of frequency analysis, there was a strong positive correlation between the values obtained for each of the 7 prey species and their true numerical proportions in the diet, and both gave exactly the same correlation coefficient, ($r = 0.73$, $p < 0.05$). Neither method gave a statistically significant correlation with diet as represented by biomass.

Prey Species	**Prey consumed**		**Spraint analysis**	
	% nos.	% mass	%freq.	Rel. freq.
Butterfish	36.9	17.4	64	24
Bullrout	9.2	6.5	53	20
Corkwing wrasse	7.8	30.7	32	12
15 - spine stickleback	35.5	29.3	50	19
Rock goby	3.5	2.6	20	8
Eelpout	5.0	3.4	16	6
Shore crab	2.1	10.2	28	11

Table 3.3. Comparison of the results of spraint analysis of spraints obtained from feeding trials with the actual diet

3.3.2. Key bones

The percentage of key bones recovered from each trial for each species is shown in table 3.4., (for paired bones this is half the total found). It was decided that the using the same bone for each species would ease spraint analysis. While the pharangeal bones and preoperculum had the highest mean recovery rates, they are only present in wrasse. The next highest rate of recovery was the premaxillae jawbone and as this bone facilitates relatively easy identification, it was chosen for further analysis.

Bone type	no. trials	no. species	mean % recovery
Dentary	5	6	41.2
Premaxilla	5	6	46.3
Articular	5	1	40.4

Table 3.4. Post - digestive recovery rates of key bones.

3.3.3. Prey size estimation

Ten specimens of four species of fish, butterfish, rockling, 15 - spine stickleback, and sea scorpion, were dissected and the premaxillae removed. The left and right premaxillae were compared via analysis of covariance and there was no significant difference in elevation or constants for any species. It therefore was decided that the same equations could be used to calculate left prey size from either left or right maxillae.

There was only sufficient bones recovered from three species of fish for regressions to be constructed, the species were butterfish, bullrout and corkwing wrasse. While a number of premaxillae were recovered, not all could be definitely attributed to a source fish, and therefore its length known. Regression equations were constructed, for these species, see table 3.5.

Species	**equation**	**r^2**	**S.E.**
Butterfish	$y = 44.65x - 8.11$	0.92	7.78
Bullrout	$y = 6.61x + 29.46$	0.89	1.31
Corkwing wrasse	$y = 6.61x + 54.50$	0.98	0.34

Table 3.5. Relationship between length of recovered premaxillae and fish length

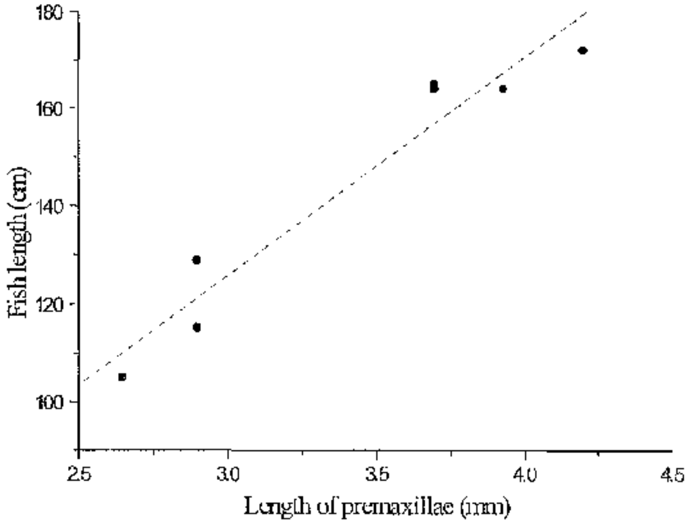


Figure 3.2. The relationship between the size of premaxillae recovered from otter spraints and the known length of the butterfish fed to the otter.

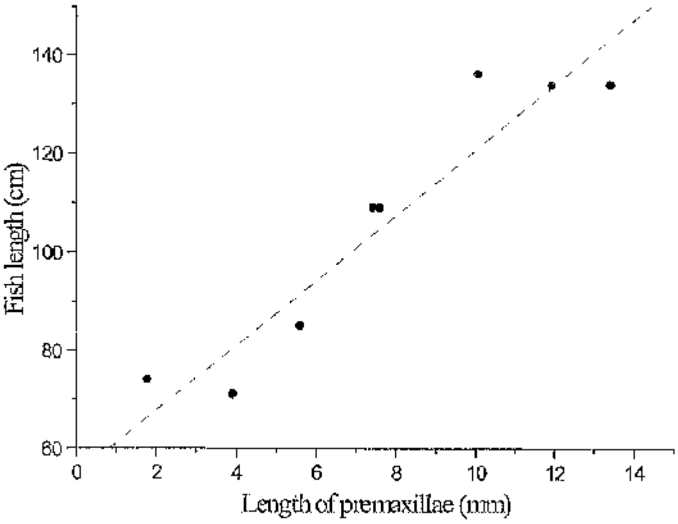


Figure 3.2. The relationship between the size of premaxillae recovered from otter spraints and the known length of the bullrout fed to the otter.

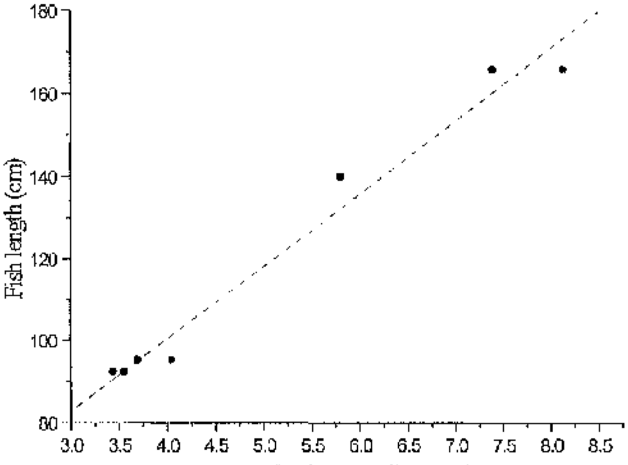


Figure 3.2. The relationship between the size of premaxillae recovered from otter spraints and the known length of the corkwing wrasse fed to the otter.

3.3.4. Relative prey number correction factors

3.3.4.1. Testing for consistency of recovery

Where the original size of fish could be determined, that is the trials that produced the bones described for size regressions above, for each species, the recovery of different sizes of bone was examined through logistic regression analysis, since Carss et al, (1998), described a logistic relationship between recovery rate and fish size, table 3.6. The fish were also divided into size classes and the proportion of bones recovered compared for each size class via χ^2 goodness of fit, to test for any other non-logistic distribution, such as described for some fresh water prey by Carss and Parkinson, (1996). None of the three species demonstrated a logistic curve or showed a significant difference in the proportion recovered in each size class, see table 3.7. Since these three species did not have a differential recovery rate with fish size, we assumed that this was true for the other marine species in our trials.

Species	χ^2	d.f.	P
Butterfish	2.01	1	0.16
Bullrout	.16	1	.69
Wrasse	.33	1	.57

Table 3.6. Results of logistic regression analysis of the recovery of a bone against the size of that bone

	χ^2	**d.f.**	**Significance**
Butterfish	1.54	2	N.S.
Bullrout	3.28	4	N.S.
Corkwing wrasse	0.43	2	N.S.

Table 3.7. Results of a statistical comparison of the proportional rate of recovery of premaxillae from different size classes of fish.

3.3.4.2. Test for consistency of recovery between trials.

The proportion of bones recovered from each trial was compared for each species of fish, via χ^2 tests, (table 3.8.), to determine whether it was consistent. All the species, except 15-spine sticklebacks, showed no evidence of a different rate of recovery between trials. This meant that correction factors, to be applied to counts of these bones found in spraints, could be calculated for these species, see table 3.9. Multiplication of the number of bones of a species found in otter spraints by these correction factors will allow relative proportions of prey numbers to be calculated. This can then be used confidently to provide an accurate overall estimate of prey numbers the animal consumed.

Species	**No. of trials**	χ^2	**d.f.**	**significance**
Butterfish	6	9.66	5	N.S.
Bullrout	5	3.12	4	N.S.
Corkwing wrasse	4	2.90	3	N.S.
15 - spine stickleback	5	11.90	4	$p < 0.01$
5 - bearded rockling	3	2.30	2	N.S.
Saithe	2	0.81	1	N.S.

Table 3.8. Comparison of recovery rate of premaxillae from different trials, for different species.

Species	**Correction factor**	**S.E.**
Butterfish	2.18	0.42
Bullrout	1.10	0.14
Corkwing wrasse	1.37	0.37
5 - bearded rockling	1.51	0.16
Saithe	1.56	0.73

Table 3.9. Correction factors for calculating relative number of prey from counts of premaxillae found in spraints.

3.4. DISCUSSION

Faecal analysis is a common method of determining an animals diet. While it can tell us definite information, that an animal ate a certain prey type, problems arise when we attempt to quantify this and say how much of a prey type it ate. Frequency of occurrence is an analytical method that attempts to overcome this, and while its accuracy has been called into question, it is still very commonly used (for example, Watt 1995, Beja 1997). Recent work with otters feeding on fresh water prey, (Carss and Parkinson 1996) demonstrated that there are large inaccuracies in the method. The current study initially examined the extent of these inaccuracies with marine prey. It was demonstrated that they are even greater than with fresh water species, in that while an accurate rank order of prey numbers can be obtained by frequency of occurrence, the rank order of biomass, which can be obtained with fresh water prey, is not accurate. The reason for this discrepancy is likely to lie in the greater variation in fish body shape of marine prey than fresh water prey (Carss and Nelson 1996)

While the only relatively accurate information obtainable from frequency of occurrence analysis is a rank order of prey numbers, it would be wrong to dismiss the method as wholly useless. It is not always absolute values that are of interest in a study, but relative values, as in comparisons of diet between habitats, seasons or years. Such comparisons have been made in most studies, and in light of the present study and Carss and Parkinson's (1996) fresh water trials, we can now evaluate the validity of these comparisons. Where the comparisons have been made statistically, by methods that use ranks, such as Spearmans Rank Correlation, (for example, as used by Mason and Macdonald, 1988), or Kendal's Coefficient of Concordance, (as used by Beja, 1997), the conclusions made are valid, in terms of rank numbers of prey. Knowledge of the length weight ratio of the prey species involved allows interpretation of these results in terms of the importance to the otters diet. However where tests involving absolute values, such as χ^2 contingency tables, (as used by, for example, Jenkins *et al* 1979, Herfst 1984, and Watt 1995) or Detrended Correspondence Analysis, (as used for example by Beja, 1991), have been applied, the validity of these comparisons must be called into question.

3.4.1. Key bones

Our work on key bones has been hampered by small sample sizes. Although our results can be considered to be preliminary, they do demonstrate that the use of key bones to quantify otter diet, with correction factors and regression equations, is feasible, and with further feeding trials, a coherent methodology could be drawn up. For our work we choose to use the premaxillae as the key bone. While there was some numerical basis for this decision, in that recovery rates were highest for premaxillae, there were also precedents for the use of premaxillae that make its use advantageous. Work is currently underway to construct a key for identification of the premaxillae of Atlantic fish, and this will be of profound use in otter diet work. It is likely that the high recovery rate of the premaxillae is related to its position in the fish' body and the manner in which the otter eats a fish. An otter will most commonly eat a fish head first, (Kruuk, 1995, pers. obs.), and therefore will first bite into it on or below the opercular flap, and subsequently chew the rest of the body as it is swallowed.

Effectively this means that those bones that are least likely to be broken up by mastication are in the front head area, such as premaxillae and pharangeal bones, and therefore are most likely to survive the digestive process intact.

Regressions of bone size against fish length have been frequently used in dietary studies and still are being used, (for example, Beja, 1997) but often these regressions have been calculated without acknowledging that the bone will change size and shape during digestion, (Pierce *et al.*, 1991). Post digestion equations eliminate these errors to some extent. There may however be some variation in the amount of breakdown of bone. Carss *et al* (1998) demonstrated that the amount of activity that occurs after feeding influences the amount of wear on a recovered bone. During our trials the otters were kept active, and since otters spraint most frequently prior to and during a feeding bout, (Kruuk, 1992), our results will reflect the situation in the wild. It is likely that there are also variations in digestion rate between individuals, however these potential errors are small in comparison with other methods of quantification, and clarification of them could be obtained by further feeding trials.

It would have been possible to calculate regressions for bone size to fish mass, and in this way derive a more direct measure of the importance of a prey item in the diet, (Pierce *et al.* 1991). However such an equation would not take into account seasonal variations in fish mass. While the relationship between fish length and bone length will remain constant, fluctuations in fish mass will also vary, hence adding a degree of error to the equation. It was therefore decided that it would be more accurate to determine fish length from bone size, and then calculate mass from length mass relationships calculated seasonally

The regression equations calculated were again hampered by a small sample size, and this meant that we were only able to do them for 3 species. The high r^2 values for these regressions show that while sample sizes are small, the correlation between post-digestion bone size and original fish length is a close one, and it can be reasonably assumed that this will be so for other species, therefore justifying further feeding trials. Such trials should be used to create regressions for other prey species and to increase the sample size of those species already done.

Size bias in the rate of recovery of key bones was suggested by Carss and Elston, (1996) after their fresh water feeding trials, in which the animals were not kept active after feeding. This bias was in both small and large fish, where the recovery rate was less than that of middle sized fish. Subsequent feeding trials by Carss *et al* (1998), during which the otters were active after feeding, suggested that the recovery rate was only reduced in large fish, and a logistic regression was described for this. In our trials, where again the otters were active, testing for either of these possibilities, (via a χ^2 goodness-of-fit test for the former, and a comparison with a logistic regression for the latter), showed there was no differential recovery rate in these trials. Since our trials follow the activity pattern of the latter freshwater trials (Carss *et al*, 1998), this is where any comparison would be valid. There are several reasons why the discrepancy in result between these may be:

1. The trials used a smaller size range of fish than Carss *et al*, and therefore the decline in recovery may only happen with very much larger fish. However there are no published details of the size range used in this work.
2. Marine fish may have bones more resistant to break-up than freshwater fish. There is, however, no evidence of this.
3. The result may be an artefact of the small sample size of these trials

Plotting out the logistic equation of recovery rate against fish size, from Carss *et al* shows that the slope evens out at approximately 50mm fish length, suggesting that it is the fact that our size range does not include very small fish that causes the discrepancy in results. It is unclear whether this will have an effect on analysis of wild spraints, since otters are generally considered to feed on larger prey (for example, Kruuk, 1995), although Adrian and Delibes, (1987) reported otters feeding on mosquito fish, *Gambusia affinis*, of 30 - 40 mm length. Carss and Elston, (1996), suggest that otters do in fact feed on smaller prey but that this is not detected by spraint analysis. Adrian and Delibes, (1987), however obtained their information on small prey items from spraint analysis, and Carss *et al*, (1998), suggested that smaller key bones actually have a better recovery rate than larger ones. Furthermore some reports of size selection for larger prey have been based on observation rather than spraint analysis, (for example, Kruuk *et al*, 1987). This suggests that reports of otters feeding on mainly large prey are genuine and that any differential recovery rate of the key bones of prey smaller than 50 mm is likely to have a minimal effect on the overall accuracy of results.

Consistency of recovery rate throughout the trials for the main prey species allows the calculation of correction factors. Previously the use of key bones has been only suggested to give minimum numbers estimates of prey types eaten, (for example, Carss and Elston, 1996). This study has shown that with these correction factors, we are able to calculate a reasonable estimate of the relative numbers of prey types. With this information, combined with regression equations, we can for the first time estimate the relative importance of different prey types in an otter's diet.

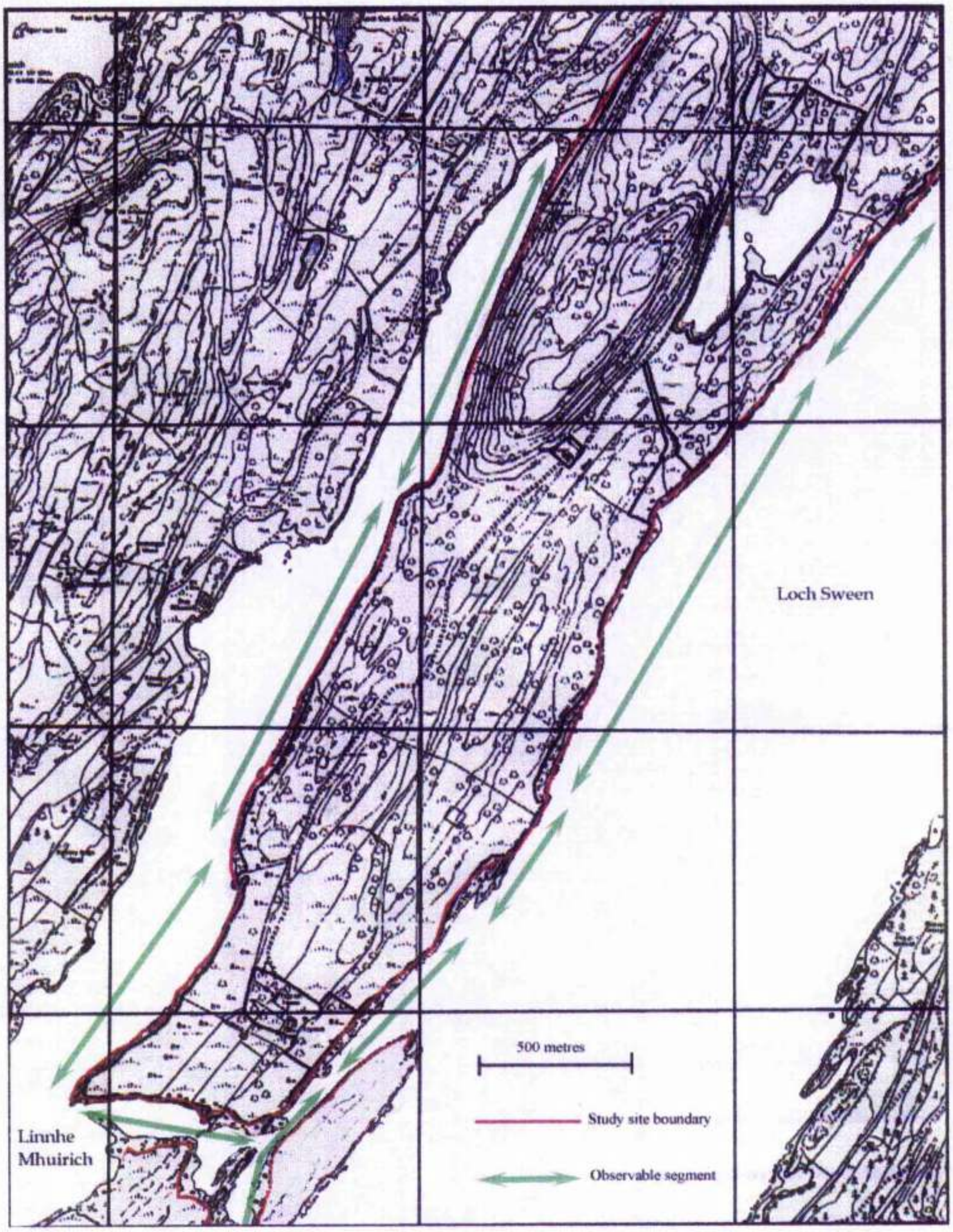


Figure 4.1. Subdivision of the Study Site into Observable segments

Chapter 4.

Seasonal Fluctuations in the Diet of the Otter at Three Habitats of the Taynish Peninsula

CHAPTER 4.

4.1. INTRODUCTION

Of the aspects of the Eurasian otter's ecology that have been examined in previous work dietary studies have been the most common. The reasons for this are simple. While direct observations of the otter can frequently be difficult to make, the otter leaves spraints, (faeces), throughout it's range (Kruuk 1992). These are easy to find, process and analyse, and from them one can determine which prey the animal has eaten (Erlinge 1968). There have therefore been numerous studies of the otter's diet, based around spraint analysis, (see reviews in Mason and Macdonald 1986, and Kruuk 1995). Potential inaccuracies in this methodology were discussed in chapter 3, (see also Carss and Elston 1997). It was concluded that for marine feeding otters, current methods can generally only give a rank order of prey numbers, though relative biomass of different prey items can potentially be calculated via regression equations and correction factors. Relatively few studies have used direct observation of the otters feeding (Kruuk *et al.* 1987, Kruuk and Moorhouse 1990, Watt 1991 and 1993), and this method allows more detailed information to be obtained, (Kruuk 1995), such as actual site, depth and time of prey capture as well possibly prey type and size. It is however likely that there will be different inaccuracies associated with this methodology, such as missing smaller prey items and, since it is impossible to observe an otter all of the time, not observing the full range of prey types. There has been no attempt to compare observation and spraint analysis. Though Watt (1991, 1993, and 1995) used both methods in his study in Mull, he did not make a direct comparison.

All of the dietary studies show that the otter is a highly specialised predator, feeding almost entirely on fish. Otters prefer to feed on fish when they are inactive and resting at the bottom of the water column (Kruuk 1995). Otters will feed in freshwater, (for example Carss *et al.*, 1990), coastal marine environments, both warm and cold (for example, Beja 1997 in Portugal and Heggberget 1993, in Norway), and brackish conditions, (for example Weir and Bannister 1977, in Norfolk). Most dietary studies have been carried out on otters feeding in fresh water, though a number have dealt with otters feeding in the sea, most notably in Scotland and Ireland. The first of these (Elmhirst 1938) simply discussed the occurrence of spraints on the island of greater Cumbrae and the possibility of determining prey species from them. No detailed study of marine diet was published until Weir and Bannister (1973, 1977) examined spraints of otters inhabiting coastal marshes in Norfolk, and Watson (1978) made a study of coastal otters in Shetland, creating an identification key for the vertebrae of common marine prey. Herfst (1984) made a more detailed study of summer marine diet in Shetland. These Shetland studies pointed to a diet largely composed of eelpout, butterfish, eel, rockling and other gadoids, cottids, flatfish, and lumpsuckers, as well as crustaceans, repeating the pattern of demersal prey suggested by other studies (such as Mason and Macdonald, 1980). A very similar suite of prey was subsequently found in further marine studies, (Murphy and Fairley, 1985, Kruuk and Moorhouse, 1990, Watt 1991, Heggberget, 1993), though eelpout lessens in importance the further south the feeding range of the otter. Wrasse and gobies also become increasingly important in more southern studies, (Murphy and Fairley 1985, Beja 1991 and 1997).

The first marine study to examine diet throughout the year was that of Murphy and Fairley (1985), who described seasonal trends in the patterns of predation, such as a peak in butterfish exploitation in the summer. Heggberget (1993), documenting coastal otters in Norwegian fjords, described a similar summer peak in butterfish predation, with a corresponding peak in that of the gadoids, particularly cod and rockling, in the winter. Kruuk and Moorhouse, 1990, also examined seasonal variations in diet, and for the first time they used observation of the otters feeding, rather than spraint analysis to describe the diet. In Shetland, eelpout were the most dominant species throughout the year; however there was seasonal variation in other species, with a winter peak in gadoids and an increase in smaller prey, such as butterfish, in spring. This work, as part of a larger study of otters in Shetland, offered the opportunity to compare the diet with data from prey population surveys, obtained via fish trapping, (Kruuk *et al.*, 1988), which will be discussed subsequently. The study by Watt, (1991, 1993 and 1995) combined data from spraint analysis, feeding observations and fish trapping, and was carried out throughout the year. Again this described a winter peak in gadoid predation, particularly rockling, and a summer peak in butterfish. There was also a spring peak in lumpsuckers, amphibians, and one of eels in the summer.

Accurate descriptions of prey size are less readily available than simple descriptions of prey profile, due to the problems of spraint analysis discussed in chapter 3. This is one of the major advantages of observation over spraint analysis. Estimation the size of prey from observations of otters feeding was first used by Kruuk and Moorhouse (1990). They tested the accuracy of both identification and size estimation by this method, by being shown a random selection of prey from a distance of and found 80% of prey correctly identified, with size estimates within 12% of the true size (Kruuk and Moorhouse 1990). Using this method, they described both seasonal and spatial effects on the size of prey taken, with an increase in the size of prey as level of exposure of the site increased, and an increase in size of prey in the winter. These two effects also interacted in that the otters tended to feed most in more exposed shores in the winter. The higher winter availability of gadoids such as cod and rockling in exposed areas, as described by trapping, was considered likely to be an important factor affecting this behaviour.

From the studies where descriptions of diet have been combined with prey surveys (Kruuk and Moorhouse 1990, Watt 1995, and Beja 1997) a clearer picture of prey selectivity in otters can be determined. In Shetland (Kruuk and Moorhouse 1990), while the otters did take advantage of seasonal peaks in prey numbers, they did not exploit the most abundant prey type, butterfish; rather they selected the more energetically profitable eelpout or rockling, and also larger prey than were relatively abundant. Watt (1995), however, found positive correlations between mean catches of prey species and their relative frequency of occurrence in spraints throughout the seasons. He related this to habitat quality, suggesting that in poorer quality habitats, such as those found in Mull, the otters selectivity was reduced; in the richer habitats of Shetland, the otters were able to be more selective due to a greater range of prey and availabilities. While prey selectivity may not be an indicator of all the indexes of habitat quality, it is likely to reflect quality from an otter's perspective. Kruuk's assertion that Shetland provides an optimal foraging environment for otters is likely to be true in the context of the high concentrations of eelpout there that are not available in other areas. The abundance of this easily captured, high-energy species in Shetland's coastal waters allows the otters a degree of selectivity not available elsewhere. Some data is also available for Portugal, where the most important food resource for otters is the corkwing wrasse, and prey selectivity is biased toward this (Beja 1997). Indeed in Portugal the coastal otters reverse the usual trend of feeding during the day, taking advantage of their prey's activity cycles (Kruuk, 1995), and feed at night. This is likely to be because, unusually for marine fish, wrasse are diurnal, (Darwall *et al.*, 1992).

There is also some evidence of individual variations in diet. Kruuk and Moorhouse (1990) found a degree of intra-specific variation with otters. While adult males and females generally tended to eat the same species of prey, females with cubs would give larger prey to their offspring, and more independent younger animals ate poorer prey. Watt (1993) described how young foraging cubs ate predominantly crustaceans, particularly shore crabs since these are easier to catch, and as their foraging skills developed the proportion of fish in their diet increased.

In the present study, it was important for us to have an accurate assessment of the otter's diet, in order to ascertain to what degree this was interlinked with variations in behaviour in response to environmental change. While we followed the example of

Kruuk and Moorhouse (1990) using observation as the main source of dietary information, we also made a study via spraint analysis to enable a comparison between data obtained by the two methods, and to allow some preliminary testing of the methodology developed in chapter 3. The questions we set out to answer were:

1. What is the diet of the Taynish otters, as described by direct observation and spraint analysis?
2. Do the results from these two measures differ?
3. Does the diet correspond with data from prey trapping?
4. How does the diet change seasonally and spatially?
5. Is the diet affected by tide state?
6. Does the size and mass of prey taken vary seasonally or spatially, or with tide state?
7. Do otters obtain different prey at different depths?
8. Does it require different lengths of dive to obtain different prey types and is this correlated with depth?

4.2. METHODS

4.2.1. Observation

The study site was divided into nine "observable segments" figure 4.1., that is areas where the whole coastline was observable from a single vantage point, (figure 4.1.). This facilitated the recording of any otter activity within set areas, the sites and recording sessions ensured that the areas were equally sampled. Each segment was studied for five continuous hours each month for 15 months, with the timing of the watch standardised, as far as possible, for time of day and state of tide. Any otter activity that occurred within the segment was recorded. When an otter was seen feeding, if possible, the type and size of prey were recorded. Size of prey was estimated by comparison with the width of the otters head, which is on average 8cm (Kruuk 1995). Prey items were recorded in nine size classes; class 1: 5 - 9 cm, class 2: 10 -14 cm, class 3: 15 - 19 cm, class 4: 20 - 24 cm, class 5: 25 - 29 cm, class 6: 30 - 34 cm, class 7: 35 - 39 cm, class 8: 40 - 44cm, and class 9: 45 - 49cm. Kruuk and Moorhouse (1990) tested the accuracy of this and found that such estimates were within 12% of the true prey size. The mass of prey items was calculated from length to mass relationships derived from fish trapping data. The length of dive was recorded as the period of submersion of the otter's head. The location of each dive was recorded on maps of the observation area using a combination of landmark triangulation, that is using landmarks distinguishable on either side of the feeding otter and noting the otters position relative to this, the orientation of the otter from the vantage point, and distance estimation. Generally the otter fed close to the shore, making this method accurate, as there was little estimation of distance necessary. Dive depth was determined from Admiralty depth soundings, and corrected for tide state. It was assumed that otters always dive to the bottom, and this assumption was borne out by personal observation, since prey was always bottom dwelling species, and by all other observers in the literature (see review in Kruuk, 1995).

4.2.2. Spraint Analysis

Spraints were collected from the coast of the study site in monthly collections for 12 months, and the place and time of collection noted. They were sealed in plastic bags and frozen. Twenty spraints were analysed for each habitat (rocky, sandy and tidal) in each season, when possible, though only 18 and 19 spraints were found in the tidal habitat, in summer and autumn respectively. Seasons were defined as in chapter 2:

Summer : June, July and August
Autumn : September, October and November
Winter : December, January and February
Spring : March, April and May

This number of spraints has been shown by several authors (Mason and Macdonald 1980, Watt 1995, and Carss and Elridge, 1997) to be adequate to contain all the important prey items. For analysis they were soaked for 48 hours in a saturated solution of a propriety biological detergent, "Biotex", to remove mucilaginous material, and consecutively washed through two sieves of mesh size 0.50 and 0.25mm. They were allowed to dry at room temperature for 24 hours and examined under a binocular dissecting microscope. Using a reference collection of bones obtained from trapping, and a key to thoracic bones (Conroy *et al.*, 1993), all identifiable prey remains were recorded, and any premaxillae were removed, identified, measured and where possible used in regression equations to calculate fish length (see chapter 3). The results were expressed as relative percentage of occurrence. This is calculated as the number of occurrences of a prey type divided by total number of occurrences of all prey types, multiplied by 100. These were then converted to a rank order of number of prey type eaten, following chapter 3, where this is shown to be the most accurate information obtainable from this methodology.

4.2.3. State of tide

This was studied at a single observation site. Observations were made, as above, from a single vantage point at the tidal rapids, over four days each month, for 15 months. These days were split into two pairs of consecutive days, and in each pair watches were carried out so that the total daylight hours were observed during them. The two pairs of days were arranged so that they were at opposite tide states with respect to the timing of high and low water. When taken as a whole season, this allowed examination of the effect of tide on prey capture, with any possible effect of the time of day eliminated. For analysis the tide was split into four states, incoming, in, outgoing, and out. The mid points of the in and out states were taken as high and low tides, as taken from Admiralty tide tables, and each state lasted for slightly more than three hours, varying according to lunar cycle.

4.2.4. Data analysis

The description of the otter diet obtained from observation was compared with the results of spraint analysis, expressed as a rank order of relative importance, using Kendall's coefficient of concordance; this uses ranked data to test the null hypothesis that the groups being compared are from different populations (Sokal and Rohlf, 1995). Observations were grouped into 3 habitat types (following chapter 2), and 4 seasons (chapter 2) for analysis. The numbers of different prey items caught at each habitat, in each season, were analysed as a three dimensional contingency table using a log-linear model (Sokal and Rohlf, 1995), having corrected the numbers for amount of otter activity observed, to determine if there were variations in the suite of items consumed, and their relative importance in these different habitats and seasons. In order to avoid too high a proportion of empty cells in this contingency table, some of the less important prey types were aggregated as follows: butterfish, eels and gobies remained as they were, rockling and other gadoids were grouped together in one prey class, as were 15-spine sticklebacks and pipefish. These two prey groups represented species of broadly the same habits and mean weights. All other prey items were grouped as a final class. The rank importance of piscine prey types as assessed by observation was compared with the catches of the fish traps (chapter 2) again using Kendall's coefficient of concordance. The effect of tide on the frequency of different prey items occurring in the diet was examined using a contingency table with prey type against tide state, and the effect of tide on size of prey was examined via a one-way ANOVA, with the data logarithmically transformed to compensate for a skewed distribution. Both the size and the mass of prey consumed were examined for seasonal and habitat effects using a two-way ANOVA, having carried out a logarithmic transformation to compensate for a skewed distribution. Mean dive times for each prey item were compared, as were dive depth. Non - parametric tests were required for the latter due to non-homogeneity of variance.

4.3. RESULTS

4.3.1. Overall Diet

4.3.1.1. Direct observation

A total of 937 prey items were observed being eaten by otters during the study, of which 283 were identifiable. The most numerous prey item was the butterfish, with 92 observations; eels rockling and gobies were also important, with 50, 29, and 28 observations respectively, table 4.1. and figure 4.2. There were significant differences in both the size (Kruskal-Wallis one-way ANOVA, $\chi^2 = 131.23$, d.f. = 9, $p < 0.001$) and the mass of these different prey items (Kruskal-Wallis one-way ANOVA, $\chi^2 = 159.75$, d.f. = 9, $p < 0.001$). Lumpsuckers and then eels were the largest prey items in terms of size, but by far the heaviest prey item was the lumpsucker, see figs 4.4. and 4.3.

Species	No. of Observations	Mean size ± S.E.(cm)	Mean mass ± S.E. (g)
Butterfish	92	16.40 ± 0.44	14.65 ± 1.02
Eel	50	23.00 ± 1.09	26.02 ± 3.56
Goby	28	11.10 ± 0.37	11.28 ± 0.22
Wrasse	5	13.00 ± 1.87	28.81 ± 7.11
Sea -scorpion	15	15.02 ± 0.82	69.39 ± 9.23
Rockling	29	16.66 ± 0.70	40.73 ± 4.62
Non-rockling gadoid	11	14.27 ± 0.79	34.98 ± 4.65
15-spine stickleback	23	11.78 ± 0.38	4.04 ± 0.31
Pipefish	11	18.03 ± 1.00	2.25 ± 0.40
Lumpsucker	4	34.52 ± 2.50	1284.85 ± 47.7
Crustacean	15	11.23 ± 1.11	96.40 ± 9.33

Table 4.1. The total number of observations of otters eating different prey items

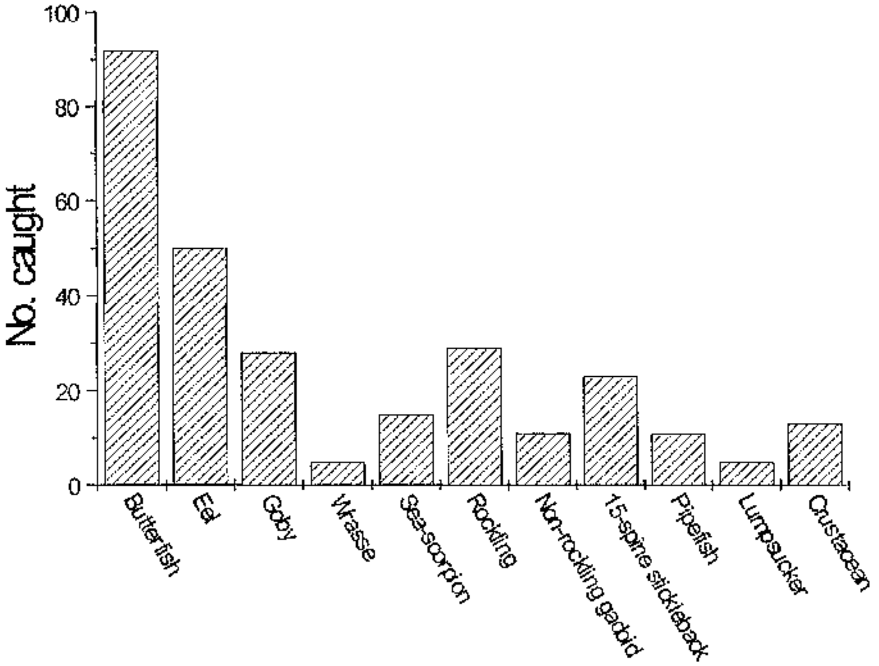


Figure 4.2. The total number of observations of different prey types being eaten by otters

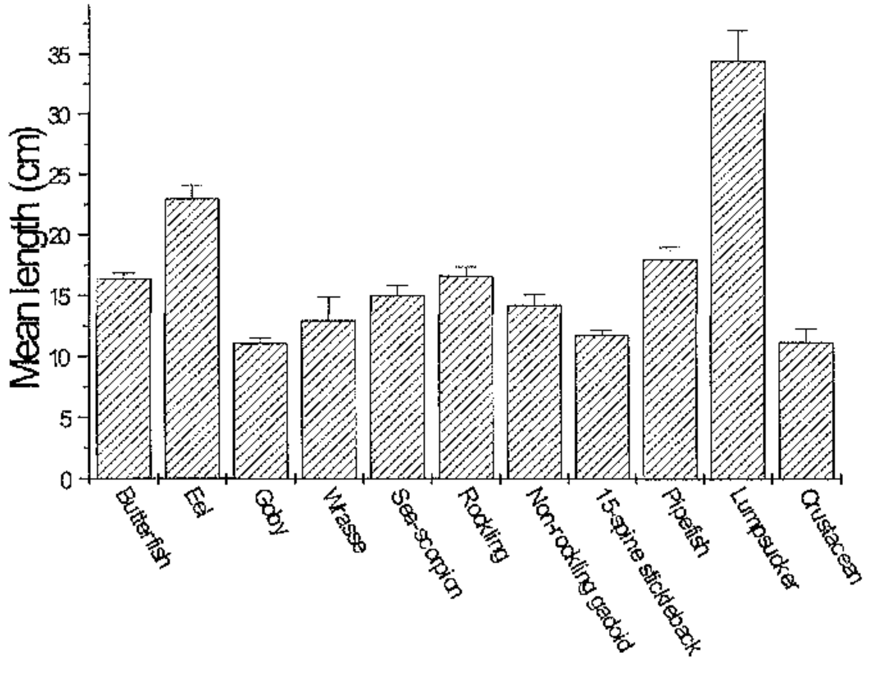


Figure 4.3. The mean length, ± standard error, of the observed different prey types consumed by otters

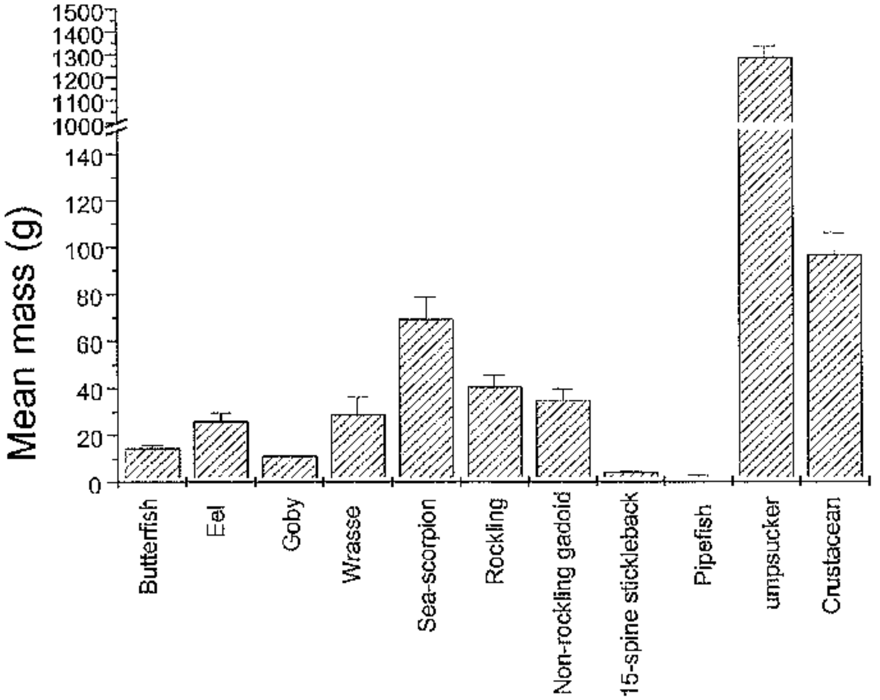


Figure 4.4. The mean mass, ± standard error, of the observed prey items consumed by otters. Note break in vertical scale

4.3.1.2. Spraint Analysis

237 spraints were analysed, yielding 805 occurrences of 20 different prey items, including 17 fish species (or type), crustacea, and unidentified birds and amphibia. Relative frequency of occurrence was calculated and a rank order of prey numbers was created, (table 4.2). The most common prey item was the black goby, followed by crustaceans. Insufficient premaxillae were found to justify application of correction factors to calculate relative biomass of prey items, as outlined in chapter 3.

Species	Frequency of occurrence	Rank by spraint analysis
Black goby	18.26	1
Crustacean	16.15	2
Butterfish	12.17	3
Eel	11.18	4
Rock goby	8.45	5
15 - spine stickleback	7.70	6
Pipefish	6.34	7
Goldsinny wrasse	5.09	8
Rockcook Wrasse	3.48	9
Corkwing wrasse	2.24	10
Cod	1.61	11
Amphibian	1.37	12
Saithe	1.24	13
Bird	0.75	14
Lumpsucker	0.50	15
Pollack	0.25	16

Table 4.2. *The rank order, in descending order of importance, of numbers of prey items consumed, as calculated by relative frequency of occurrence in spraints.*

4.3.2. Comparison of Observation and Spraint Analysis

When the data on the main prey items obtained from observation and spraint analysis are ranked and compared, table 4.3., there was found to be no significant similarity between them (Kendall's coefficient of concordance, $W = 0.65$, $\chi^2 = 11.68$, d.f. = 9)

Species	Rank from observation	Rank from spraint analysis
Butterfish	1	2
Eel	2	3
Goby	4	1
Wrasse	10	4
Rockling	3	9.5
Non - rockling gadoid	7	7
Sea - scorpion	5	9.5
Stickleback	6	5
Pipefish	8	6
Lumpsucker	9	8

Table 4.3. Comparison of the ranked data (in descending order of importance) on otter diet obtained via observation and spraint analysis.

4.3.3. Comparison of Prey Observations and Fish Traps

The observations of prey taken by otters were ranked using observations, and compared with the ranked total catches of the fish traps, over the same 15 month period, see table 4.4. and figure 4.5.; the largest discrepancies were with butterfish and gobies. There was found to be no significant similarity between them, (Kendall's coefficient of concordance, $W = 0.48$, $\chi^2 = 8.73$, d.f. = 9).

Species	Rank from observation	Rank by trap
Butterfish	1	8
Eel	2	5
Goby	4	1
Wrasse	10	2
Rockling	3	7
Non - rockling gadoid	7	3
Sea - scorpion	5	6
Stickleback	6	4
Pipefish	8	9
Lumpsucker	9	10

Table 4.4. The numerical importance of prey types from trapping and observations of otters feeding.

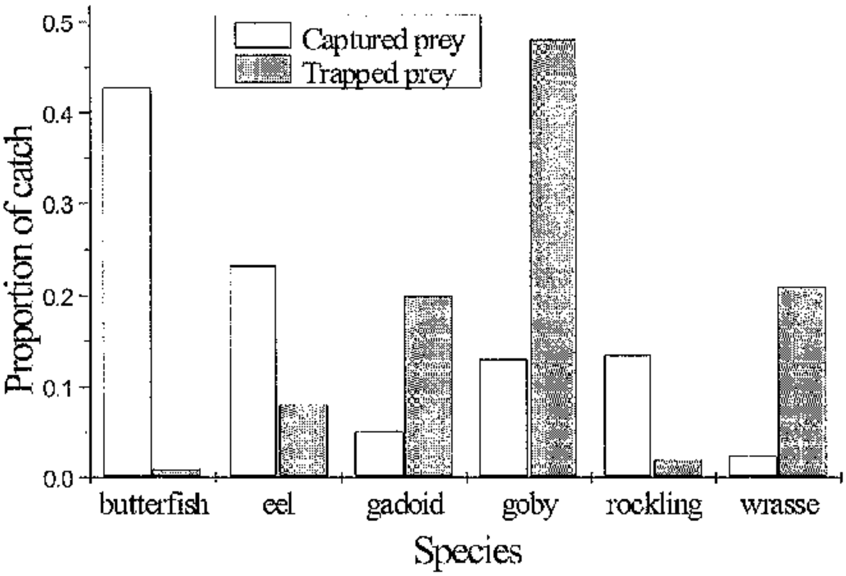


Figure 4.5. Comparison of fish caught by otters and in fish traps, expressed as proportion of the total catch

4.3.4. Habitat and Seasonal Effects

A three-dimensional frequency table of numbers of the main prey types in each habitat, in each season was constructed. Log - linear analysis revealed that the most significant model that could be applied to the table was the one that did not include any interactive term, **log p = x + y + z**, where x, y, and z represent habitat, season and species respectively (Pearson $\chi^2 = 1370$, d.f. = 61, $p < 0.001$). This indicates that each factor is having a separate effect, without interactions. Table 4.5. shows the individual effects of habitat, season and species, all of which were highly significant. The most significant factor was habitat, followed by prey type, followed by season. Therefore there were significant differences in the numbers of different prey types caught in different habitats, in different seasons. Figure 4.6. shows the differences in overall frequencies of prey caught in different habitats, with all seasons aggregated, with the largest number of prey caught in habitat 3, the tidal habitat. Very few prey were caught in the sandy habitat, habitat 2, in comparison with the other two. Figure 4.7. shows the differences in overall numbers of prey in different seasons, with all habitats aggregated. The largest amounts of prey were caught in the winter, and the other seasons show broadly similar catches. Figures 4.8. - 4.11. show these data in more detail, describing the different prey items caught in each habitat, in each season. While these interactions were not as significant as the above model they do show important trends. Butterfish are common in every season, except the winter in the tidal habitat, while they are important in the rocky habitat except in the spring. They are never taken in the sandy habitat. Eels were important in the tidal habitat in the summer and autumn, and rockling and other gadoids were important in the tidal and rocky habitats in the winter.

Factor	Pearson χ^2	d.f	significance
Habitat	1695	69	<0.001
Season	1314	68	<0.001
Species	1468	66	<0.001

Table 4.5. *Individual effects of habitat, season and species on the observed number of fish eaten by otters, as described by the log - linear model* **log p = x + y + z.**

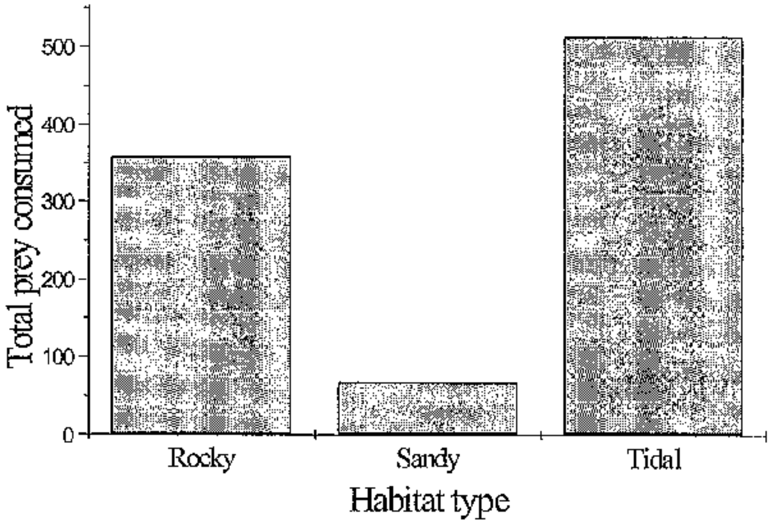


Figure 4.6. The total catches of all prey, with the seasons combined, in the three habitats.

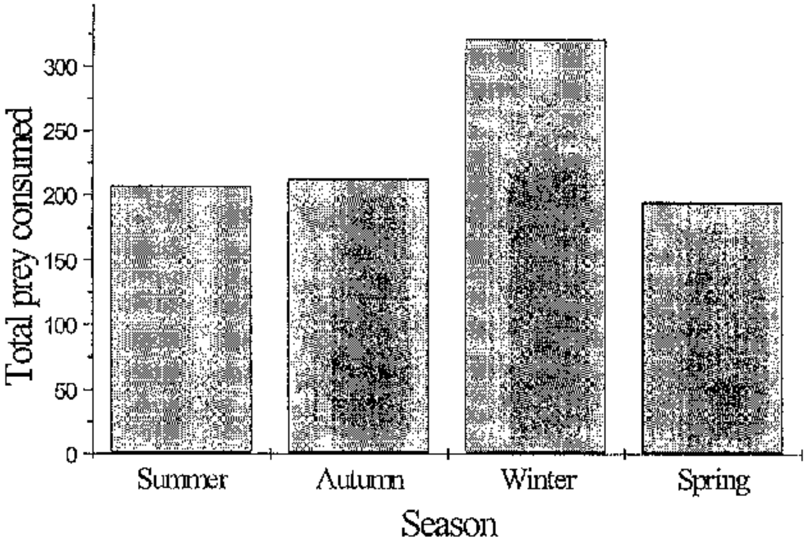


Figure 4.7. the total catches of all prey, with the habitats combined, in the four seasons

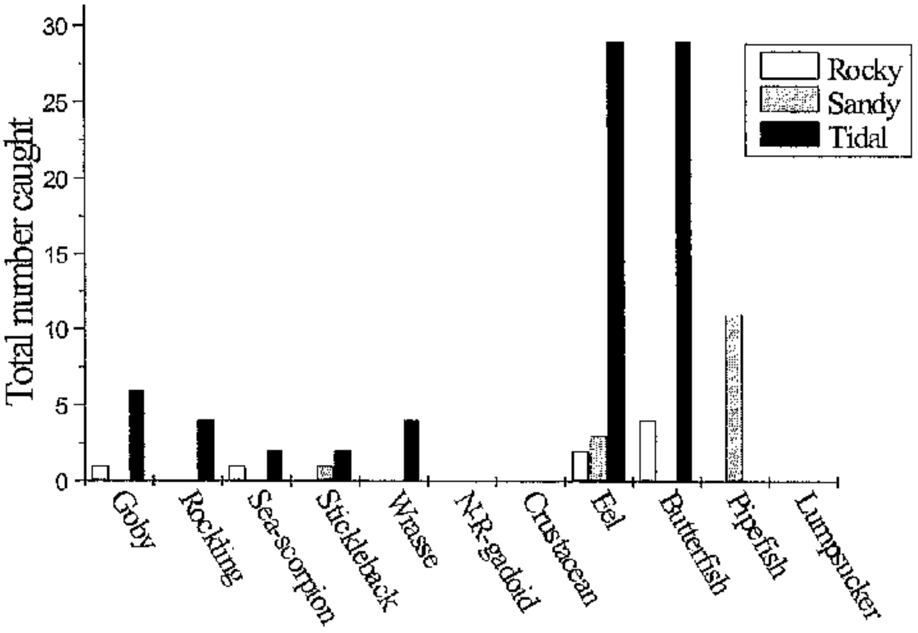


Figure 4.8. The number of observations of otters feeding on different prey types, in the three habitats, during the summer.

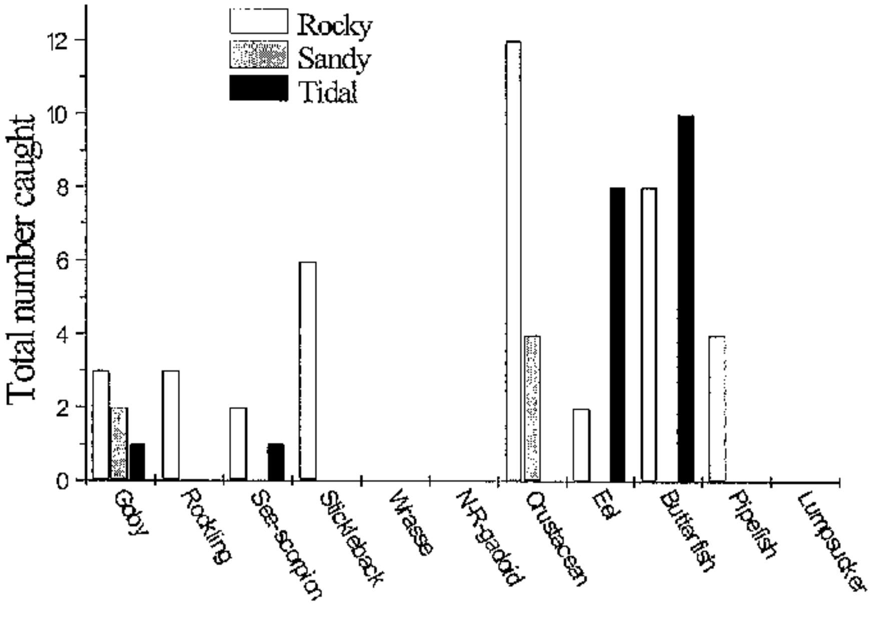


Figure 4.9. The number of observations of otters feeding on different prey types, in the three habitats, during the autumn

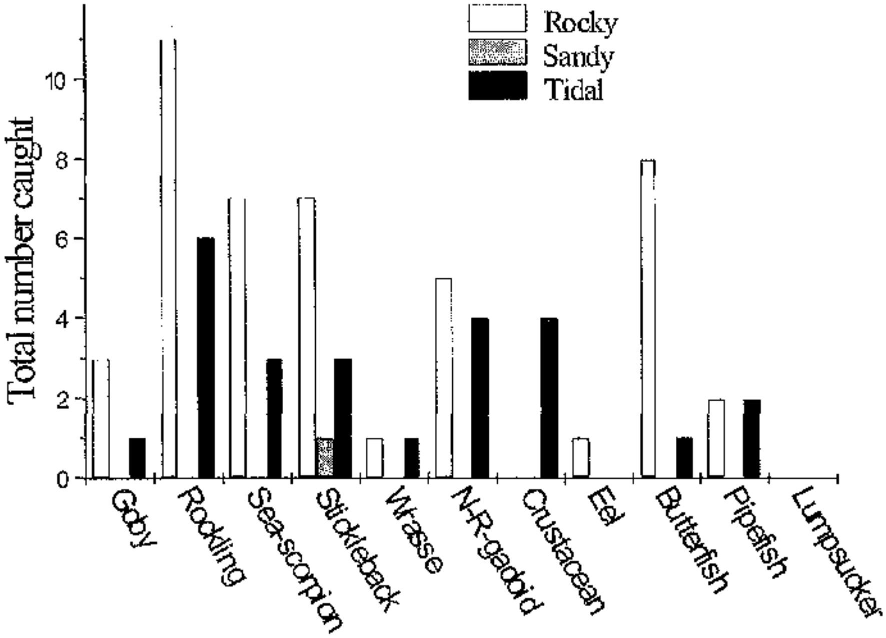


Figure 4.10. The number of observations of otters feeding on different prey types, in the three habitats, during the winter

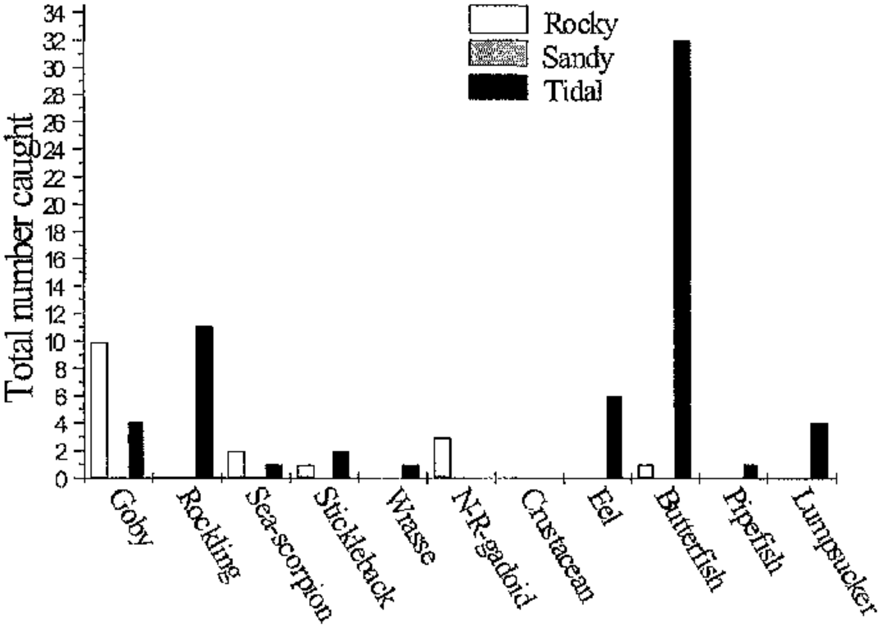


Figure 4.11. The number of observations of otters feeding on different prey types, in the three habitats, during the spring

4.3.5. The Effect of Tide

The state of the tide was found to have no significant effect on the relative numbers of different prey items taken by otters, (χ^2 contingency table, $\chi^2 = 33.4$, d.f. = 27) nor did it have a significant effect on the size of prey taken, (one-way ANOVA, with data logarithmically transformed to normalise distribution, F = 2.34, d.f. = 3, 284)

4.3.6. Prey Size and Mass

The mean size and mass of all prey taken by otters at different seasons from different habitats were compared using two-way ANOVA, having carried out a logarithmic transformation of the data to normalise the distribution. Both season and habitat had a significant effect on the size of prey taken (see table 4.6), and there was also a significant interaction between the two factors, with the effect of season differing between the habitats, figure 4.12. The biggest prey are caught in the tidal habitat in the summer autumn and spring, and the sizes from different prey are similar in the winter. In the summer prey were larger in the sandy habitat, but smaller in the autumn. In the spring no observations were made of prey size in habitat 2. Differences in the mean mass of all prey items (table 4.7.) were only significant between habitats, and there was no significant interaction.

Factor	F	d.f.	sig.
Season	11.32	3, 284	<0.001
Habitat	15.96	2, 284	<0.001
Interaction	6.60	5, 284	<0.001

Table 4.6. Results of 2-way ANOVA examining the effect of habitat and season on the size of prey observed being taken by otters, and the interaction between them.

Factor	F	d.f.	sig.
Season	1.22	3, 284	N.S.
Habitat	4.69	2, 284	<0.01
Interaction	0.18	5, 284	N.S.

Table 4.7. Results of 2-way ANOVA examining the effect of habitat and season on the mass of prey observed being taken by otters, and the interaction between them.

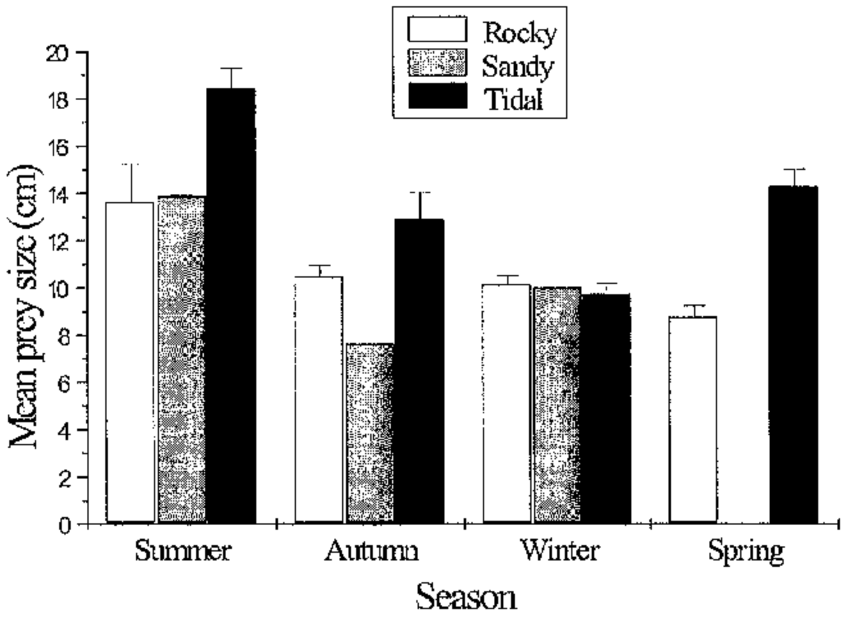


Figure 4.12. The mean size of all prey types combined, in different seasons and habitats.

4.3.7. Depth of prey capture

There were significant differences between the depth that the different prey types were caught by otters (Kruskal-Wallis one-way ANOVA, $\chi^2 = 32.46$, d.f. = 10, $p < 0.001$), see figure 4.13. Crustaceans were taken at the greatest depth, followed by eels, though the eels showed a large amount in variation. Most of the other species were in broadly the same range of depth, 2 - 4 m, and wrasse were caught in the shallowest water, under 2m.

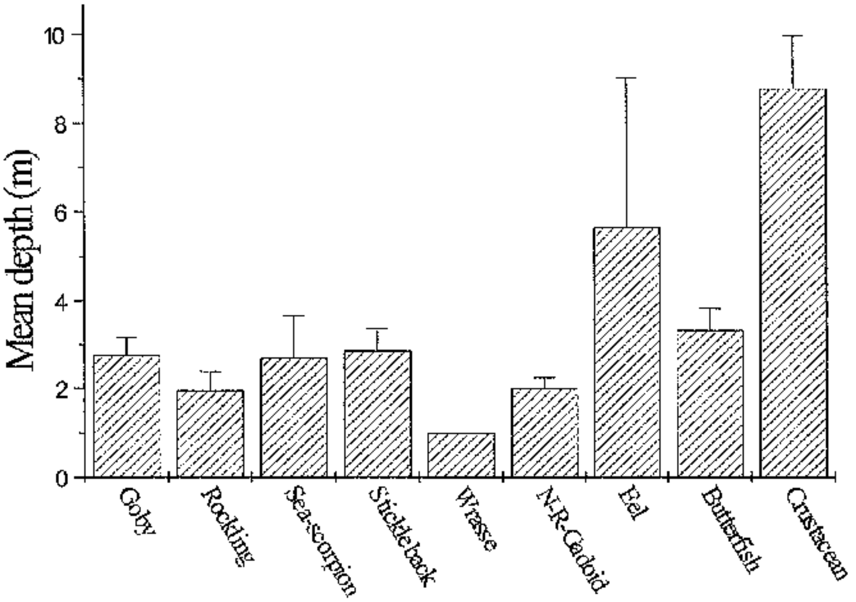


Figure 4.13. The mean depth of capture by otters, ± standard error, of the different prey types

4.3.8. Dive duration and depth

The duration of the successful otter dive times for the different prey types were also significantly different (Kruskal-Wallis one-way ANOVA, $\chi^2 = 29.80$, d.f. = 10, $p < 0.01$), see figure 4.14. While the depth of successful dives was correlated with their duration, (Spearmans rank correlation, $r = 0.51$, $n = 112$, $p < 0.001$), when the dives are grouped into prey species, and the mean dive time for a species correlated against the mean depth of capture of that species, there is no significant correlation for mean dive duration for each prey type against mean dive depth (Spearmans rank correlation, $r = 0.55$, $n = 1$). Crustaceans, which were on the whole edible crabs, were found at the greatest depths, and also had the longest dive times. Rockling and wrasse, however, despite being caught in relatively shallow water had comparatively long dive times associated with their capture.

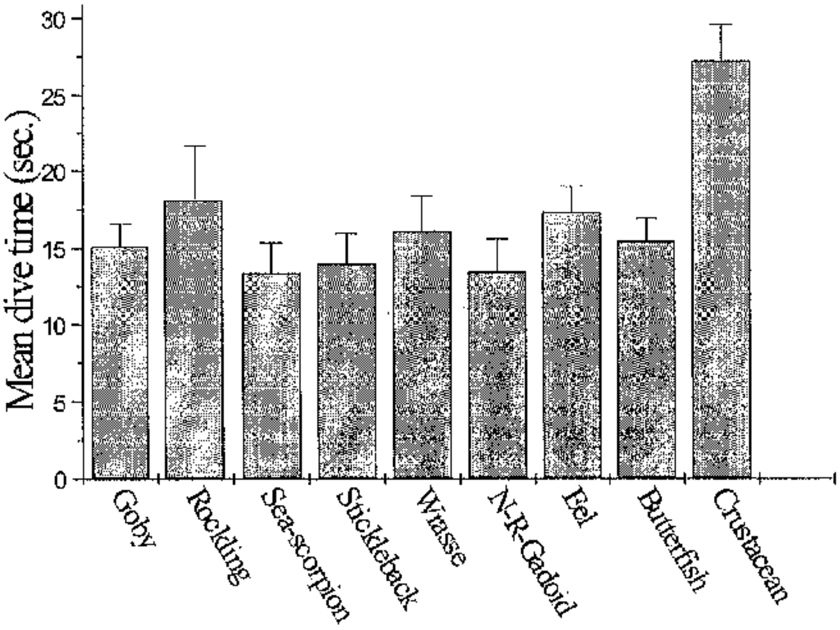


Figure 4.14. The mean dive duration for the capture of the different prey species.

4.4. DISCUSSION

Dietary preference has been described as a "tendency to eat more of a prey type than would be expected based on it's abundance in the habitat", (Sih, 1993), and Kruuk (1995) has described the Eurasian otter as one of the most specialised carnivores with respect to their dietary preferences. It is clear from numerous studies that they prefer to forage on bottom-dwelling fish, and that they prefer to do so when the fish are inactive. Within this fairly narrow band of prey types it has been suggested that the degree of selection that an otter shows in its prey choice can reflect how optimal its environment is (Kruuk, 1995, Watt, 1995) where a high degree of selection reflects a high quality environment. The underlying question in this study is how selective is the otter in this area, and can we understand the adaptive significance of the observed dietary pattern.

In order to describe the diet of the Taynish otters, two methods were used, direct observation and faecal analysis, and there are limitations to both. The limitations of spraint analysis have been examined at some length in chapter 3. In summary

1. The only accurate information obtainable from frequency of occurrence quantification of spraint analysis of marine prey is a rank order of prey numbers.
2. Relative biomass of different prey items can be calculated via regression equations and correction factors. These however are only at a preliminary stage and therefore cannot be done for all prey species.

Kruuk (1995) suggests that direct observation of prey eliminates these problems, and allows more information on for example time and site of prey capture, but this method also has limitations namely:

1. Small prey items cannot be identified and this may bias the results.
2. The prey recorded are biased towards the environments in which the otter can be observed feeding. It is very unusual for example to make observations of otters feeding in a terrestrial or subterranean environment, however it is known that they do so, feeding on birds mammals or invertebrates.

A combination of methods can give us some useful information, for example while observation may miss predation on mammals, hair would be found in spraints, and accurate biomass information can be obtained from observation. These limitations, from both methods, could therefore be overcome to some extent by the use of a combination of methods, yet there have been no studies to date that do so. While Watt (1990) used both methods he neither compared nor combined them, using them rather for different purposes, that is spraint analysis for dietary description and observation for quantifying foraging behaviour. In this study observation was used for the main body of our information, and used spraint analysis was used to identify any gaps in this.

4.4.1. Overall diet

Both spraint analysis and direct observation describe the diet of the otters at Taynish as confirming all other studies, in that it is almost entirely composed of bottom dwelling fish. In Taynish we can conclude that the most important prey items are butterfish. It also correlates strongly with other comparable studies, such as Mason and Macdonald (1980), Murphy and Fairley (1985) and Watt (1995) in that there are high proportions of butterfish, cottids, rockling, non-rockling gadoids, gobies, eels and crustaceans. Differences with the Shetland studies are not surprising. Eelpout were a far commoner component of the diet in Shetland, however these are rarer in the west coast of Scotland than in Shetland (see chapter 2, and Kruuk *et al.*, 1988). Gobies and wrasse are more important in the diet of these otters than those in Shetland and such prey items are far commoner in the west coast than in Shetland (Kruuk *et al.* 1988). It would seem therefore that any dietary differences between this study and others can be accounted for in terms of prey availability rather than predator choice.

4.4.2. Comparison of methods

The two methods of diet description differed in the relative importance assigned to different prey species. It is important to note that there are differences as would be predicted by the limitations of observation as a method of diet description; that is, there is no avian, mammalian or amphibian prey noted in the observational data but these were present in spraints. In assessing relative importance only the key prey species were included (butterfish, eel, goby, rockling, non-rockling gadoid, and wrasse). The Kendall's coefficient of concordance uses ranked data and the feeding trials described in chapter 3 suggested that spraint analysis would give an accurate rank order of prey numbers. The fact the rank order we obtained is not the same as that obtained from observation could a reflection of the limitations of the two different methods. For example, we predicted that observation would not detect smaller prey, and two of the larger discrepancies in the data sets are wrasse and gobies. From the trapping data, (see chapter 2), the mean length of wrasse available to otters is 8.04cm (s.e. = 2.29) and that of gobies is 9.21cm (s.e. = 2.07). Where a measure of the length of unidentified prey was available, (n = 120), the mean length was 9.21cm (s.e. = 0.27), and while the majority of unidentified prey were not assigned a size class, because they were not seen clearly, it seems likely that they would be similarly of a small size. Therefore it is reasonable to deduce that the discrepancy between the two methods is largely due to a bias created by unidentified prey in observation. This demonstrates that the best method of assessing the otters diet is not through either method in isolation, rather in the two combined. It also should is that spraint analysis has pointed out a level of identification that would be impossible to obtain from direct observation, in that it tells us black gobies are more important in the diet than rock gobies whereas with observation we could only define the prey as a goby, without knowing the actual species. The same is true for the wrasse, where in spraints we can distinguish, corkwing, goldsinny and rockcook wrasse, and the non-rockling gadoids where we can distinguish cod, pollack and saithe. This information from the spraints is limited to only what species are present, information on prey size and otter behaviour relevant to the prey such as dive time and location of capture cannot be found in this manner, but it is precisely this class of information that is obtainable from observation.

Another aspect of the observational method is that it is better at picking up very large prey items, such as lumpsuckers, than spraint analysis. This is due to the fact that with such prey items, the otter does not consume the skeleton, only the flesh, so there is little or no occurrence of undigested hard parts in the faeces. This has also been noted by Kruuk (1995) with respect to dogfish, where the otter commonly only eats the liver.

One final discrepancy between the methods is the importance of rockling in the diet. Observations showed them to be an important component of the winter diet at Taynish, however they were one of the lowest ranking prey items in spraint analysis. There is no obvious reason why this might have been, except that the rockling bones may have been confused with other non-rockling gadoids in analysis.

4.4.3. Comparison between observation and traps

When the data for the most important prey from observation and trapping were ranked and compared, they were found to be different. Following the example of Kruuk and Moorhouse (1990), this would suggest that otters are being selective in their prey choice, and that this demonstrates that they are in an optimal environment (Kruuk, 1995). However the data merits closer examination before this conclusion can be drawn. If we examine figure 4.3. we can see that the biggest discrepancy is in the importance of butterfish in the two groups. As described in chapter 2, there are problems with the use of stationary traps to catch butterfish and therefore trapping data for this species is unreliable. Even bearing this in mind however, figure 4.3. demonstrates that there are large differences between all the prey groups. With the exception of the gadoids, trapping shows the smaller group, that is the gobies, as being commoner than are present in the diet, and the larger prey types, eel and rockling as being less common than in the diet. This would suggest that the otters are selecting for the less common but more profitable prey types. Wrasse are far less common than in the diet than in the traps, which may be because the wrasse are diurnal in habit (Darwall *et al.*, 1992) and so are harder for otters foraging during daylight to catch. The traps however show no such selectivity. The non - rockling gadoids also do not match in the two data sets. All these species are generally pelagic, but can be found resting in kelp beds at different points in their lifecycle or daily activity cycle (Howes 1991). It is likely that the otter will tend to catch them only in the winter when the adults rest during the day in kelp beds (Sarno *et al.* 1994). However the majority of the prey from the trap catches are caught the summer and are likely to be of age group 1 juveniles, which spend their first summer in (Sarno *et al.* 1994). They are however not resting, and this makes them unsuitable prey for the otter, and again there is a contrast in size, the adults predated upon are fewer but of higher food value than the numerous juveniles that the traps catch. Therefore the discrepancy between results is due to sampling of different stages in the life cycle of the prey, and a selection of prey size by the otter.

Overall therefore, the data supports the conclusion that otters are selecting for larger prey items, and this is a reflection of the quality of the habitat.

4.4.4. The influence of season and habitat on relative frequencies of prey types

In order to analyse the seasonal and habitat effects on the foraging of the otters we constructed a three - dimensional contingency table of frequencies of prey types and examined the trends present using a log - linear model. The most significant model was the one represented by the equation **log p + x + y + z**. Other models with interactive terms were also significant but none were a significant as the above model, therefore this model will provide the closest fit to the data. This becomes clearer if examined with respect to overall frequencies, figures 4.6. - 4.5. The significance of the difference between the number of fish of all species, caught in all seasons is stronger than it would be examining these individually, for example in each season separately. This is also true for the overall frequencies between species and between habitats. The habitat differences between catches are the most significant. As can be seen from figure 4.4. The largest number of prey are caught in habitat 3, the tidal habitat, though the difference between this and the rocky habitat, habitat 1, is an effect of the greater amount of watches carried out here to examine the effect of tide. This discrepancy would not have affected the results, since the prey figures were corrected for amount of observed activity. This is not true for the second habitat, in which dramatically less prey were caught, suggesting that this is a less than optimal habitat for the otters. This is supported by the trapping data (Chapter 2), which described a consistently lower biomass of catch in this habitat than in the other two. The lack of dense algal beds in this habitat would also support this, as will the fact that there is a very high proportion of low quality food, such as gobies, 15-spine stickleback and pipefish caught here, suggesting a reduced ability for prey selection. Chapter 5 will examine the possibility that this is reflected in the distribution of the otters around the Taynish peninsula.

In the log - linear model, the second most significant factor was prey type, and the relative frequencies of prey types have been discussed above under overall catches.

The analysis finally describes a significant difference in the catches between seasons. Kruuk (1995) modelled the energetic requirements of foraging otters, based on previous studies of the oxygen uptake of captive otters (Kruuk *et al.*, 1994) which had demonstrated an increase in metabolic rate with a decrease in water temperature. His model described an increase in foraging activity of the animal as a consequence of decreasing water temperature. While the model described foraging effort as actual time spent foraging, this equates directly with the actual mass of prey consumed. Our results have shown there is no significant seasonal variation in the mean mass of the prey of otters consumed (though there is a caveat to this, as will be discussed subsequently) so in order for the otter to increase its food intake, as described by the model, it would need to eat numerically more prey. It is likely that this is the reason for the greater amount of prey taken by the otters in the winter at Taynish.

Other seasonal and spatial trends in relative consumption of different prey species are notable, though were not obvious from the log - linear analysis due to aggregation of some of the prey types, and the strength of the significance of the non - interactive model. In common with other Scottish coastal otters, (for example Mason and Macdonald, 1980, Watt, 1995) eel and butterfish dominated catches in the summer, while rockling and other gadoids were important in the winter. Spring was almost entirely dominated by butterfish, which lay their eggs and guard them at this time (Quazim, 1957) so they will be more vulnerable to predators. The same is also true for lumpsuckers, which, while they occurred infrequently in the diet, were important in terms of mass. They only occurred in the spring in the otter diet, and, as described elsewhere (Clutton-Brock, 1991), this is a function of male egg guarding during this time. Lumpsuckers are an offshore species, the females only coming inshore to spawn and the males to guard the eggs, in the spring. The egg guarding males are vulnerable to the otters, a major cost of parental care (Clutton-Brock, 1991) and this is reflected in the data, figure 4.9. Also notable from the data is a peak in crustacean predation, almost entirely edible crabs, during the autumn, which is also associated with foraging in deeper water. Potential influences on this very specific behaviour will be described in chapter 9.

4.4.5. The effect of tide on prey selection

Tide was shown to have no effect on the relative frequencies of prey taken. This would correspond to our knowledge of prey behaviour, and the fact that otters prefer to capture prey when it is least active (Kruuk *et al.*, 1988). Koop (1990) demonstrated in the laboratory that both rockling and butterfish follow diel activity cycles rather than tidal, and Hesthagen (1976) found no evidence of tide related behaviour in the black goby. Where the tidal range is small, intertidal and subtidal fish show a reduced dependence on the tide as an entrainment of their activity cycles (Gibson, 1969), and the tidal range at Loch Sween is extremely small, maximum 1 meter, due to the presence of a amphidromic centre in the adjacent Sound of Jura (Earle, 1982). All of this evidence points to diel rather than tidal prey behavioural cycles and it is therefore not surprising to discover that tide has no affect on the suite of prey captured. There may be other tidal effects on otter behaviour, such as reduced depth, and changes in the accessibility of dense kelp forests due to strong currents. These will be discussed subsequently in chapter 7.

4.4.6. The influence of habitat and season on the size and mass of prey taken

There was a significant seasonal and habitat effect on the overall size of prey taken, as well as a significant interaction between the two factors. In general the largest prey were taken in the tidal habitat, though not in winter, when the size of prey was fairly constant. The largest prey were taken in the tidal rapids during the summer and this is due to the large proportion of eels being captured then. The mean size of prey in this habitat will also have been raised by the amount of very large lumpsuckers taken. Some caution should be shown in examining mass with respect to season, due to the possibility of seasonal change in the length mass relationship. This may mean that there is differences in mass of prey that have not been shown by this analysis. For example, Sayer et al. (1994) described how several species of fish become quiescent in the winter, including rockling, wrasse, and butterfish, and it is likely that some body mass is lost during this period, hence changing any length weight relationship. This change in prey mass may be another reason why more prey are eaten in the winter, (see above), to compensate for their reduced food value.

4.4.7. Dive Time and Depth

Clear differences emerge in the depth that the prey items are caught at, and these are likely to be a function of prey distribution. Most are found in relatively shallow water, 1 - 3 m, but eels are caught deeper still, though there is much variation in this species and the crabs are caught in the deepest waters, up to 10m. The correlation between dive depth and dive duration is not a surprising one, given that with otters always foraging on the bottom, there will be a longer travel time. The lack of a correlation in this relationship when it is subdivided into species, however demonstrates that it is not only depth that causes variation in dive time, but also the catchability of the prey item. This, and the effect that temperature can have upon it, will be explored in greater detail in chapter 5.

4.4.8. Conclusions

1. The diet of the otters feeding in the waters around the Taynish peninsula broadly reflects that of other studies, being composed almost entirely of bottom dwelling fish, such as butterfish, eels, gobies and rockling, captured when they are least active.
2. While there are advantages and disadvantages to both direct observation and spraint analysis as methods for describing diet, the best overall picture of the otters diet is obtainable through a combination of both.
3. The otters are selective in their choice of prey, where possible they will choose heavier prey items.

4. There is variation in the feeding behaviour both seasonally and spatially, and this is best reflected in actual total frequencies of prey eaten. The largest difference is between habitats, the sandy habitat, habitat 2, being the poorest in terms of numbers of prey caught. More prey are caught in the winter and this is likely to be due to the increased metabolic demands of feeding in colder water.
5. Different prey items tend to be caught at different depths, however variations in dive times are not solely a reflection of depth, suggesting variation in the ease of catching different prey.

CHAPTER 5

THE ROLE OF TEMPERATURE-MEDIATED FLUCTUATIONS IN BIOMASS IN DETERMINING FORAGING SITE CHOICE

CHAPTER 5

5.1. INTRODUCTION

An animals choice of foraging site will be influenced by a number of biotic and abiotic factors, and a knowledge of these factors is essential for the understanding of an animals habitat requirements and for the implementation of practical conservation management strategies. For predators, the key biotic factors will be related to prey, such as prey distribution and size, and for predators foraging in an aquatic environment, many key factors will be related to hydrography, (Wanless *et al.*, 1993). Fluctuations in the population densities of prey species can have profound effects on the choice of foraging site in diving predators, though in contrast to many land predators, it can be very difficult to demonstrate this since animals forage out of view, beneath the water surface and/or far from land based observation points. Radio-telemetry, however, has greatly increased our capacity to study aquatic predators and to link their behaviour to aspects of the distribution and abundance of their prey. For example using radio-tracking, it has been shown that the common guillemot has to travel for greater distances to foraging sites in years when there are low prey abundances (Monaghan *et al.* 1994).

There has been much discussion on the habitat requirements of the Eurasian otter, (Kruuk, 1995), particularly in relation to conservation, (for example Macdonald and Mason 1983, Mason and Macdonald, 1986). Historically the most used technique for determining habitat use by otters has been by surveys of the occurrence of spraints.

Such surveys have involved little else but the counting of the numbers of otter faeces found in different areas. While such information can be of value in determining that an otter has been in that particular area, it is difficult to extrapolate any further information from this. That the otter spraints are likely to serve a communicative, as well as excretive, function has been discussed at some length elsewhere (for example Erlinge 1968, Mason and Macdonald 1986, Kruuk 1992 and 1995). Kruuk (1992) hypothesised that sprainting is used as a signal to conspecifics of the recent usage of a resource, such as a feeding patch. As part of the evidence for this Kruuk cites the scarcity of spraints during seasonal abundances of prey, and their copiousness during periods of low prey availability. He further suggests that the use of other resources, such as fresh water pools for coastal feeding otters, may similarly be signalled by sprainting since such areas are frequently sprainting sites. However during dry summers, when such pools are frequently restricted, we would expect an increase in sprainting behaviour, due to the diminishing resource, but in fact there tends to be less sprainting (Conroy and French 1987, *pers. obs.*). This does not detract from the overall body of evidence of there being a communicative function of sprainting, which creates difficulties in using it to gauge relative otter numbers. Particularly, there are large seasonal variations in numbers of spraints that can be found. (Conroy and French 1987, Macdonald and Mason 1987), and this is partly explained by Kruuk (1995) in that he has observed otters sprainting more in the water in summer. Such large fluctuations will produce inaccuracies in any survey of otter distribution carried out via spraint counts. It is therefore likely that much data on habitat requirements may be flawed due to the biases in the data based purely around the distribution of spraints (Kruuk *et al.*, 1986, Mason and Macdonald, 1987, Kruuk and Conroy, 1987).

As mentioned above, a far more accurate method for determining the range and habitat use of an animal that is difficult to observe directly is radio telemetry. A radio-transmitter is attached to, or implanted in, an animal and the signal from this allows the position of the animal to be determined from a distance by one or more receivers (Amlaner and Macdonald 1980). Radio-tracking has more recently given valuable data on habitat utilisation by freshwater otters (for example, Kruuk *et al.* 1993, Durbin 1998), but for coastal otters this has only been thoroughly carried out in Portugal, (Beja 1995), and all studies are somewhat hampered by small sample sizes, largely due to the difficulties of catching the otter and implanting the transmitter, (Melquist and Hornocker, 1979). Due to the important thermo-regulatory function of the otters pelt, and the amount of time spent grooming it, particularly in marine habitats, (Nolet and Kruuk, 1989) it is vital that the radio transmitter is implanted intraperitoneally (Kruuk 1995). Some radio-tracking was carried out with coastal otters in Shetland before this limitation was described, with the transmitter attached to the fur by a collar or harness, but the behaviour of the animal was modified to such an extent that the results must have been biased (Kruuk 1995). The need to implant the transmitter of course makes the whole radio-tracking procedure much more invasive.

In freshwater, radio-telemetry studies (Kruuk *et al.* 1993, Durbin 1998) have shown that narrow, gravel rich, sections of water are preferred by foraging otters, though again conclusions are limited by small sample sizes. These radio-telemetry studies have cast doubt on the traditionally held beliefs, derived from spraint surveys, that certain habitat features, such as riparian vegetation, are important for otter distribution (Durbin 1998).

For otters foraging in a marine habitat, perhaps the most crucial environmental constraint is the availability of fresh water, (Kruuk and Moorhouse, 1991). This resource is necessary for the washing of salt, which compromises the thermo-insulatory function of the pelt (Kruuk and Balharry, 1990), out of the animals fur. This requirement for fresh water is reflected in the otters preference for coastal habitats which are gently sloping and poorly drained, as opposed to cliffs or agricultural areas. This explains to some extent why otters are relatively common on the west coast of Scotland, but not the east, (Green and Green 1987, Kruuk 1995). Underlying geology, particularly the permeability of the rock will also affect this, (Kruuk 1995).

In Shetland, Kruuk and Moorhouse (1990 and 1991) hypothesised that, as well as access to fresh water, it was important for an otter to have access to different habitats within their home range in order to be able to exploit seasonal variations in the prey abundance of different habitats. This was particularly associated with winter peaks in gadoid predation, on exposed coasts, and summer peaks in eelpout predation, on sheltered coasts. It has been argued (Kruuk and Moorhouse 1990 and Kruuk 1995) that this explains the social grouping of the otters in such areas, where several females share a group range, thereby allowing exploitation of habitats that fluctuate seasonally in quality.

There are a number of advantages and disadvantages associated with both direct observation and radio-telemetry as means of obtaining information about otter usage of habitats. Direct observation has the considerable advantage that there is not the need to capture the animal, which can take a considerable amount of time with, and perform invasive surgery upon it. With Eurasian otter populations considered vulnerable, there are strong ethical as well as logistic arguments against this. Furthermore, direct observation allows for data to be obtained from more individuals than can be captured and successfully implanted with functional transmitters. Also observation allows you to see precisely what the animal is doing, which frequently is not possible with radio-tracking. Conversely radio-telemetry allows for the precise identification of individuals and, in the case of otters, potentially creates the opportunity for more information on terrestrial behaviour to be collected. Finally radio-telemetry would allow data on the possibility of coastal otters foraging nocturnally, as may occur in the winter (chapter 7). The ideal study would be one in which both methods were used, but for the purposes of this study, it was decided that direct observation would allow a good quality and quantity of data to be collected without the logistical and ethical difficulties of radio-telemetry.

Our study site around the Taynish peninsula encompassed different marine habitats. On the other hand, fresh water pools and holts were abundant and uniformly distributed on the land associated with these, due to a degree of homogeneity of the coastal terrestrial habitats. Therefore it gave the opportunity for us to examine variations in the choice of foraging site, without confounding terrestrial variables.

Our explicit hypothesis was that habitat selection would be governed by available prey biomass, and this in turn would be affected by environmental variables, particularly water temperature. From chapter 2 we have already determined that there is an interaction between available biomass and season, and this may further influence foraging habitat choice by otters.

We therefore set out to test the hypothesis that otters forage preferentially in areas where there is the highest available biomass for any particular water temperature by examining the following questions:

1. Whether the available biomass of the three habitats fluctuated with water temperature, and whether this relationship was the same for all three habitats.
2. Whether the otters followed patterns in biomass in their choice of foraging habitats, and if not what other factors could have influenced this.

5.2. METHODS

5.2.1. Temperature mediated fluctuations in biomass

The fish-trapping regime (chapter 2) provided data on the interaction between biomass and mean monthly water temperatures. Biomass was measured as the total monthly weight of catches, excluding crustaceans, in the fish traps in each of the three habitats, rocky, sandy and tidal. The mass of crustaceans was excluded from this measure for two reasons; firstly, the large numbers of crustaceans, particularly shore crabs did not reflect their importance in the otter diet (chapters 2 and 4), and secondly a large part of the body mass of crustaceans compromises the carapace, which the otters do not eat (Kruuk 1995). Otters tend to only eat crabs, because of the high costs associated with them when they are inexperienced, (Watt 1993), with the exception of edible crabs, which have a high food value, see chapter 9. The mean monthly water temperatures of the three habitats were calculated as the arithmetic mean of the temperatures measured at 2m depth during all watches carried out at each habitat during a particular month. In temperate shallow waters there is homogeneity of temperature throughout the water column (Clark 1987). The temperatures were recorded on a Salinity, Conductance and Temperature (S.C.T.) meter after each watch was completed. The relationship between biomass and temperature was calculated for each habitat using Analysis of Covariance, (Sokal and Rohlf, 1995) on the SPSS.7 statistical computing package, with biomass as dependant variable, habitat as the factor, and water temperature as the covariate.

5.2.3. Seasonal fluctuations in habitat utilisation by otters

For 15 months, July 1995 - September 1996, otter watches were carried out along the coastline of the Taynish peninsula. For the purposes of this the three key habitats of the area were subdivided into observable segments, where the whole coastline was observable from a single vantage point allowing all otter activity within each area to be recorded, and each area was observed for 5 consecutive hours every month. These sites and recording sessions ensured that all areas were equally sampled. The timing of the watches was standardised to coincide with an early morning receding and low tide to eliminate the possibility of biases created by time of day or state of tide, which may influence the amount of otter activity (Kruuk and Moorhouse 1991, chapter 6). During the watch any otter activity was recorded and the location marked on maps of the observation area. The timing of dives was recorded, and foraging use was recorded as the overall time an otter spent underwater during the observation session. The overall time an otter was in view was also recorded, as a measure of activity, as was the proportion of the time the otter was in view that it was underwater. If two otters were present detailed observations would be made of one and a record of the others general behaviour, that is in the water or on land, made. The time the second otter was in the water was then assigned a value of underwater time from the mean proportion of time that was spent underwater obtained from observations of otters at a similar time of day and tide state, and time of year. In practice this occurred very few times. These measures of activity were then corrected for the distance of coastline observed for that particular watch, by dividing the amount of time underwater by the length in km of the shoreline. Studies by Kruuk and Moorhouse (1991) in Shetland demonstrated that length of coast is the most consistent measure of the range of marine foraging otters, (as opposed to quantity of water or overall area). The watches for each of the habitats were aggregated, and analysed using an ANOVA General Linear Model, including foraging usage per km as dependant variable, biomass, water temperature and mean prey catch per minute as covariants and habitat as the factor. The results were compared with the predictions obtained from the relationships between biomass and water temperature, both in terms of water temperature, and time of year.

5.3. RESULTS

5.3.1. Temperature mediated fluctuations in biomass

An Analysis of Covariance with temperature correlated against biomass showed that for each habitat there was a correlation between biomass of catch and water temperature. The relationship was different for each habitat and there was thus a significant interaction between habitat and temperature, table 5.1. and figure 5.1. The interaction largely arises because, unlike the other two habitats, there is no increase in biomass with temperature in the rocky habitat; further the increase in biomass with temperature was much faster in the tidal than in the sandy habitat. As can be seen in figure 5.1., at temperatures below 10°C the highest biomass was in habitat 1, the rocky habitat, whereas at temperatures above 10°C the highest biomass was in habitat 3, the tidal habitat. At no point was the biomass in habitat 2 more than that in the other two habitats.

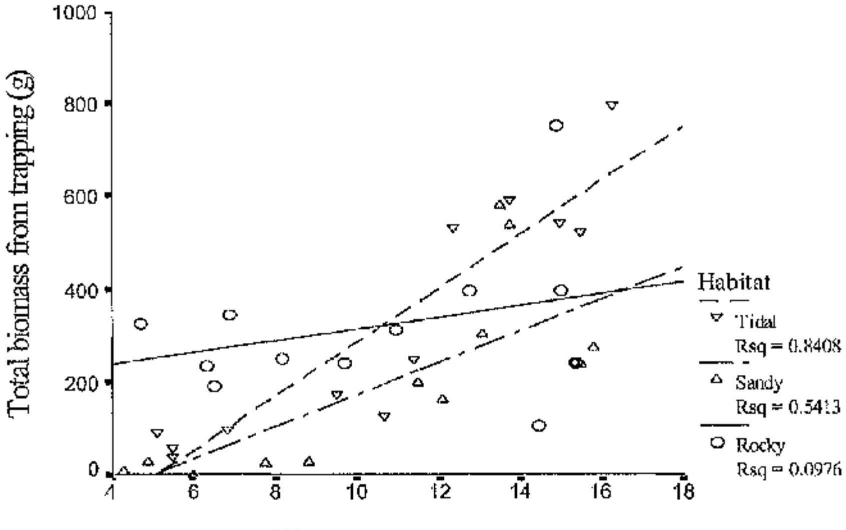


Figure 5.1. The total monthly biomass from fish traps set in the three habitats, in relation to mean water temperature

	D.F.	F	Significance
Habitat	2, 34	4.68	<0.05
Water temperature	1, 34	6.63	<0.001
Interaction term	2, 34	4.88	<0.05
Model	5, 34	10.80	<0.001

Table 5.1. Fluctuations in available biomass, as determined from stationary trapping, in relation to mean monthly water temperature in three habitats surrounding the Taynish peninsula

From this result we would predict that, if available biomass is the main determinant of otter usage of a foraging site, then otters would forage mostly in habitat 1, (the rocky habitat) when temperatures were below 10.7°C and switch to a preference for habitat 3, (the tidal habitat) in temperatures above 10.7°C. Furthermore the data would predict that at no point would habitat 2, the sandy habitat, be preferred.

5.3.2. Seasonal variation in habitat utilisation by otters

The three measures of otter activity produced slightly different results.

1. The mean overall time an otter was observed per 5 hour bout, corrected for coast length, differed between habitats, (ANCOVA, d.f. = 2, 33, F = 6.434 $p < 0.01$) (figure 5.2) though none of the covariates, that is available biomass, water temperature or catch rate were correlated with this when included in the model, nor were there significant interactive terms.
2. Mean actual foraging time, as measured by time underwater corrected for length of coast, also differed between habitats, (ANCOVA, d.f. = 2, 33, F = 3.94, $p<0.05$), figure 5.3., and correlated positively with biomass, (ANCOVA, d.f. = 1, 34, F = 3.62, $p < 0.05$), figure 5.4., with no significant interactive term. The correlation with biomass, while statistically significant, was however a very weak one

(adjusted $r^2 = 0.04$). There was no significant relationship with the other two covariates, nor were there any significant interactive terms.

3. The proportion of the time an otter was in view that it was underwater showed no variation with habitat and was correlated with none of the covariates.

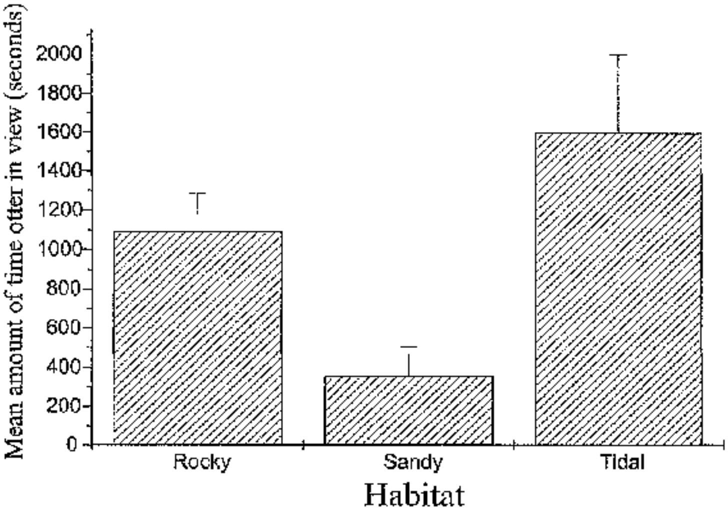


Figure 5.2. The mean amount of time per five-hour watch, ± standard error, that an otter was in view, in the three habitats, over the whole study.

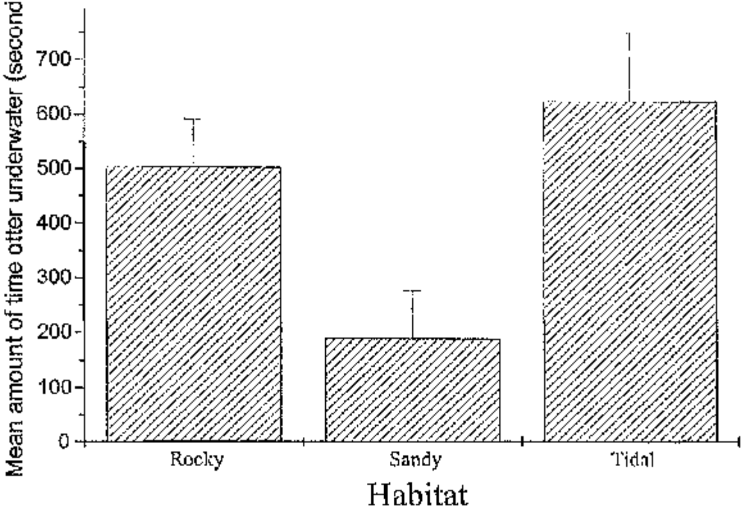


Figure 5.3. The mean amount of time per five hour watch, ± standard error, that an otter was underwater, in the three habitats

Both measures 1 and 2 indicated that most activity occurred in habitat 3, the tidal rapids. In order to determine whether any underlying pattern of foraging site choice corresponded with our predictions from biomass, we split the observations into two groups, to correspond to the temperature ranges of the biomass predictions, that is less than 10.7°C and greater than 10.7°C, figure 5.5., and examined the relative amount of foraging, using the second measure of this, in the three habitats. Our prediction stated that at the lower temperature range, the otters would prefer to forage in the rocky habitat, and in the higher range they would prefer to forage in the tidal habitat. In other words we would have predicted an interaction between habitat and temperature range. Analysis using a two–way ANOVA revealed that there was no significant interaction between these two factors (d.f. = 2, 46, $F = 0.14$). Temperature range also had no effect on amount of foraging, (d.f. = 1, 46, $\mathbf{F} = 0.02$), although there were differences between the habitats, (d.f. = 2, 46, $f = 4.02$, $p < 0.01$). As can be seen from figure 5.5., there was no difference between the patterns of foraging site choice in the two temperature ranges. However the data does fit our predictions in that the sandy habitat is foraged least by the otters.

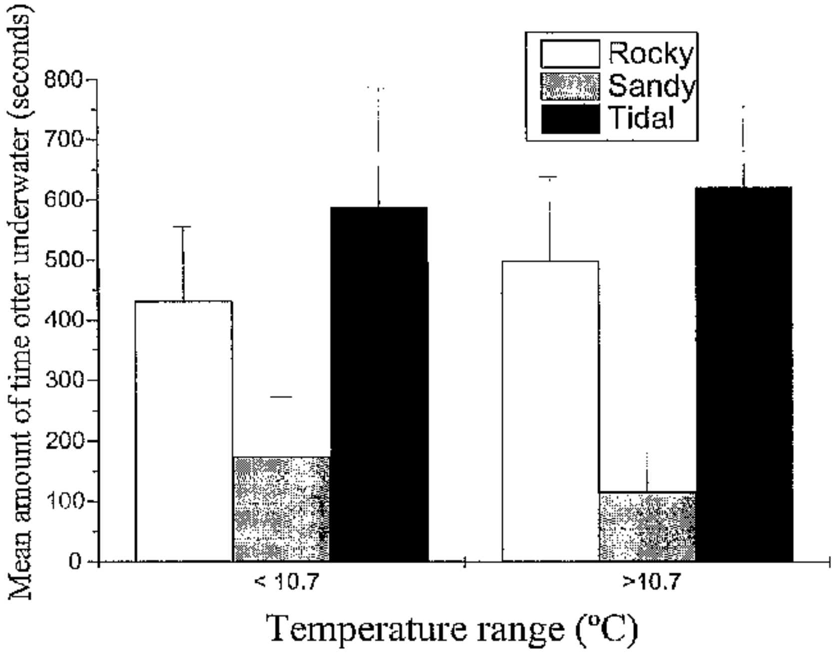


Figure 5.5. The mean, ± standard error, amount of time per five-hour watch that an otter was underwater, in the three habitats, in two temperature ranges

In order to examine further the data for variations in this overall pattern of foraging site choice, we subdivided the data into months, figure 5.6., and analysed it by using a two-way ANOVA., with month and habitat as the two factors, and again using underwater time corrected for length of coastline as the dependant variable. There was no significant variation in the amount of foraging observed in the different months (d.f. = 11, 24, F = 1.08), nor did this interact with habitat (d.f. = 21, 24, F = 1.19). While there were no significant interactions between month and habitat, there were deviations from the overall pattern of the most otter usage being in habitat 3. As shown in figure 5.6. these are in the months of September, October and November, when there was more activity in Habitat 1, and February and August, when there was more activity in habitat 2.

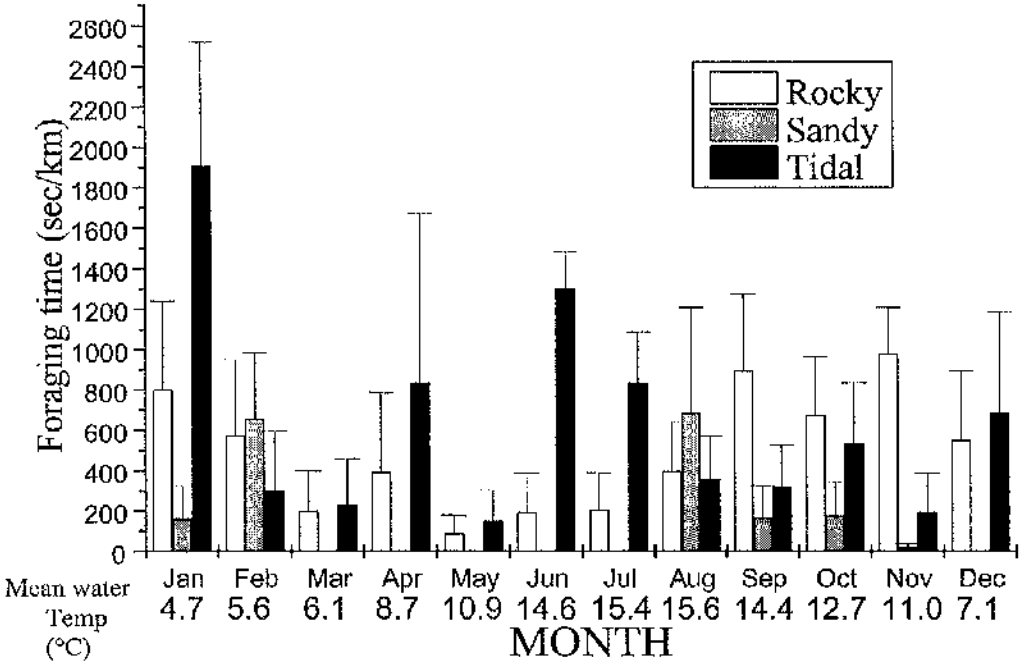


Figure 5.6. The mean time, ± standard error, that an otter was underwater, in the different habitats, throughout the year.

5.4. DISCUSSION

Densities of prey can have profound effects on the foraging site choice of diving predators (Monaghan *et al.* 1994). In this chapter we examined the effect of temperature driven fluctuations in prey density on foraging site choice in the Eurasian otter. Our results showed that while there were some correspondences between observations on site choice around the Taynish peninsula and predictions based solely on biomass, this did not fully account for the distribution patterns

5.4.1. Fluctuations in biomass

Re-examination of the fish trapping data (chapter 2) in the context of water temperature demonstrated not only a positive correlation between water temperature and total monthly biomass, but that this relationship differed significantly between the three different habitats (Figure 5.1). From these relationships it was possible to predict which habitat the otters would prefer to forage in, over the range of temperatures described. Before examining this relationship there are a few points that should be clarified.

As discussed in chapter 2, the traps used in the fish trapping regime depend on the behaviour of the fish for catches, (see also Kruuk *et al.* 1988), and as described in chapter 6 and elsewhere (for example Fraser *et al.* 1993) the behaviour of the fish varies with water temperature, with a reduction in activity with depressed water temperatures. A consequence of this may be that some or all of the effect of water temperature may be due to changes in the fish behaviour rather than in actual population densities. Following Kruuk *et al.*, (1988), in chapter 2 we compared the relative ranking of prey catches in the traps in different months, with the assumption that behavioural changes would affect all species in broadly the same manner. Therefore if the ranks had changed seasonally, this could be taken as a confirmation that temperature mediated changes in fish behaviour were not the determinant of change in the catches of the traps. While our results, like those of Kruuk *et al.* (1988), confirmed this, they do not altogether eliminate the possibility that temperature does have an influence on catches. Furthermore it is not entirely clear what this influence would be, since the reduced activity at lower temperatures will both reduce the likelihood of a fish entering the trap, it will also reduce its ability to escape. Our data show that there are differences between habitats in the relationship between water temperature and catch, and this further reinforces the belief that catches from fish traps are not simply a function of temperature mediated behavioural changes to the fish.

5.4.2. Measures of usage

In our description of the otters' habitat use we used two measures, the overall time an otter was in view and the total underwater time, and as third measure we determined the proportion of the total time that an otter was underwater. There was little difference between the first two, although the second, underwater time, produced a significant but very weak correlation with biomass, while the first did not. Both measures are likely to have different useful applications. The first measure, the whole period an otter is in view, includes resting and recovery periods as well as travelling time, and as is the more useful in terms of descriptions of overall usage of an area by otters. As such it is reasonable to expect that biomass would not have an effect. The second measure, the total amount of time an otter is underwater, is related entirely to foraging behaviour, and so while its use is perhaps more restricted, it will conversely be more precise. For this reason, and because it is foraging behaviour that this study is particularly concerned with, it is this measure that we shall use subsequently.

The proportion of total time that an otter was underwater was measured to examine if there were differences in how an otter allocated time in the habitats, or in different water temperatures. That there were no differences or relationships suggests either that the otters allocate time to separate activities in much the same way in any conditions or that the differences we were observing were too subtle to cause any detectable change.

5.4.3. Habitat choice

From the data obtained from fish trapping and water temperature we predicted the habitat preferences of foraging otters in relation to biomass and water temperature. While overall the otters foraged preferentially in the tidal habitat, and this was the habitat with the overall highest biomass, the actual data of changing use of habitats in relation to biomass only matched the predictions to a limited extent. This suggests that available biomass does plays a role in foraging habitat choice, but that other factors are also important. Some of these possibilities will now be discussed.

5.4.3.1. Prey choice

For the purpose of our predictions we assumed that the available mass of prey, in grams, would be the key factor in habitat choice. What this does not take into account is differences in prey value, particularly calorific value and lipid content, and variations in costs of obtaining and handling certain prey items. Calorific analysis by other workers, (Norman 1963, and Nolet and Kruuk 1989) gave the highest calorific values of the commonest prey types to be butterfish, (5.01 kj/g, Nolet and Kruuk 1989) and eels, (6.08 kj/g, Norman 1963). All other factors being equal, we would predict that the otter would choose such prey over lower value prey. Our data from observations of dive times of different prey (chapter 5) showed that capture times of the commonest piscine prey are broadly similar, and, although eels have the second longest capture time, any such differences are small.

From the observations of otters feeding (Chapter 4), for much of the year, the most important prey types are eels and butterfish. Furthermore the fish trapping data clearly shows that more eels are caught in habitat 3 than habitat 1, and while the accuracy of stationary trapping as a method of assessing butterfish populations is questionable, all the catches of butterfish were in habitat 3. This is strongly suggestive that at least some of the deviations from our predictions are associated with the otters choosing more profitable prey, using calorific value rather than simple mass as an important criterion of habitat choice.

However, the data from fish trapping also shows that the most eels are caught in the traps in habitat 2, and so while this may well explain why most otter foraging is carried out in this habitat it in August, there is no foraging carried out here in the other summer months. Therefore we must conclude that factors other than prey mass and quality (as expressed by calorific value) are influencing choice of habitat. It may be that rather than a single prey species determining site fidelity, it is also the range of species available that is important, and while there are high catches of eels associated with the summer months in habitat 2, there are few other prey of value, whereas both habitats 1 and 3 have a range of species available. There may also be other features of the habitat that influence the otters choice, such as algal cover, and this will be discussed subsequently.

A further deviation from our prediction occurs in February, when again the greatest amount of activity occurs in habitat 2, the sandy habitat. Unfortunately during observations in this month it was impossible to identify the prey species taken in habitat 2, largely because they were too small or visibility was too poor. Other observations from this time suggest that the most important prey are 15-spine sticklebacks and to a lesser extent gadoids. Fish trapping shows the largest number of 15-spine sticklebacks were caught in February in habitat 2, so it may be that this species is dominant in the choice of foraging site at this time. However, the 15-spine stickleback is a poor quality prey species for otters, the lowest of all the common prey in terms of mean mass of those caught by otters, (4.04g ± 0.31, chapter 4), while the gadoids are of reasonably good quality, both in terms of mass and calorific value (rockling; 40.73g ± 4.62, 3.83 kj/g, non-rockling gadoids 34.98g ± 4.65, 4.29 kj/g, mean masses from chapter 4, calorific contents from Nolet and Kruuk, 1989). Therefore it is not clear why the otter would show a preference for this species. In general the prey quality available to otters is reduced in winter, (for example Kruuk and Moorhouse 1990) and it may be quantity of sticklebacks rather than quality that is the important factor, but this is not clear from any of the data.

5.4.3.2. Algal cover

Dense, canopy forming algal species, particularly *Laminaria* spp., are important for coastal foraging otters because their prey species will use them for cover when they are resting (Kruuk 1995), the period in which the otters will forage for them the most. Of the three habitats, only 1 and 3 had these species of algae present in large numbers (Earll 1984, Lumb, 1984), whereas habitat 2 is more associated with *Zostera* beds (*Ibid.*). These latter beds only provide dense cover for a short period in the summer, coinciding with the period in August of marked otter usage of the habitat. Both habitats 1 and 3 possess large areas of *Laminaria* forest, but they are of a slightly different nature. In habitat 1 there is typically a broken rock and boulder substrate, dominated almost entirely by *Laminaria saccharina* and *L. hyperborea*,. In habitat 3, there is also a similar substrate with *Laminaria* growths, but they are interspersed with Maerl beds, gravel and muddy sediments and there are also areas of pebble substrates, dominated by encrusting calcareous algae and *Ophiocomina nigra* (a species of brittlestar), (Lumb 1984). Kruuk *et al.* (1990) examined a number of microhabitats along a Shetland coast, which differed significantly in their usage by foraging otters. Within the range of these there was little difference in the amount of prey caught and its size, nor was there a difference in their proximity to other resources such as resting sites and freshwater. Where there was a perceptible difference was in the amount of openings in the canopy forming algae species. It was hypothesised that these assisted the otters in foraging by allowing them to get straight down to the stems and holdfasts and move horizontally, rather than having to work their way through the dense canopy of the fronds (Kruuk 1995). The nature of the varied substrate in habitat 3, and the resultant patterns of vegetation, may therefore be preferable to a forging otter rather than the more dense and uniform pattern in habitat 1, creating a further influence on the otters choice of foraging habitat.

5.4.3.3. Availability of depth

Another aspect of the habitats that will be a factor in the choice of foraging site for otters is the availability of deeper water in which to forage. While otters generally forage in water less than 3m deep, (Nolet *et al.* 1993) in warmer water they will forage deeper (chapters 8 and 9). The only habitat around the Taynish peninsula which has depths greater than 5m is the rocky habitat, and this may account for the use of this habitat in September and October, (figure 5.6.) in contrast to our predictions based simply on biomass.

5.4.2.3. Species diversity

In chapter 2 we calculated a Shannon-Wiener species diversity index for the different habitats. This demonstrated that the highest species diversity was in the tidal habitat. While it would be false to simply say this was the reason for greater overall otter usage of the area, it is likely that the two factors are linked. It may be profitable for an otter to forage in an area where it does not need to be reliant on a single important prey species, rather for it to have a range of species to choose from. The higher species diversity, and the higher biomass, are likely to reflect the overall quality of the tidal habitat, a fact noted by other studies on the area (see review in Lumb 1986) and in the habitat's listing as a Site of Special Scientific Interest. Overall therefore it is likely that the otters show a preference for this habitat because of its general quality, in terms of biomass, algal cover and species diversity

5.4.2.3. Terrestrial variables.

Terrestrial variables, such as access to fresh water, ease of entry and exit to sea, bolt holes, are all likely to be important in determining habitat choice. However in this study there was considerable homogeneity of the terrestrial environment close to the shore , so such factors can be eliminated from our discussion.

5.4.3. Conclusions

1. Otters feeding around the Taynish peninsula show an overall preference for one habitat, the tidal habitat, however there are monthly variations in this
2. The preference for this habitat is likely to be due to overall habitat quality, as reflected by biomass, algal cover and species diversity.
3. There is a positive relationship between biomass and water temperature but it is different in each of the habitats. The variations in habitat use can be partly linked to the fluctuating biomass of the them, though this does not completely account for the changes

4. Other possible causes of these changes include a preference for certain prey, eels and butterfish, due to calorific content, a preference for foraging in habitats with broken algal cover, and seasonal exploitation of deeper water.

CHAPTER 6.

THE EFFECT OF TEMPERATURE REDUCTION ON THE ACTIVITY AND ESCAPE RESPONSE OF PREY OF THE EURASIAN OTTER

CHAPTER 6

6.1. INTRODUCTION

Foraging behaviour, in any predator, will to a large extent be influenced by the behaviour of its prey (Sih 1993), and variations in the preys tendency to move will be a major factor in determining the predators attack behaviour (Sih 1993). Ectothermic animals, such as fish, are subject to temperature as a major environmental influence on their behaviour (Fraser *et al.*, 1993), and so the behaviour of their predators is also likely to be affected by it. Cold water temperatures are frequently associated with enforced inactivity in crevices or under rocks in marine fish (Sayer *et al.*, 1994), though this has been mistaken for downshore migration in the past (for example with wrasse, Fielder, 1964, and butterfish, Watt, 1995). During these periods of torpor the fish are likely to be exposed to an increased predation rate by predators such as the Eurasian otter.

On the west coast of Scotland the diet of the otter is dominated by butterfish, (Mason and Macdonald 1980, Watt 1995, and see also chapter 4), and this is one of the species known to enter a state of torpor during cold water and retreat into crevices, (Sayer *et al.* 1994). While it is sensitive to changes in temperature of as little as 0.03°C (Gibson 1969) it seems to be more tolerant of low temperatures than other infralittoral species. For example Jones and Clark (quoted in Gibson 1969) described a large "winter kill" of marine fish during an extremely cold winter. Many species became locally extinct; others took several years for their populations to recover;

however butterfish numbers were unaffected. Despite this there have been no studies examining directly the effect of temperature on butterfish behaviour.

There are five species of wrasse that are associated with the Scottish coast, and they all inhabit inshore waters amongst rock and algal cover (Darwall et al. 1992). Several of these species, such as goldsinny, corkwing and rockcook, are known to show temperature mediated behavioural change, as well as going into torpor at low temperatures (Sayer *et al.*, 1994), their growth and feeding intensity are temperature related (Darwall *et al.*, 1992). Wrasse are important components of the otters diet in Portugal (Beja 1995), and have also been recorded as prey items in Ireland (Murphy and Fairley 1985) and Scotland (chapter 4)

A number of species of gobies inhabit the coastal waters of the British Isles (Wheeler 1978), and some of these, notably the black and rock gobies, can be a relatively important food source to the otter (chapter 4). While there have been some studies examining the influence of light (Hesthagen 1976) and hydrostatic pressure (Northcott 1991) on the activity of black gobies, and a number of studies on the behavioural ecology of gobies (for example Ota *et al.* 1996), including studies on behaviour mediated predation risk (Magnhagen, 1993), there has been no work to date describing any temperature related effects on activity and consequent predation risks.

There have been a number of suggestions that water temperatures have a profound effect on the foraging behaviour of otters (Kruuk 1995) with recent work demonstrating that there are increased metabolic costs associated with foraging in lower water temperatures (Kruuk *et al.* 1994). Kruuk and Carss (1996) modelled these metabolic costs in terms of the energetic input, expressed as fishing effort per day, required to offset the metabolic costs of foraging at different water temperatures. Their model predicted that in colder temperatures it would be necessary for an otter to forage for longer in order to meet its metabolic requirements. These predictions are, however, based on a constant potential capture rate of prey, though the model does allow for some variations in its interpretation. The otters feeding at Taynish (chapter 4) and elsewhere on the Scottish coast (Watt 1995), catch more profitable prey in the winter particularly the gadoids, such as rockling and cod, and so while there may be increased foraging costs in low water temperatures, due to increased energy requirements for thermoregulation, there may also be increased benefits related to changes in prey availability. This shall be examined more closely in chapter 8. Furthermore if the prey show temperature-mediated fluctuations in behaviour, as described above, their vulnerability to predation may be increased in colder water temperatures. This would be a further benefit to offset the increased costs incurred by a predator foraging at low water temperatures.

We therefore set out to test the hypothesis that temperature mediated changes in the behaviour of the prey affected the foraging behaviour of the predator. In order to do so we determined:

1. If there was a reduction in activity in some of the prey species of the otter and if this reduced activity level was reflected in a consequent reduction in escape response.

2. Whether any fluctuations in these behaviours resulted in a change in the foraging behaviour of otters in the wild, in terms of the capture time required for each of these prey items.

6.2. METHODS

6.2.1. General Activity Level

Live specimens of butterfish and corkwing wrasse were obtained by trawling along a five-mile stretch of coastal water at Dunstaffnage, Oban, Argyll. They were transported to Glasgow and placed in a large storage tank, which was kept aerated, and at a constant temperature of 11°C. The tank was filled with sand, gravel, rocks and seaweed, as well as plastic tunnels, in order to closely mimic the natural habitat. A constant phototperiod of 12 hours was given each day, from 8 a.m. to 8 p.m. The animals were allowed to acclimatise to captive conditions for a minimum of five weeks.

Three observation tanks were set up, each was 90 cm long, 30cm wide and 45 cm deep, the bottom covered with sand and broken shells, with larger stones on top. There was an area of seaweed, *Fucus serratus* and *F. vesiculosis*, and tunnels and crevices were created to allow for hiding places. Each of the observation tanks was kept in a separate room of different ambient temperature, and the water in the tank was thereby kept at three temperatures, 5°, 10° and 15° C. The water was not allowed to fluctuate more than 0.5°. Continuous aeration and water circulation was applied.

For each experiment, two individuals of the same species were removed from the holding tank and placed in an observation tank. Following Stott (1970) who described an excess of activity in perch, *Perca fluvatilis*, immediately after handling, and to allow acclimatisation, the fish were left for 48hrs. Activity was recorded as an instantaneous time sampling procedure (Boniface 1994) with a recording of each animal scored as either active or stationary. This was repeated every two minutes, giving a total of ten scores for each animal. This was then repeated again for a further five bouts, with a twenty minute recording period every hour for six hours, giving a total of sixty scores for each animal at each temperature. The two animals were then removed and a further two conspecifics were put in the tank, and the same procedure followed. The procedure was followed for six fish of both species at three different temperatures. The same fish were used for all experimental temperatures, so a 48-hour period of acclimatisation was allowed before each experiment. Feeding regimes were not varied at any point.

The results were expressed as the proportion of the sixty scores that the fish was in motion, and then arcsine transformed to allow for parametric analysis. To examine the data for any relationship between activity level and water temperature, analysis of covariance (Sokal and Rohlf 1995) was used, with activity as the dependent variable, individual fish as the factor, and water temperature as the covariant. This allowed such any relationship between activity and temperature to be examined while taking into consideration any individual variations in response.

6.2.2. Escape Response

Corkwing wrasse and butterfish were collected from Dunstaffnage bay by beam trawling and kept as outlined above for general activity studies. Rock gobies were obtained from the stationary trap regime (See Chapter 2) and kept in the same holding tanks as the butterfish and wrasse. An experimental tank was built, measuring 124 x 30 x 24 cm, containing a transparent plastic cylinder of 18 cm diameter and 56 cm long. The cylinder was marked at 1 cm intervals along its full length. A Panasonic video recorder was focused upon the cylinder. Water temperature within the experimental tank was modified following Harper and Blake (1990) by adding plastic bags filled with either hot or frozen water, and leaving until the temperature stabilised. This was carried out as it allowed more variations in temperature than the method described above for general activity studies. Temperature was constantly monitored to prevent fluctuations of more than 0.5° C. An acclimatisation tank was also built containing rocks and gravel as above, and this was maintained at the same temperature as the experimental tank.

The animals were allowed to acclimatise for 24 hours in the acclimatisation tank before each experiment, and then they were placed in the experimental tank and left undisturbed for one hour. With the video recorder running, an escape response, that is swimming down the cylinder in the opposite direction from a stimulus, was provoked. Following Eaton and Emberley (1991) the stimulus was a prod to the head region with a glass rod. The procedure was repeated five times for each individual, which was then removed, weighed and placed in the holding tank. This procedure was carried out for seven rock gobies, eight wrasse and ten butterfish, at five different temperatures, 16°, 11°, 8°, 6° and 4°C.

From the video recordings of the experiments, the mean speed exerted by each animal for the duration of each escape response, and the acceleration from the start to the end of the cylinder during each response was calculated. The relationship between water temperature and speed and acceleration of escape response was calculated by Analysis of Covariance (Sokal and Rohlf 1995), with activity or speed as the dependant variable, individual and sequence of response as the factors, and the water temperature as the covariant. Analysis by this method allowed consideration to be made of individual variations in response, and for any effects of habituation or fatigue.

6.2.3. Otter Behaviour

During observations of otters feeding (see chapter 4), the duration of successful dives were measured. Where the prey was identifiable this was recorded. The temperature of the water in which any feeding was observed was measured at 2 m depth using a CTS meter. The duration of dives, for each prey type, were then examined for any relationship with water temperature, using correlation analysis.

6.3. RESULTS

6.3.1. General Activity Levels

For both the two fish species tested, that is butterfish and corkwing wrasse, there was a highly significant relationship between activity and water temperature, with activity decreasing as temperature decreases, table 6.1. There was no individual variation in activity, nor was there an interaction between individuals and activity at different temperatures.

Species		D.F.	F	significance
Butterfish	Individual	5,18	0.26	N.S.
	Temperature	1,18	80.83	<0.001
	Interaction	5,18	0.54	N.S.
Wrasse	Individual	5,18	0.63	N.S.
	Temperature	1,18	10.05	<0.001
	Interaction	5,18	0.66	N.S.

Table 6.1. The relationship between water temperature and activity in butterfish and corkwing wrasse

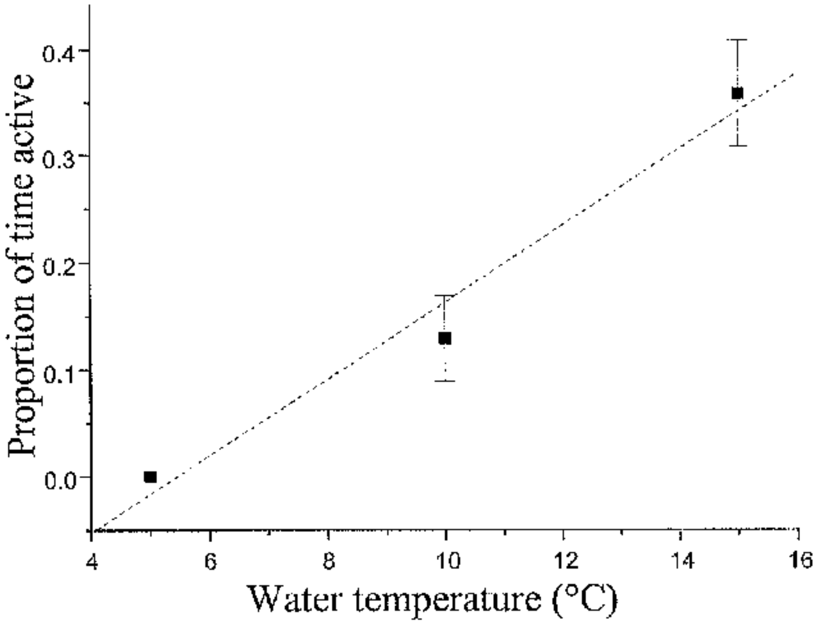


Figure 6.1. The relationship between water temperature and the proportion of time that a butterfish is active

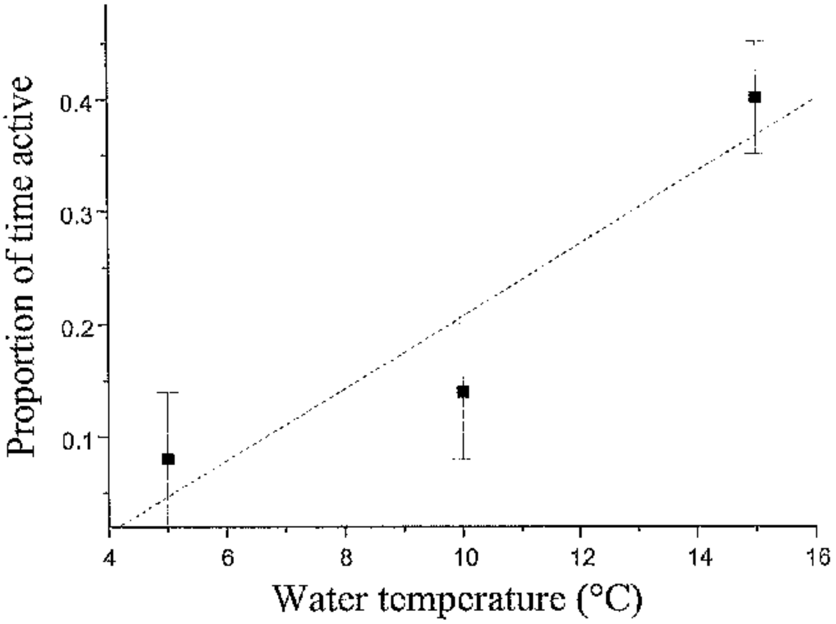


Figure 6.2. The relationship between water temperature and the proportion of time that a corkwing wrasse is active

6.3.2. Escape Response

For all 3 species there was a highly significant positive relationship between both the speed and the acceleration of the escape response and water temperature, see table 6.2. In all species this relationship was stronger for speed than acceleration. With butterfish there was no significant individual variation, nor was there a habituation or fatigue effect, expressed as the number of previous times the escape response had been elicited. There was however significant individual variation in the speed of the response in wrasse, though this did not interact significantly with temperature; that is the variation in speed attributable to water temperature was the same for all individuals, though actual speeds were different. There was no significant habituation effect in this species, nor did this interact with temperature. Rock gobies did not show individual differences in speed or acceleration, however there was a significant interaction between the individuals speed and water temperature, that is the relationship between water temperature and the speed of escape response was different for each individual. Again there was no habituation effect or interaction term.

			Speed			**Acceleration**	
Species		D.F.	f	sig.	D.F.	f	sig.
Butterfish	individual	9,250	1.00	N.S.	9,250	0.88	N.S.
	order	4,250	2.24	N.S.	4,250	1.51	N.S.
	temp.	1,250	46.37	<0.001	1,250	22.08	<0.001
	int. 1	9,250	0.75	N.S.	9,250	0.71	N.S.
	int. 2	4,250	1.76	N.S.	4,250	1.76	N.S.
			$r^2 = 0.27$			**$r^2 = 0.25$**	
Wrasse	individual	8,225	2.18	<0.05	8,225	1.42	N.S.
	order	4,225	1.13	N.S.	4,225	0.51	N.S.
	temp.	1,225	83.92	<0.001	1,225	46.50	<0.001
	int. 1	8,225	1.96	N.S.	8,225	1.12	N.S.
	int. 2	4,225	1.67	N.S.	4,225	0.47	N.S.
			$r^2 = 0.39$			**$r^2 = 0.26$**	
Rock goby	individual	6,175	1.59	N.S.	6,175	1.03	N.S.
	order	4,175	1.62	N.S.	4,175	0.38	N.S.
	temp.	1,175	132.76	<0.001	1,175	31.01	<0.001
	int. 1	6,175	2.88	<0.05	6,175	1.44	N.S.
	int. 2	4,175	2.33	N.S.	4,175	0.49	N.S.
			$r^2 = 0.54$			**$r^2 = 0.29$**	

Table 6.2. *The results of the ANCOVA investigating the relationship between water temperature and escape response, expressed as speed and acceleration, in butterfish, corkwing wrasse, and rock gobies. Int. 1. is the interaction between individual and temperature, int. 2 the interaction between order and temperature*

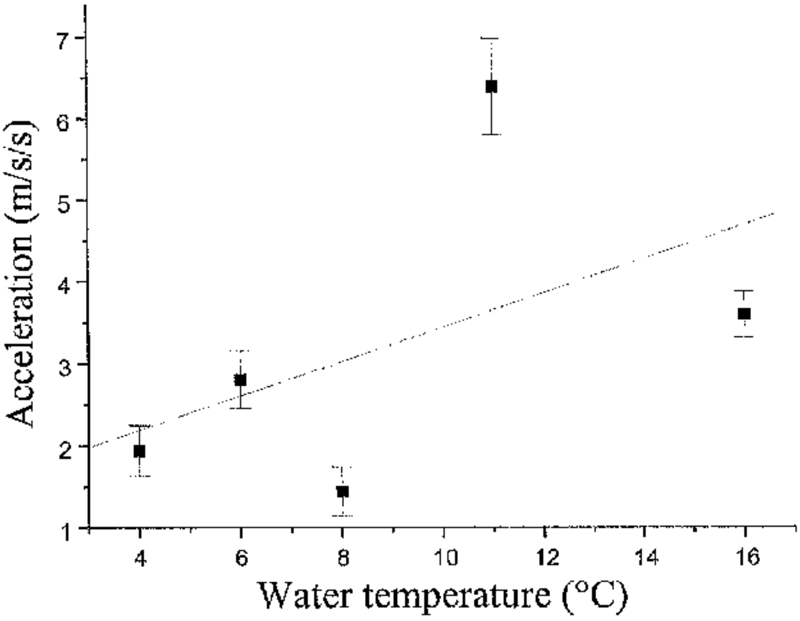


Figure 6.2. The effect of water temperature on acceleration, during the induced escape response, of the butterfish.

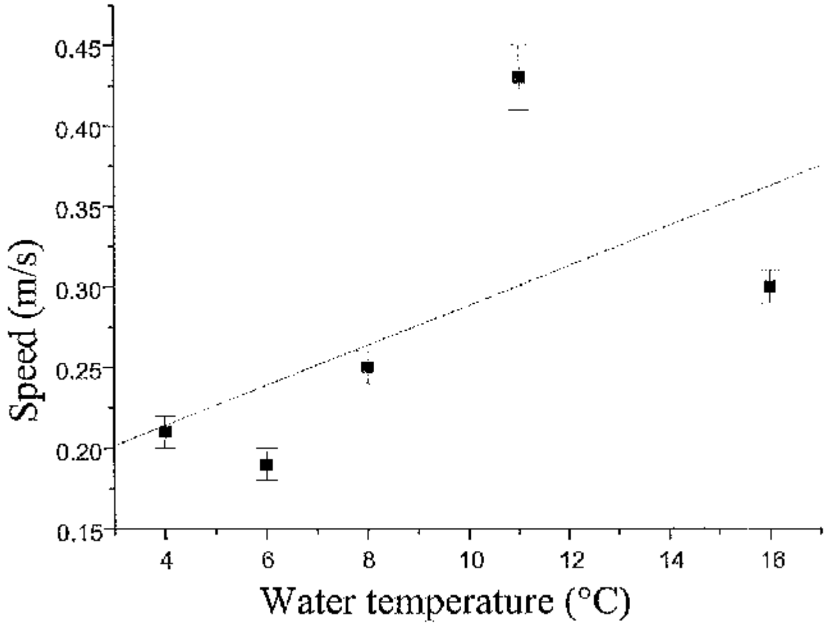


Figure 6.3. The effect of water temperature on the speed of the induced escape response of the butterfish.

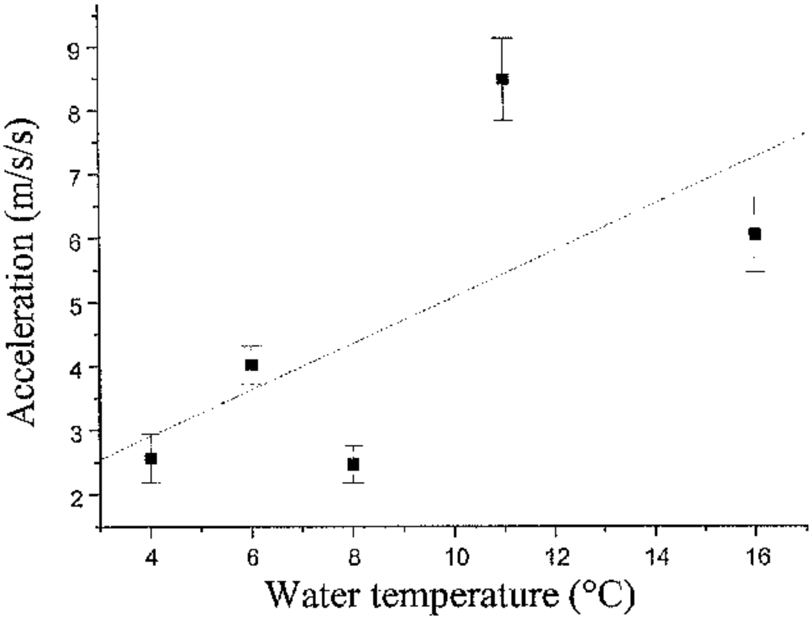


Figure 6.5. The effect of water temperature on acceleration, during the induced escape response, of the rock goby.

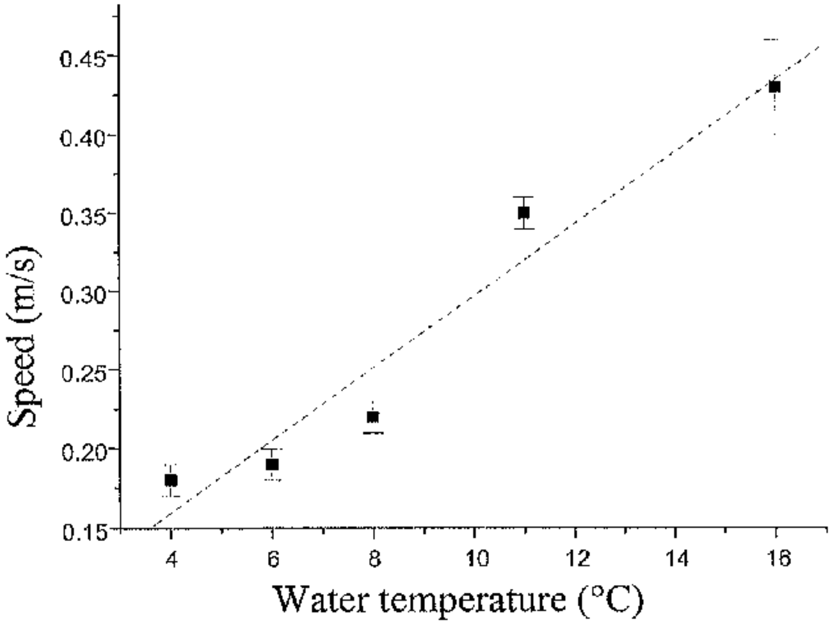


Figure 6.6. The effect of water temperature on the speed of the induced escape response of the rock goby

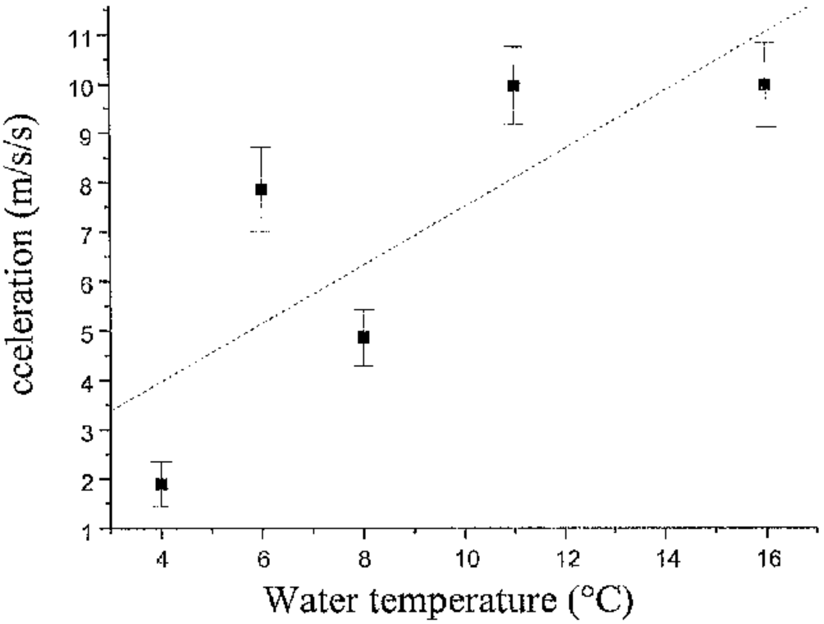


Figure 6.6. The effect of water temperature on acceleration, during the induced escape response, of the corkwing wrasse.

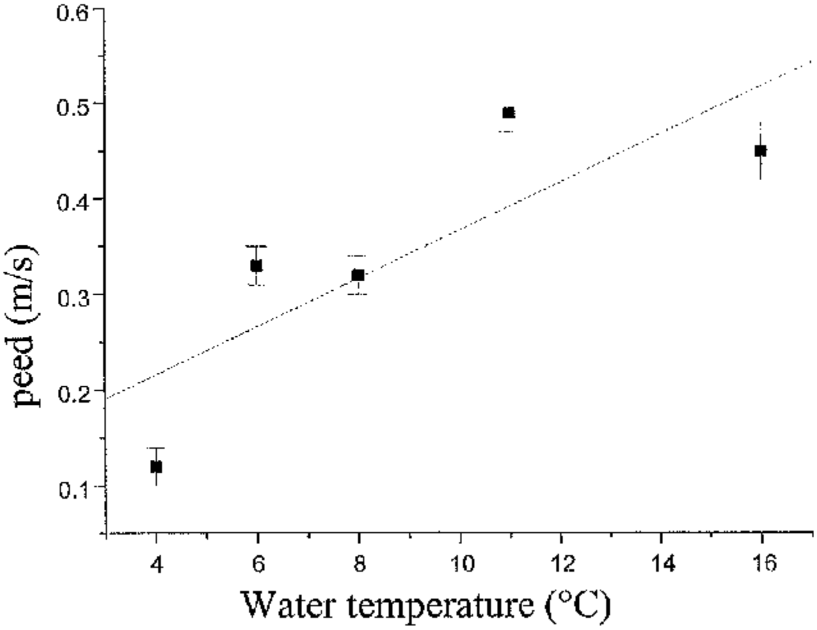


Figure 6.7. The effect of water temperature on the speed of the induced escape response of the corkwing wrasse.

6.3.3. Otter Behaviour

The data on butterfish and gobies was analysed by Pearson's correlation coefficient, and that on wrasse by Spearman's rank correlation, due to a small sample size. None of the dive durations required to catch the three prey items showed any significant variation with the temperature of the water in which they occurred, table 6.3.

	n	R	sig.
Butterfish	87	0.02	N.S.
Wrasse	7	0.59	N.S.
Goby	27	0.12	N.S.

Table. 6.3. *The relationship between the duration of dive preceeding capture of prey and the temperature of the water, for three prey species, butterfish, corkwing wrasse and gobies.*

6.4. DISCUSSION

Temperature mediated fluctuations in prey behaviour may under certain circumstances have dramatic effects on the foraging behaviour of a predator. In this study, however, while it was clearly shown that the activity and strength of escape response of some of the piscivorous prey of the Eurasian otter were significantly compromised by low water temperatures, we found that there was no variation in the amount of time associated with the capture of these prey with fluctuating water temperatures. From our experimental data we would have expected dives in colder water temperatures to be shorter, due to the fish being easier to catch. Clearly, stronger influences affect the ability of the fish to escape predation, and in order to understand them, an examination of the foraging behaviour of the otter is required. First, however, we shall discuss the fish behaviour in more detail.

6.4.1. Fish behaviour

The decline in activity and swimming speeds in three fish species we have described has been similarly found in other species (for example in rainbow trout, *Salmo gairdneri*, Webb 1978). This decline may be related to physiological aspects of the fishes musculature, in that white glycoltic muscles, which are associated with fast swimming speeds, are recruited less at low temperatures, (Rome *et al.* 1984), as well as the overall decline in speed of responses in cold water associated with ectothermy.

Such a reduction in activity and startle responses will be a serious constraint on these fish, since it makes them highly vulnerable to predation. It is therefore likely that they have evolved mechanism to counterbalance this. Traditionally (for example Wheeler 1969) it was thought that many inshore fish species migrated offshore into deeper water during the winter months to avoid the coldest temperatures and associated risks. However in light of the discovery by Sayer *et al.* 1994, that relatively large numbers of these fish can be found within crevices and under rocks, in a state of quiescence, during the winter, the main compensatory response to the increased predation risk is likely to be concealment. The effectiveness of this concealment is evident in the fact that for so long it was believed that these animals had migrated offshore

However all three of these fish species are still predated on during the winter by otters, (chapter 4), so presumably any concealment is not complete. It is likely that there are only a limited number of available sites for concealment available, and so it is poorer quality individuals that are vulnerable to predation by the otters, while the better quality animals will have obtained good sites of concealment and therefore have a higher chance of survival.

With this hypothesis, we would expect that capture times of these prey would be reduced in the winter, because of reduced activity as already stated, but also because the fish are of poorer stock. Conversely however, because we are examining overall capture times, and cannot witness everything that happens during the otters dive cycle, it may be that once a prey item is found the capture time is shortened, but that the otter has to increase its search time to detect such hidden prey.

One further finding of this work was that we detected no habituation in any of our experimental animals, despite them being exposed to a fairly large number of stimuli. There may be several reasons for this.

1. That the animals need to be exposed to a greater number of stimuli before any habituation occurs
2. That the animals are stressed by the experimental conditions and therefore are less likely to be pacified by habituation
3. That the unpredictable nature of the sublittoral habitat precludes the advantages of habituation.

6.4.2. Otter behaviour

It is likely that otters hunt for food by touch, using their vibrissae, or whiskers, rather than by sight. Green (1977) describes an experiment where removal of these vibrissae greatly reduced an otters ability to successfully hunt, and the fact that freshwater feeding otters feed largely at night (Kruuk, 1995) also supports this. Kruuk (1995) describes watching captive otters in a feeding tank turning their whiskers down and forward to maximise the contact area with its surroundings. Otters also feed when their prey are inactive or vulnerable (for example, Carss *et al.* 1990, Beja 1995, Kruuk 1995) choosing prey that rest demersally, particularly, in marine environments, amongst weed (Kruuk and Moorhouse 1990).

An overall reduction in activity, as described by our experiments in this chapter, would affect only the components of an activity cycle where the animal is active, rather than those periods when it is naturally resting. Similarly the escape response of an inactive animal is likely to be less than that of an active animal. Since the otter is feeding on fish when they are inactive, it is likely that the level of overall activity, when the animal is active, will have little influence on the catchability of the prey. While decreased water temperatures also significantly reduced the escape response, our experiments were carried out with active animals, giving no real indication of how the animal would respond to disturbance when resting. Indeed it may be the movement from a disturbed animal that is picked up by the foraging otters vibrisae, so a reduced response may not necessarily increase the vulnerability of the prey. Overall, however, the results suggest that the reason why, despite the reduction in general activity and escape response of its prey species with depressed water temperatures, the behaviour of the otter in foraging for this prey is not significantly affected is because of the otters habit of foraging for these prey when they are already inactive.

Implicit in this hypothesis however, is the relationship between the timing of the otter's feeding and the activity of the prey. Where the activity of the prey is reduced by low temperatures, it is likely that any activity cycle will be altered, indeed temperature dependant shifts in the activity cycle of fish have been described elsewhere (Fraser *et al.* 1993). The change in the behaviour of the fish species predated on by the otter suggested by our data and the literature (particularly Sayer *et al.* 1994) is one of a collapse of the activity cycle into a continual state of quiescence.

The implications of this on a predator such as the otter would be changes in the timing of foraging, rather than on such variables as capture time. In such circumstances foraging would no longer be restricted to distinct periods corresponding with the activity of the prey, and may either follow a different pattern governed by external factors, or may break down all together. These possibilities will be examined in chapter 7.

We can therefore draw the following conclusions from this part of our overall study:

1. That there is a decrease in activity in some of the important prey species of the otter in depressed water temperatures, and this reduction is also reflected in the strength of the escape response, determined as both speed and acceleration.
2. Despite this there is no significant reduction in the capture times of these prey items in low water temperatures. This may be due to either the fact that otters predate on these species when they are inactive anyway, or that while there may be faster capture times, the time to find the prey may be longer

CHAPTER 7.

THE EFFECT OF TEMPERATURE-MEDIATED FLUCTUATIONS IN THE BEHAVIOUR OF PREY ON THE ACTIVITY CYCLE OF THE OTTER.

CHAPTER 7

7.1. INTRODUCTION

The partition of an animal's time into an activity cycle, and the partitioning of the cycle between different activities such as feeding, resting and breeding activities will be dependent on a number of factors, such as prey movements and the threat of predation. Since these factors can change seasonally, there may be resultant shifts in activity patterns. For example, woodcock, *Scolopax rusticola*, feed during the night in spring, but in the summer feed during the day (Hirons and Owens 1982). This is due to a switch from pasture to woodland habitat driven by increase in grass length in the pasture.

Similarly, the activity patterns of the Eurasian otter are thought to follow those of its prey species in that they prefer to forage for prey when it is inactive, and resting on the bottom of the water column (Kruuk 1995). This explains the nocturnality of fresh water foraging otters, and the diurnality of marine foragers. In freshwater, otter prey, particularly salmonids, are largely active during the day, (Westin and Aneer 1987), though this can change in lower water temperatures (Fraser *et al.* 1993), and there may be resultant shifts in the otters foraging behaviour (Carss *et al.* 1990, Kruuk 1995). Some important marine prey types, such as eelpout and rockling, are nocturnal, and probably because of this, marine foraging otters are diurnal (Kruuk and Moorhouse 1990, Watt 1991), though in Portugal where the main prey, corkwing wrasse, are diurnal, the coastal otters are nocturnal (Beja 1991).

Diurnal and nocturnal activity cycles can be further broken down into time of day or night, and with coastal otters as with all marine life, the state of tide may also have a role in determining activity patterns. In Shetland, Kruuk and Moorhouse (1990) described seasonal shifts in coastal marine otters activity patterns. In the winter, there was a single peak in otter activity before noon, in the summer there was a peak two or three hours after dawn, and a second lesser peak in the early evening. There was, however, no statistical evidence provided for this trend, neither was a possible explanation advanced. The same study examined patterns of tidal effects on foraging, and described a statistically significant decrease in preference for foraging during rising, falling, low and high tides, respectively. Interestingly, when the observations were partitioned into male and female otters, the males showed a stronger effect, and for females the effect was no longer statistically significant. The authors also stated that they believed that there was more activity at low tide, but that the otters were harder to observe due to exposed weed. However they based this claim largely on data from a single radio-collared otter, which was likely to be showing abnormal behavioural patterns due to the attachment of the transmitter (Kruuk 1995). The tidal effect was related again to the activity of the prey species, particularly eelpout and rockling, which were most active during high tide, the time of least otter activity. Unfortunately the study was not able to correct the tidal observations for time of day, and the comparisons between tide state were made only in the summer (Kruuk pers. comm.), so seasonal effects could not be examined.

These preferences for foraging during changing tides, and in the early morning and evening, can be equated with the pattern of predator activity following prey behaviour by the following hypothesis. Rather than choosing to prey on fish when they are wholly inactive, that is during the day and at low tide, the otters prey upon them during the interface from active to inactive, that is when they are emerging from, or entering into, cover. It is possible that the prey are easier to catch when at the entrance to cover, rather than when fully sheltered. Another possibility is that a moving tide, as when incoming or outgoing, moves the kelp fronds in a single direction, facilitating easier access through gaps between them. Such hypotheses are unfortunately virtually untestable. However the less elaborate hypothesis, as initially proposed by Kruuk and Moorhouse (1990), that otters time their foraging to coincide with trends in the activity patterns of their prey, remains testable. Much of Kruuk's work (see review in Kruuk, 1995) reinforces this idea, as does Beja's (1991) description of the nocturnal coastal feeding otters in Portugal feeding predominantly on diurnal prey. A further implication, as described in chapter 6, is that if there were fluctuations in the behaviour of the prey, then the behaviour of the predator would shift to meet these changes. Such fluctuations could be the changes in the behaviour of fish associated with depressed water temperatures (for example Webb 1978, Fraser *et al.* 1993). In chapter 6 we described a reduction in both overall activity and in the escape response of some common otter prey species with depressed water temperatures, and Sayer *et al.* (1994) described how many marine fish entered a state of quiescence during low water temperatures. Effectively this state of torpor means that the fish no longer have an activity cycle, they are inactive constantly. The implication of this for a predator such as the otter is that there would no longer be any requirement to follow the prey's cycle. Foraging activity could then be dependent on other, abiotic factors, or indeed none at all, in other words a constant level of activity throughout the day. This could, in part, explain the seasonally fluctuating patterns of the daily activity cycle of the Shetland otters as described by Kruuk and Moorhouse

(1990). From this we can hypothesise that where we may see variations is in the timing of foraging, in that when the prey are constantly inactive there is no longer any need to time foraging to coincide with the prey's periods of inactivity. Kruuk and Moorhouse (1990) had suggested that these periods of foraging were at low tide and early in the morning, but were unable to test this through a range of water temperatures. We therefore set out to test the hypothesis that temperature mediated changes in the activity cycle of prey will be reflected by seasonal fluctuations in the timing of foraging by otters.

To do so we attempted to answer the following questions by carrying out observations throughout the tidal cycle and at different times of day in a single habitat:

1. Does tidal state and time of day affect the amount of otter foraging activity?
2. Does this change in relation to water temperature?
3. Can any changes therefore be related to the effects of water temperature on prey activity?

7.2. METHODS

Observations were carried out for 15 months, from July 1995 to September 1996, of a single area, the tidal rapids at the Taynish peninsula, a site wall used by foraging otters (see chapter 5), from a vantage point that afforded a complete view over the area. These observations were made over four days each month. The four days were split into two pairs of consecutive days, and in each pair watches were carried out so that the total daylight hours were observed during them. The two pairs of days were arranged so that they were at opposite tide states. This meant that in every month, observations were made during every possible combination of time of day and tide state. All otter activity was recorded during this period. Also recorded were wind speed, cloud cover, rainfall and overall visibility. Wind speed was measured using a hand held anemometer, manufactured by "Dwyer Instruments Inc.". Cloud cover were expressed as 0 - 25%, 26 - 50 %, 51 - 75 %, and 76 - 100 %, rainfall and visibility were ranked, none, light, medium or heavy, and poor, fair or good, respectively. Although these measures are somewhat subjective, because the same observer always scored them, they were consistent.

For analysis, the tide was split into four states, incoming, in, outgoing, and out. The mid points of the in and out states were taken as the highest and lowest points, taken from Admiralty tide tables, and each state lasted for slightly more than three hours, varying according to lunar cycle. The mean day length of each month was partitioned into three equal, concurrent segments, morning, midday and evening. All observations therefore were during a known time of day and state of tide. Otter foraging activity was measured as the total time that an otter was underwater during observations of the particular combination of tide state and time of day. If two otters were present detailed observations could not be made simultaneously on both. Therefore, one otter was described in detail and a record of the others general behaviour, that is in the water or on land, made. The time the second otter was in the water was then assigned a value for actual underwater time from the mean proportion of time that was spent underwater obtained from observations of otters at a similar time of day and tide state, and time of year. In practice this only occurred five times. The data were expressed as a proportion of the total time that observations were made in that combination of conditions, in that month. This was arcsine transformed to allow parametric statistical analysis.

The following analysis were then carried out:

1. *Checking for weather effects*

To eliminate the possibility that activity was influenced either directly by the non-aquatic weather, such as cloud rain and wind, or indirectly by affected the observer ability to see the otters, the results were tested for variations in amount of foraging activity recorded in different weather conditions. A Kruskall-Wallis one-way ANOVA was applied to each of the ordinal weather variables, that is cloud cover, rainfall and visibility, with otter foraging activity as the dependent variable, and a Pearson's product moment correlation coefficient calculated for wind speed against otter foraging activity. The non-parametric ANOVA was used with the ordinal data sets due to heteroscedasticity caused by large differences in group size.

2. *Relationship between day length and foraging time*

To eliminate the possibility that recorded foraging activity was simply a function of day length, in that that was the time the animals were visible, the monthly amount of foraging activity was tested for a correlation with day length, via a Spearman's Rank Correlation.

3. *Effects of season, tide and time of day*

To test for variations in the amount of otter foraging activity between tide states and time of day, an ANOVA General Linear Model was designed, including month, tide state and time of day as factors, with arcsine transformed foraging effort, as described above, as the dependent variable. The model tested for the effects of month, tide and time of day, and interactions between month and tide, and month and time of day.

7.3. RESULTS

7.3.1. Weather Effects

None of the weather variables had a significant effect on the amount of otter activity observed, (Kruskall - Wallis one way ANOVA for rain, cloud cover and visibility, Pearson's correlation coefficient for wind speed, see table 7.1. and figures 7.1 – 7.4. for data amount of observation time under different rainfall and cloud cover conditions.) While none of the observations were made under certain conditions, since the data are based on proportion of observation time, this bias has been corrected.

Variable	D.F. / n	χ^2 / r	significance
Wind speed	174	-0.02	N.S.
Cloud cover	4	0.98	N.S.
Rainfall	3	1.97	N.S.
Visibility	2	4.93	N.S.

Table 7.1. The effects of weather variables on the amount of otter activity observed.

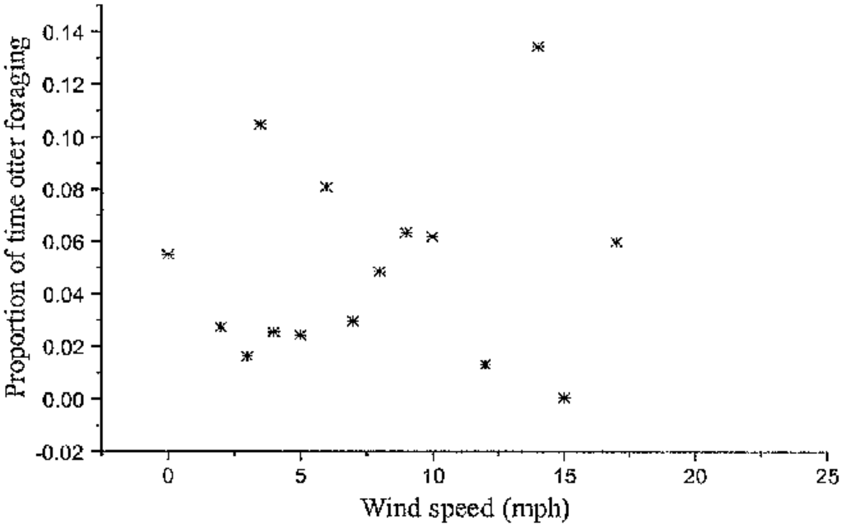


Figure 7.1. The proportion of observation time that an otter was seen foraging, in relation to wind speed

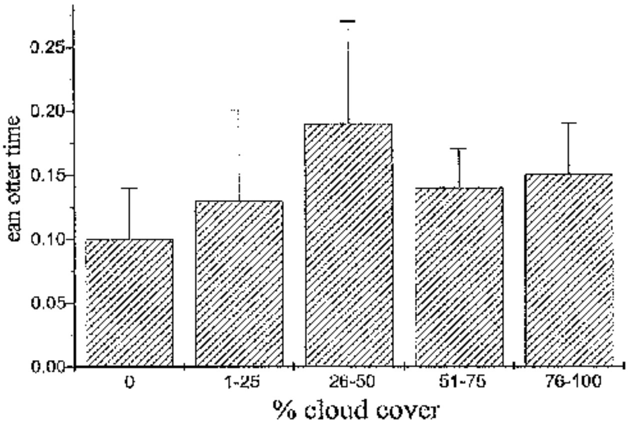


Figure 7.2. The mean otter time, that is the proportion of observation time that an otter was underwater, with standard errors, under different percentage cloud covers

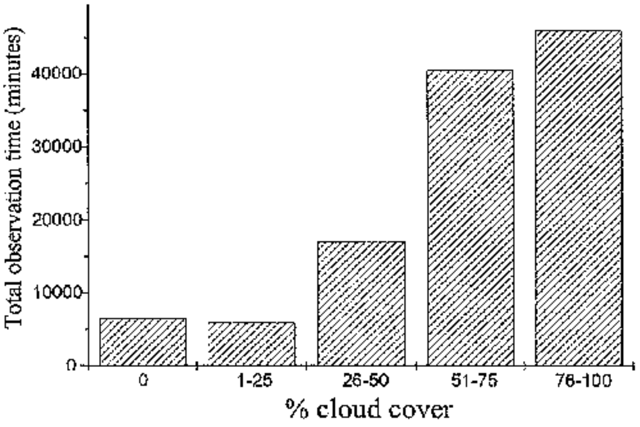


Figure 7.3. The total observation time under different percentage cloud covers

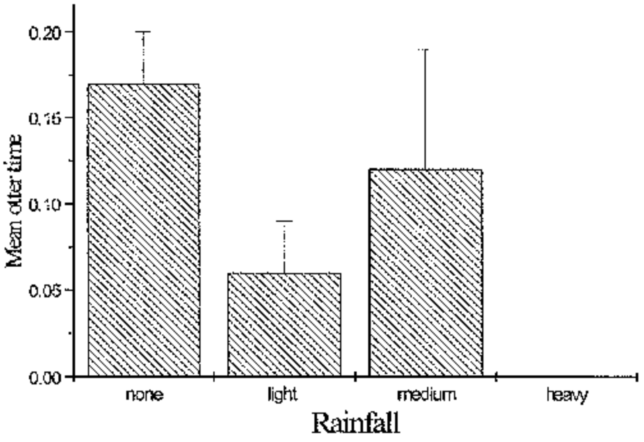


Figure 7.4. The mean otter time, that is the proportion of observation time that an otter was underwater, with standard errors, in different rainfall conditions

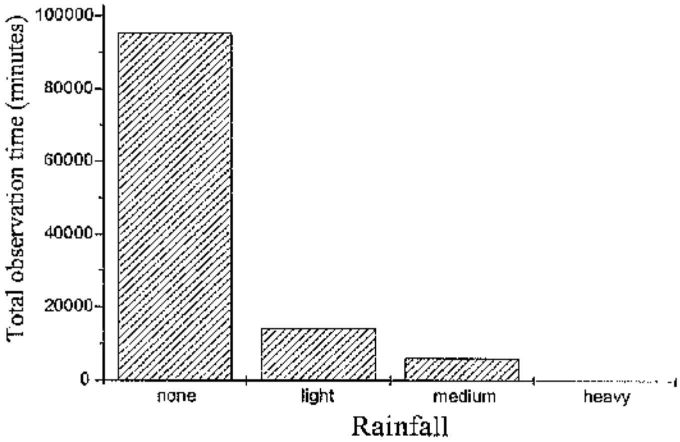


Figure 7.5.The total observation time under different rainfall conditions.

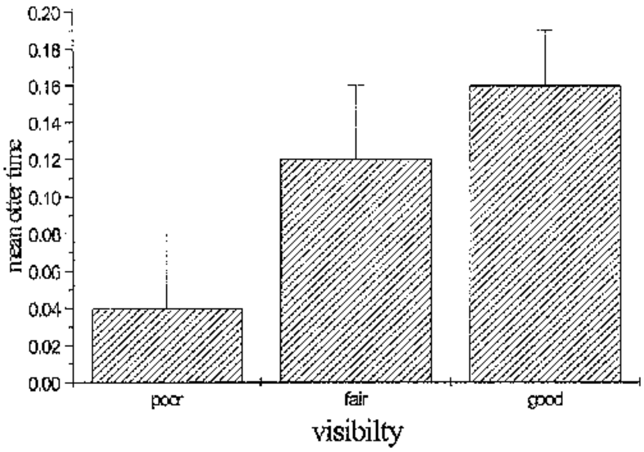


Figure 7.6. The mean otter time, with standard errors, that is the proportion of observation time that an otter was underwater, in different visibility conditions

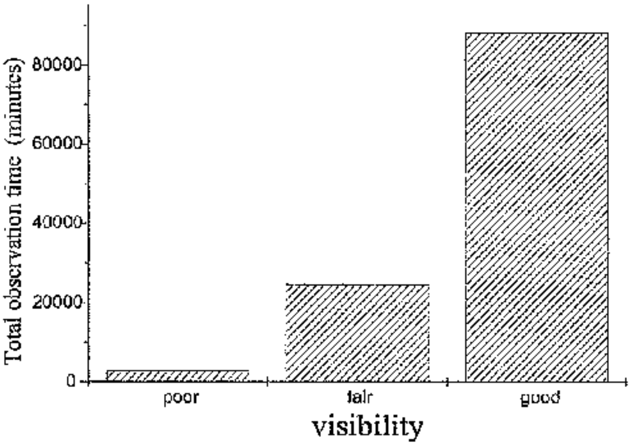


Figure 7.7. The total amount of observation time in different weather conditions

7.3.2. Relationship between day length and activity

There was no significant relationship found between length of day and amount of otter activity, (Spearman's rank correlation, d.f. = 10, non significant)

7.3.3. Effects of month tide and time of day

During January 1996, complete observations of all tide states and time were not made do to adverse weather conditions, and so this month was excluded from subsequent analysis. The results of the ANOVA model examining the effects of month, state of the tide and time of day on the amount of otter foraging occurring are summarised in table 7.3.2. The state of the tide did not have a significant effect on foraging activity, nor did it interact significantly with month, but both month and time of day were significant factors and there was a significant between them.

The changes in preference for different times of day in the different season are shown in figure 7.5. In the summer and autumn, there is a preference for foraging in the morning, followed by the evening, with the least foraging occurring in the midday. In the spring, morning is the still the most important foraging time, but midday is more important than evening, and in the winter, the most foraging activity occurs in the evening, followed by midday, then the morning.

Factors & Interactions	D.F.	F	Sig.
Time of day	2,192	5.08	< 0.01
Tide state	3,192	0.61	N.S.
Month	10,192	2.97	< 0.01
Month*Time of day	20,192	2.08	< 0.01
Month*Tide state	30,192	1.15	N.S.
Model	65,192	1.77	< 0.01

Table 7.2. Summary of the results of an ANOVA General Linear Model, testing the effects of month, tide state and time of day on the proportion of observation time that an otter was actively foraging.

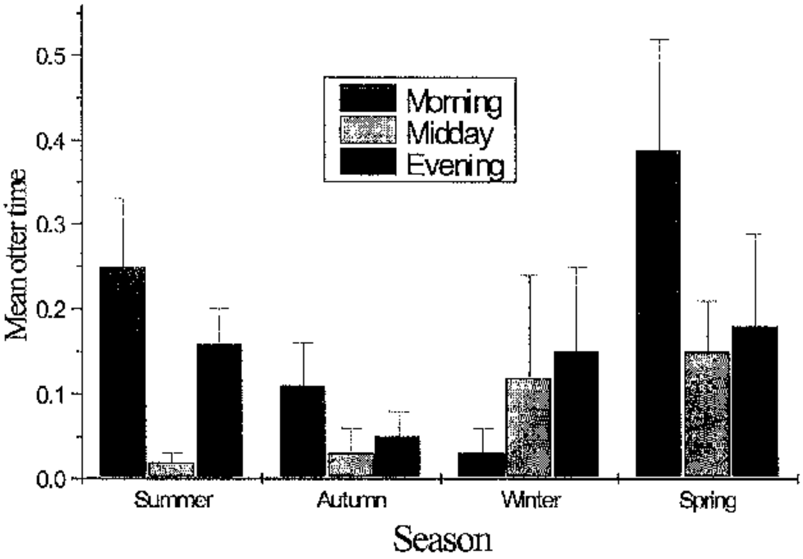


Figure 7.8. The relative occurrence of otter foraging at different times of day, expressed as otter time, that is the mean proportion of the total observation time, with standard errors, in different seasons.

7.4. DISCUSSION

In chapter 6 it was demonstrated that while there were reductions in both the activity and the escape response of some otter prey with depressed water temperatures, there was no change in the actual capture time of these species, despite it being likely that they are easier to handle in colder water. This was considered as potentially being due to the otter predating upon these species when they are inactive anyway, therefore a decrease in activity would not affect capture times. From this we hypothesised that where we may see variations is in the timing of foraging, in that when the prey are constantly inactive there is no longer any need to time foraging to coincide with the prey's periods of inactivity. Kruuk and Moorhouse (1990) suggested that these periods of foraging were at low tide and early in the morning, but were unable to test this through a range of water temperatures. This observation regime was therefore designed to test the above hypothesis by observing otter activity throughout the year at all times of day and tide state at the same location. Since all observations were from the same point, the regime was also allowed the testing of any climatic effects on the amount of underwater time being recorded.

7.4.1. Limitations of the Data

In the study of foraging patterns of otters feeding in Shetland carried out by Kruuk and Moorhouse (1990), they discussed some problems with their data that invalidated the potential for carrying out the class of ANOVA models for analysis that we have used in this study. It would therefore be appropriate to discuss these limitations and the manner in which we have sought to overcome them in this design.

7.4.1.1. Independence of Observations

Kruuk and Moorhouse quantified otter activity as number of dives. Because their observations were frequently of a long run of dives by the same otter, during a single foraging bout, the observations were not always independent of each other, invalidating a basic assumption of parametric statistical analysis. Our data took the form of total underwater time per observation period as a measure of foraging activity, and therefore the independence or not of a run of dives was not in question, allowing parametric analysis to proceed. It is possible that there remains some non-independence since it was often the same otters observed throughout the study. However since an overall proportion of activity was taken for each combination of tide state, time of day and month, such an effect was minimised.

7.4.1.2. Quantification of Observation Effort

In the Shetland study, there were a number of "imponderable" variables, such as weather, visibility and particularly the shape of the coastline. These invalidated any measure of observation effort needed to make valid comparisons between these areas. However, our observations were made from a single point by a single observer, eliminating observer and topographical biases. By measuring climatic variables, and overall visibility, and testing them for effects, we found that there were not any such influences on the amount of time underwater being recorded. In all this meant that we could take observation effort simply as the time spent observing the area for otters, and proceed with analysis.

7.4.1.3. Small Sample Size

The Shetland study, like our own with around nine adults, was based around only a limited number of individuals, and Kruuk and Moorhouse felt that this limited the validity of possible analysis. While it is true that some of the trends described could be due to idiosyncratic behaviours of the otters, there is no real means of overcoming the problem when working with a rare and somewhat elusive species such as the otter. Therefore the possibility of the low sample size influencing our results is something that must be borne in mind when interpreting them. It does not however invalidate them, and at their simplest they can be viewed as the trends in a small population of otters. Extrapolation to the species as a whole should be done with caution, but still is valid to some extent. While it would have been helpful to identify individual otters and test for differences in their foraging patterns, in practice it was often very difficult to identify an otter with the required degree of confidence. Otters on the Scottish west coast do not have the same distinctive throat patches associated with Shetland and many fresh water populations, so individual identification is harder, particularly when the animal is feeding.

One final limitation of our data and one not discussed by Kruuk and Moorhouse, was the possibility of two otters foraging at the same time, in the same area. As described in the methods we assigned an estimated foraging time to the second otter to analyse such situations. In practice this only occurred on five occasions, and on two of these there was a second observer present to time the otter. Using this method is therefore unlikely to bias the data given the large numbers of observations that were made.

7.4.2. Weather Effects

None of the measured climatic variables had a significant effect on the amount of otter foraging recorded. However when examined graphically, both rainfall and visibility would be expected to have an effect, (figures 7.4. and 7.6. respectively). The explanation for this can be seen in the figures (figures 7.5. and 7.7.) showing the amount of actual observation time that was undertaken under these conditions. There were very few observations carried out in either poor visibility or heavy rainfall, and so it is likely that the results of the statistical tests were accurate. As such we can be reasonably confident that the results we have obtained with regard to the other variables such as the state of the tide and time of day are not artefacts of the weather.

7.4.3. State of Tide

Our examination of how state of the tide influences the activity patterns of otters produced no significant result, neither did it interact significantly with the time of year. This is contrary to the finding of Kruuk and Moorhouse (1990) who did find significant preferences for certain tidal states. There are several reasons why this might be so;

1. Loch Sween has an exceptionally low tidal range due to the presence of an amphidromic node adjacent to it in the sound of Jura. This is a point where two tidal currents meet, and in Loch Sween the currents cancel each other out to a large extent, reducing overall tidal fluctuation's. Gibson (1969) stated, as one would expect intuitively, that for fish to show tidal mediated behavioural patterns they must be exposed to relatively strong tidal changes. The fish in Loch Sween are not exposed to such changes for the majority of the time, and therefore may not display

tidally mediated activity patterns, in which case neither would otters predating upon them.

2. The important prey species discussed by Kruuk and Moorhouse are rockling and particularly eelpout, which while a common and important prey species in Shetland seems almost entirely absent from Loch Sween (chapter2) which is at the lower reaches of its range (Wheeler 1969). Many of the otters behavioural patterns in Shetland are based around this species, as are Kruuk's observations and hypothesises for coastal otters (see review in Kruuk 1995). In Loch Sween, a far more important prey species is the butterfish (chapter 4), though rockling are seasonally important, and these are not subject to the same tidal behavioural *zeitgebers* as the eelpout (Kruuk et al 1988, Koop 1990, Kruuk 1995). Again where the prey species is unaffected by tide, we would largely expect the predator to also be.
3. Kruuk and Moorhouse, while observing more otters in outgoing and incoming tides suggested that there was in fact more activity in lower tide states, but that the otters were harder to see due to visible weed, though this was not quantifiable. There is therefore the possibility that there was more otter activity at low tide at Taynish but it was not observed. As stated in 7.1., Kruuk and Moorhouse backed up this statement by referring to radio-tracking data, which was largely based around a single female fitted with a radio-harness. This female showed a number of unusual behaviours due to this apparatus being fitted, probably due to it affecting the function of the pelt and the otter's ability to groom (Kruuk 1995). Bearing this in mind, this is not a convincing argument.
4. The significant fluctuations in otter activity with tidal state reported by Kruuk and Moorhouse (1990) were only significant for observations of males. The vast

majority of our observations, where the animal could be sexed, were of females, and as such our data does in fact match that of Kruuk and Moorhouse.

The lack of an interaction between either tide state and month and tide state and time of day can be explained simply as there being no preference for foraging at a given tide state, and this lack of preference remains the case despite changes in season and time of day.

*7.4.4. **Time of Day***

While Kruuk and Moorhouse demonstrated graphically that otters showed a preference for foraging at certain times of day, and that these preferences changed with season, they presented no statistical evidence to support it, because of problems of quantifying observational effort and the independence of data (see *7.4.1.*) In this study we dealt with these problems, to some extent, and attempted to quantify otters preference, or lack of it, for foraging at certain times of day. We found significant differences in the time of day when most foraging occurred and also found a significant interaction between this and the month the observations were being made. However the pattern was not as would have been expected from our hypothesis. Our hypothesis predicted that there would be no difference in the relative amounts of otter foraging between the different times of day during the winter months, due to the quiescence of the fish at this time. However while the pattern was different from that of the rest of year, where overall, in a manner similar to Kruuk and Moorhouse's Shetland observations, there was a peak in activity in the morning, then a lesser peak in the early evening. However in winter there was not the levelling out we predicted, rather a pattern of preference for the later part of the day, then the middle, then the morning.

A potential explanation of this winter pattern is that with the removal of the stimulus of following the prey's activity cycle the otters can forage when it is most profitable with respect to other variables. In any shallow body of water, throughout the day the water will get warmer. The observed preference for feeding later in the day may simply be because the water is warmer then, so heat loss is reduced. Unfortunately we did not measure daily changes in water temperature, so we could not test this hypothesis, however such changes are likely to be very small in Scotland in the winter, so this explanation is unlikely. Such continual measurements would therefore be recommended for any future studies.

It should also be pointed out we have based our hypothesis around the evidence of a reduction in activity of three species of prey and extrapolated this onto other prey species. In chapter 4 we demonstrated that gadoids were important prey during the winter months, and not at other times of the year (see also Watt 1991 and 1995), and we do not know directly how their behaviour is affected by water temperature. Sayer *et al.* (1993) did find 5 - bearded rockling during their winter searches of crevices, but this gives us no indication of activity. The rockling are caught more in fish traps in the winter as well, but this could be taken as evidence of an increase or a decrease in activity, or as changes in population size. Experimental evidence of the behaviours of all the important prey species are required before any conclusions can be completely justified.

One further possibility is that with the suggested breakdown of the preys activity cycle, otters feed not only during the day but also at night, so large shifts in behaviour may have occurred but not been noted by our sampling method.

7.4.5. Conclusions

1. The state of the tide had no significant effect on the foraging behaviour of otters at the Taynish peninsula. This is likely to be due to firstly that the tidal range is small so the fish are unlikely to demonstrate behavioural changes mediated by tide that the otters could exploit. Secondly, the main prey species, the butterfish does not show strong tidal behaviours. The time of day does affect otter foraging, activity being highest in the morning most of the year. This is likely to be due to the behavioural cycles of its prey.
2. The lack of influence of the tide does not change throughout the year. The effect of time of day changes seasonally. In the winter otters prefer to forage later in the day. This effect may be linked with a state of torpor of the prey species in cold water.

CHAPTER 8.

THE EFFECT OF WATER TEMPERATURE ON THE FORAGING PARAMETERS OF THE EURASIAN OTTER

CHAPTER 8

8.1. INTRODUCTION

Divers are defined by Houston and Carbone (1992) as animals which "hunt for food below the surface of the water and return to the surface to breathe". Such animals are subject to a range of physiological constraints peculiar to their mode of life and the medium within which they forage, and a range of morphological and behaviour adaptations have evolved to cope with these.

The term "central place forager" was introduced by Orians and Pearson (1979) to describe an animal that returns regularly to the same place when foraging, for example travelling between food patches. Houston and MacNamara (1985) pointed out that this description could also apply to diving foragers, since they always return to the surface. Following this definition, Kramer (1988) used this to apply the marginal value theorem to divers. The marginal value theorem is one of the most widely used optimal foraging models, and it describes a loading curve of diminishing returns to a predator feeding in a patchy environment, where the predator spends time travelling between, and foraging within patches (Krebs and Kacelnik 1991). The model is used to predict the optimal time to spend feeding in a patch, one of the determinants of which is the time it takes to travel to the patch. Kramer (1988) applied this approach to describe the optimal foraging time for divers, using oxygen consumption as the currency. In this model the loading curve was no longer used to describe rate of food intake, rather it described the rate of replenishment of oxygen stores in the post dive recovery period. Kramer identified three components of the dive cycle, surface time, foraging time, and the time spent travelling between these, and said that the animal would want to maximise the proportion of the cycle spent in the foraging patch. His model predicted that as foraging time increased, so would surface time and total underwater time. This model was formalised and extended by Houston and Carbone (1992) to allow predictions about the time spent foraging and the average rate of oxygen consumption underwater to be made. One key prediction of their model was that the time spent in a foraging area would first increase and then decrease as the travel time from the surface to the foraging area and back again increases.

Unfortunately these models are limited in application by the assumption that the animal has to have the ability to eat underwater. It is the basic prediction of Kramer that an animal will maximise the proportion of time spent foraging that is not applicable to predators feeding on single prey items on the surface, since foraging will cease with the capture of prey. The models can however be successfully used to describe the some aspects of the metabolic requirements of diving animals regardless of where they eat their prey, (see for example Houston and MacNamara 1994). Houston and Carbone (1992) recommend the use of a previous model dealing with single prey loaders (Houston and MacNamara 1985), for situations where the forager eats at the surface.

Subsequent to this, there have been a number of modifications to the basic model, examining the optimality of diving behaviour in the context of, for example, swimming speed (Thomson *et al.* 1993), mixed metabolic pathways (Carbone *et al.*

1996), and differential respiratory physiology (Walton *et al.* 1998). However most of these models have concentrated on the dive cycle, as defined by Kramer (1988), despite the fact that this may not account for all the metabolic costs of diving. In a number of mammalian and avian studies, the metabolic rate has been shown to be elevated for over an hour after diving (de Leeuw, 1996), therefore the complete costs of foraging are not being met during the dive cycle alone. De Leeuw (*Ibid.*) made a distinction between three types of diving cost:

1. the metabolic rate during submergence
2. the average metabolic rate during the dive cycle
3. the costs of diving as the excess over resting costs, including the whole period of elevated metabolism due to diving.

He demonstrated that in tufted ducks, *Aythya fuligula*, all the metabolic costs of diving were not included in the parameters of the dive cycle. Furthermore, his data showed that while the metabolic rate during the dive cycle did not change with fluctuations in water temperature, the overall diving costs did. This suggested that during diving, energy is mainly used to overcome hydrodynamic forces, and the extra costs of being underwater particularly thermoregulatory costs, are paid off after diving. Similarly, MacArthur (1984) had described a correlation between the decline in body temperature after diving and the post-dive excess oxygen consumption in muskrats.

Such thermoregulatory costs to foraging underwater are a consequence of the high heat carrying capacity of water, which is approximately 23 times that of air, (Schmidt-Nielson 1983). The costs of foraging in relation to thermoregulation have been discussed for several species, for example tufted ducks (Bevan and Butler 1995), Common and Thick-billed murres (Croll and McLaren 1993), and Minke whales, *Baleanoptera acutorostrata* (Folkow and Blix 1992). Fluctuations in these costs in relation to water temperature water have been examined in tufted ducks (de Leeuw 1996) as described above, as well as a number of other animals such as beavers, *Castor canadensis* (MacArthur and Dyck 1990) and the Australian water rat, *Hydromys chyrogaster*, (Dawson and Fanning 1981). Of these mammals, the former showed a linear increase in its metabolic rate with a decrease in water temperature, whereas the latter showed little fluctuation.

For the Eurasian otter, a predator that obtains virtually all its food from the water, the metabolic costs of foraging in cold water would be an important influence on foraging behaviour. Metabolic rates, expressed as oxygen consumption, were measured in captive otters by Kruuk *et al.* (1994), and the results demonstrated a large negative effect of water temperature on metabolism. Therefore it would be expected that there would be shifts in foraging behaviour during exposure to colder water temperatures to compensate for this increased physiological demand. However field studies carried out on otters foraging in fresh water in a range of temperatures showed no obvious effects of water temperature on foraging behaviour (Kruuk *et al.* 1997). However this study only examined the parameters of foraging associated with the dive cycle, that is underwater and surface time, as well as the overall length of bout. There was no attempt made to measure the overall recovery period after such a bout. Following de Leeuw (1996), we would expect there to be no direct correlation between these parameters and water temperature, with the metabolic costs of thermoregulation being met after the foraging behaviour was completed. Otters intersperse their foraging with periods of time on land, during which they groom and rest (Nolet and Kruuk 1989), and these are distinct from overall resting periods when the otter will frequently retreat into a holt. The grooming is likely to be related in part to maintaining the insulatory function of the pelt, particularly for otters foraging in the sea. Similar grooming and preening behaviour associated with diving has been found in murres (Croll and McLaren 1993), muskrat (MacArthur 1984), American mink, *Mustela vison*, (Stephenson *et al.* 1988) and sea otters, *Enhydra lutris*, (Costa and Kooyman 1982). Such vigorous grooming may also serve as a form of non-shivering thermogenesis, a means for the animal to raise its body temperature.

In the light of the insight by de Leeuw that the thermoregulatory costs of diving are met during the recovery period after a diving bout, which may involve grooming behaviour, and the study by Kruuk *et al.* (1994) demonstrating that otters suffer high metabolic costs associated with foraging in low water temperatures, we can hypothesise that such recovery periods would be longer after an otter forages in depressed water temperatures. Using the data from Kruuk *et al.* (1997) obtained from otters implanted intraperitoneally with heat sensitive radio transmitters, this prediction was quantified mathematically in collaboration with Dr. G. Ruxton as follows.

We assume that otters alternate between foraging periods in the water where they lose heat and periods on land where heat is recovered. We further assume that while the otter is in the water its core temperature drops according to Newton's law of cooling, as described by the equation below, where;

T_B = otter body temperature

∂T_B = the change in body temperature

t = time

∂ t = the change in time

T_w = water temperature.

α is a constant that controls the rate that heat is lost, the higher the value of α, the faster heat is lost.

$$\frac{\partial T_{\mathrm{B}}}{\partial t} = -\alpha(T_B - T_w)$$

If the otter enters the water (t = 0) at temperature $T_B = T_{B1}$, then we solve the equation above to find the temperature at any subsequent time as below:

$$T_B(t) = T_w + (T_{B1} - T_w)\exp(-\alpha t)$$

Upon leaving the water the otters body temperature, T_B, rises according to a similar equation, with a constant = β and T_M = maximum body temperature:

$$\frac{\partial T_B}{\partial t} = \beta(T_M - T_B)$$

If it leaves the water at temperature T_{B2}, then the temperature at subsequent times can be found by solving the equation above to give:

$$T_M(t) = T_M + (T_{B2} - T_M)\exp(-\beta t)$$

If we pick the temperatures T_{B1} and T_{B2} at which the otters enters and leaves the water respectively, then we can rearrange the above to give the lengths of time that it spends on land τ_L, and in the water τ_W :

$$\tau_L = \frac{-1}{\beta} In\left(\frac{T_M - T_{B1}}{T_M - T_{B2}}\right)$$

$$\tau_W = \frac{-1}{\alpha} In\left(\frac{T_{B2} - T_W}{T_{B1} - T_W}\right)$$

We can plot these equations as follows (figure 8.1.)

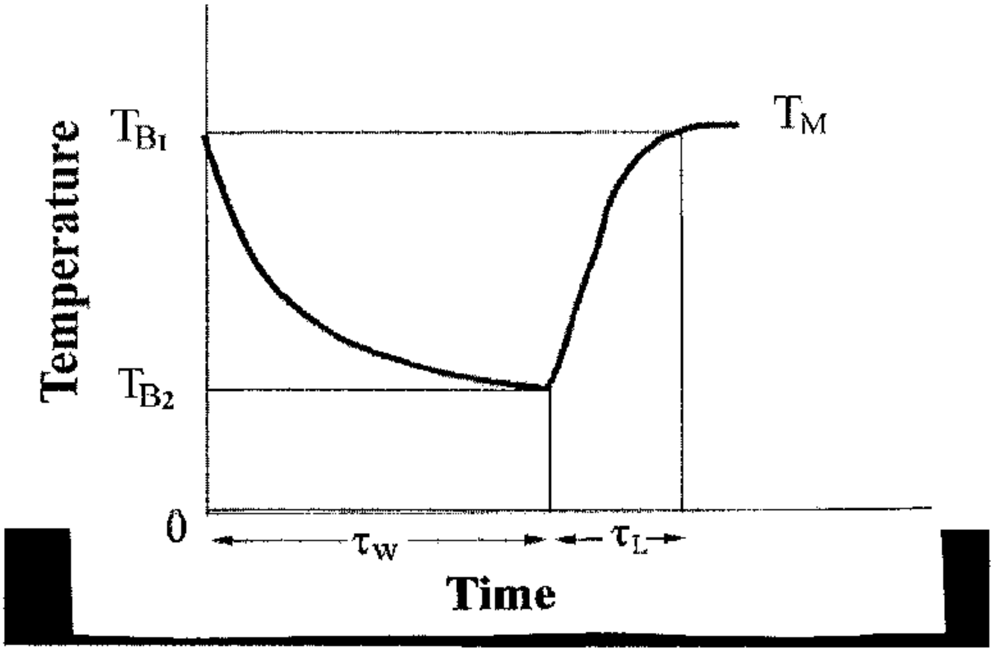


Figure 8.1. The modelled relationship between loss of body temperature (T_B) *in water*(τ_W) *and the compensatory gain on land,* (τ_L)*, over time*

We wish to find the combination of T_{B1} and T_{B2} which optimises the fraction of time that the otter spends in the water i.e. which maximises the relationship:

$$\frac{\tau_W}{\tau_W + \tau_L}$$

Below we plot this fraction of time for the unique optimal pair of values of T_{B1} and T_{B2} independently found for each of various different values of water temperature T_W. The other model parameters α and β and T_M were calculated from data presented by Kruuk *et al.* (1997), which were obtained from temperature sensitive radio transmitters. T_M was assigned the mean of the core body temperatures recorded, 38.1°C, and α and β were determined from estimates of T_{B1} and T_{B2} obtained from graphical data in Kruuk *at al.* (*Ibid.*) using the following formulae, derived from those above:

$$\alpha = \frac{-1}{\tau_W} In\left(\frac{T_{B2} - T_W}{T_{B1} - T_W}\right)$$

$$\beta = \frac{-1}{\tau_L} In\left(\frac{T_M - T_{B1}}{T_M - T_{B2}}\right)$$

Below, we demonstrate graphically how the optimal value of $\frac{\tau_W}{\tau_W + \tau_L}$ varies with water temperature:

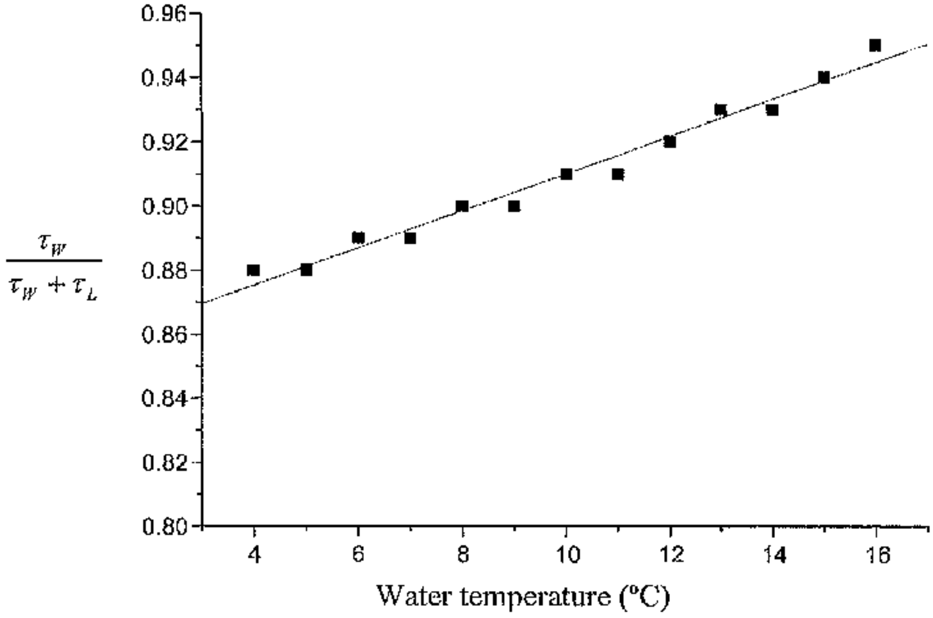


Figure 8.2. The optimum proportion of time allocated to recovery on land or foraging in water at different water temperatures.

Therefore this simple model predicts that as water temperatures decrease, the otters will spend proportionately more time on land. Further simulations show that this result is robust against plausible changes in parameter values.

This model can be used to predict the amount of recovery time an otter will spend on land relative to the length of the preceding foraging bout, at different water temperatures.

8.2. METHODS

Observations were made of otters feeding along the coast of the Taynish peninsula, where a range of depths was available. Using a Psion 2 personal organiser, modified with a data logging package written by Dr. M. Burns of Glasgow University, the lengths of dives were recorded. A complete dive was scored as from the point of submersion of the head, to the point of the surfacing. Dives were recorded as either successful or unsuccessful. Where possible the position of the otter in the water was recorded onto maps using terrestrial markers as guides, and depth was obtained from Admiralty depth sounding charts, corrected for tide state. A feeding bout was recorded as the whole of a period that the otter was in the water, without coming onto land, and success rate during that bout was measured as the proportion of dives that were successful. If the otter came onto land to eat, the bout was considered to be terminated, however if it ate prey in the water it was not. When prey was captured, if possible it was identified and an estimate of its size made by comparison with the width of the otter's head and assigned to a size class (see chapter 4 for more details). Its weight was calculated from length mass equations obtained from the fish-trapping regime and from Nolet and Kruuk (1989). For unidentified prey a mean value was used for that size class. A mean rate of prey intake was then calculated and this was expressed as grams per hour. When it was possible to observe a complete foraging bout, that is from the point of initiation, when an otter was clearly seen to be entering the water and the subsequent period on land, without losing sight of the otter, the length of time in the water and on land was recorded. This was only done for such periods when the otter had not gone onto land to consume prey, as this would have affected the actual recovery time on land. The temperature of the water was recorded at two metres depth using a Salinity Conductance Temperature (S.C.T.) meter. Clark (1987) described the temperature in temperate shallow water as being constant throughout the water column, so this figure was assumed to be correct for all dives.

The following parameters were tested for the effect of water temperature upon them:

1. The mean depth of dives occurring at any water temperature.
2. Dive duration, for unsuccessful dives only. Fluctuations in successful dives have been examined in chapter 6.
3. Inter-dive recovery period, for unsuccessful dives only, to eliminate any time spent consuming prey, and only for dives that did not precede going onto land, so as to eliminate travel time to land.
4. The ratio between surface recovery time and dive duration, subject to above caveats.
5. The proportion of dives that were successful within each foraging bout
6. The rate of prey intake, in grams per hour
7. The proportion $\frac{\tau_W}{\tau_W + \tau_L}$, where τ_W = time in water, and τ_L = time on land.

All these were analysed for fluctuations with water temperature. Parameters 1, 2 and 3 were analysed by means of a multivariate ANOVA model, with dive duration, surface pause and arcsine transformed surface to dive ratio as dependent variables and water temperature and depth as the covariants, 4 and 6 were analysed by non-linear regression analysis, and 5 by Pearsons product moment correlation coefficient.

8.3. RESULTS

A total of 5495 dives were recorded, of which 743 were successful and 4752 were unsuccessful. The mean duration of an unsuccessful dive was 16.25 seconds ± 0.16 (± standard error) and that of successful dives was 15.14 seconds ± 0.33. Figures 8.3. and 8.4. show the distribution of successful and unsuccessful dives respectively. The mean rate of food intake was 467 grams per hour (± 68)

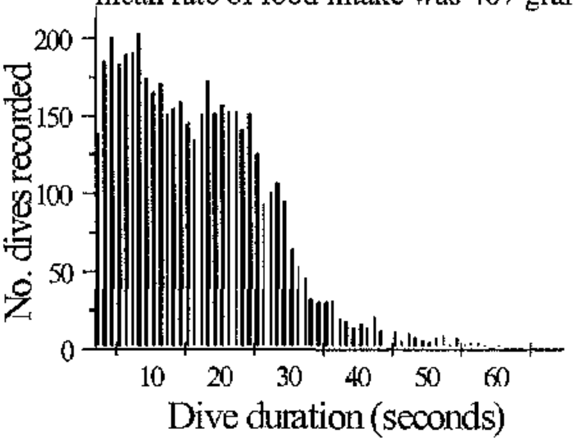


Figure 8.3. The durations of unsuccessful dives

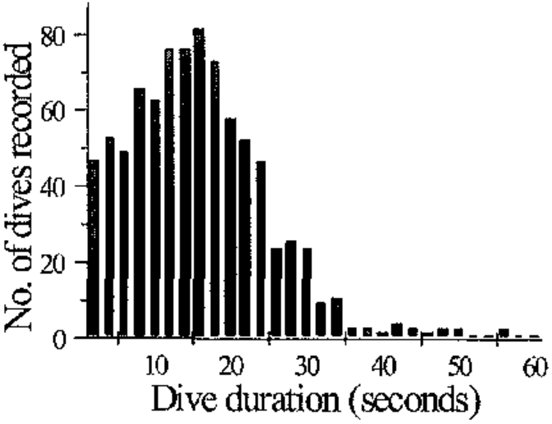


Figure 8.4. The durations of successful dives

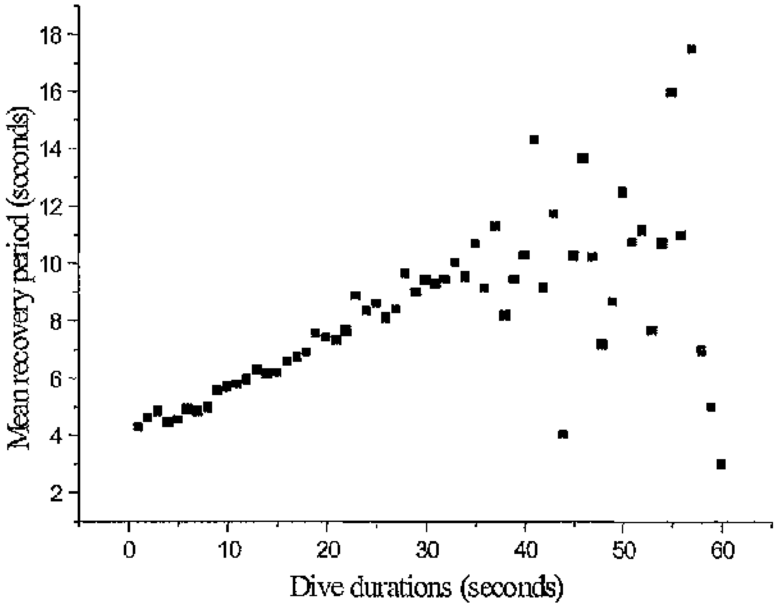


Figure 8.5. The relationship between dive time and the subsequent recovery period for unsuccessful dives. Recovery time expressed as means to reduce data noise.

The mean surface time following successful dives was 6.68 seconds ± 0.007, and after successful dives (where the otter did not take the prey on land, n = 690) 13.33 ± 0.33. The mean surface to dive ratio for successful dives (where prey was not taken on land) was 1.47 ± 0.008, and that for unsuccessful dives was 0.73 ± 0.002. There was a highly significant correlation between the dive time and recovery period (Pearson's product moment correlation coefficient, $r = 0.35$, $n = 4752$, $p < 0.001$). Figure 8.5. shows this relationship between dive duration and subsequent recovery period. The relationship is strongly linear up to dive durations of around 35 seconds.

Of the 2392 dives where the depth was known, both successful and unsuccessful, the mean depth was 2.99m ± 0.005 (± standard error). The maximum depth recorded was at 18.75 metres. The distribution of dive depths is shown in figure 8.6.

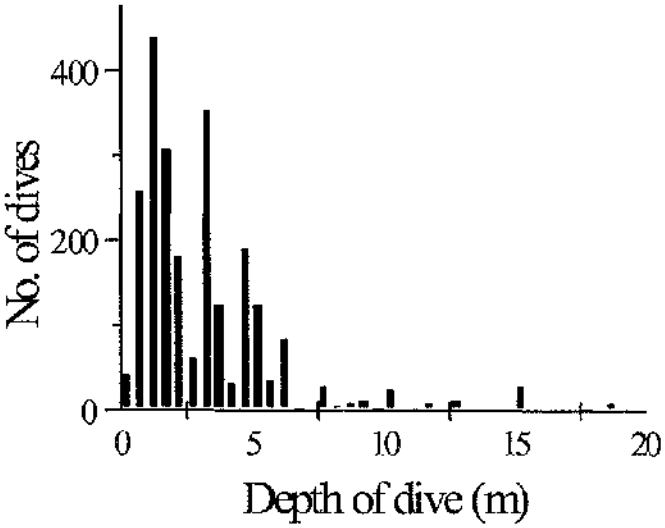


Figure 8.6. The occurrence of all dives at different depths

8.3.1. Effects of water temperature

(a)The dive parameters

The water temperatures recorded ranged from a minimum of 4.0°C to 16.5°C. Data was analysed by non-linear regression analysis and using a multivariate MANCOVA model, with dive duration, surface recovery period and Arcsine transformed surface to dive ratio as dependent variables, and water temperature and depth as covariants.

1. There was a significant alternative exponential relationship between water temperature and the mean depth of dives. The relationship can be described by the equation:

$$y = 26.62.x - 3.06.x^2 + 0.11.x^3 - 63.63,$$

(non-linear regression, $r^2 = 0.79$, df = 15, $p < 0.001$) see figure 8.7.

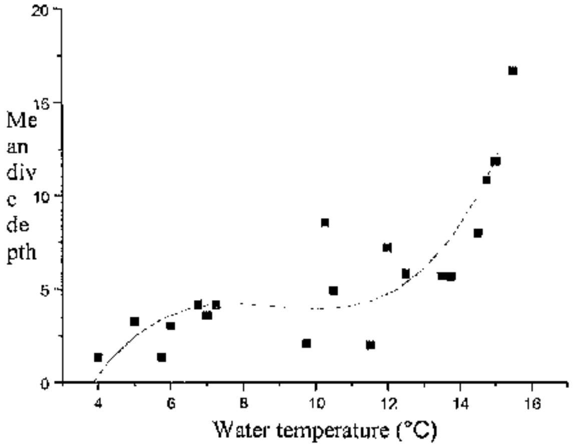


Figure 8.7. The relationship between water temperature and the mean depth of dives

2. There was no independent relationship between water temperature and dive duration, p=0.174, but there was a significant relationship between dive duration and depth, (MANCOVA, adjusted $r^2 = 0.178$, $p<0.001$, , see figure 8.8.)
3. There were weak, but statistically significant relationships between both water temperature (MANCOVA, adjusted $r^2 = 0.039$, $p<0.001$) and depth (MANCOVA, adjusted $r^2 = 0.179$, $p<0.001$) with surface time, see figures 8.9. and 8.10.
4. There were very weak, but statistically significant relationships between the dive to surface ratio with both water temperature (MANCOVA, adjusted $r^2 = 0.023$, $p<0.001$) and depth (MANCOVA , adjusted $r^2 = 0.008$, $p<0.001$), see figure 8.11. and 8.12.

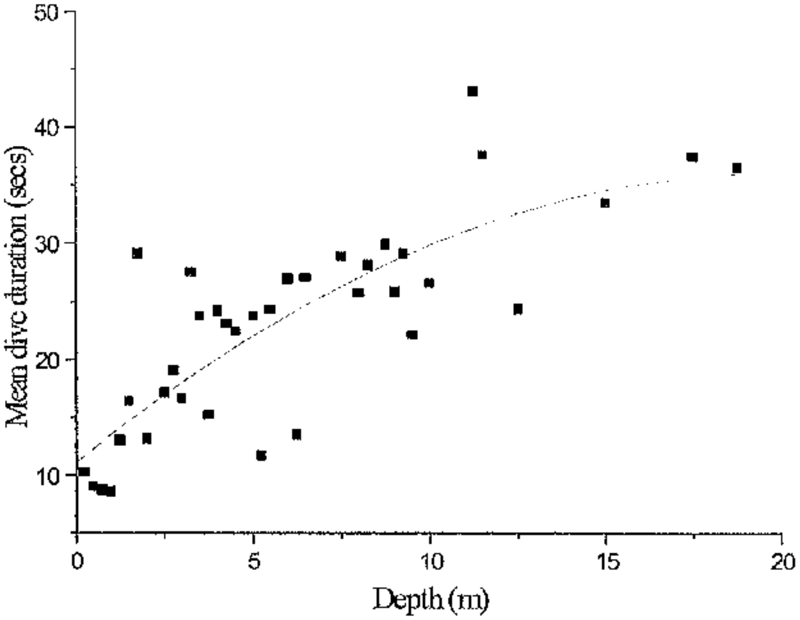


Figure 8.8. The relationship between dive duration of unsuccessful dives and depth. Dive duration shown as a mean to reduce data noise

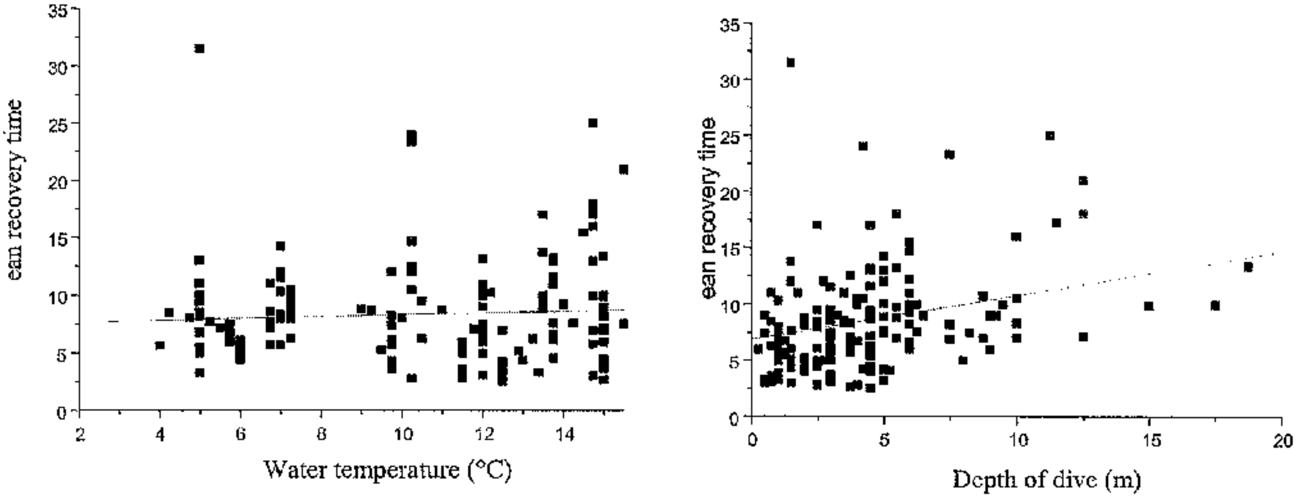


Figure 8.9. The relationship between water temperature and surface recovery time for unsuccessful dives

Figure 8.10. The relationship between the depth of dive and surface recovery time for unsuccessful dives.

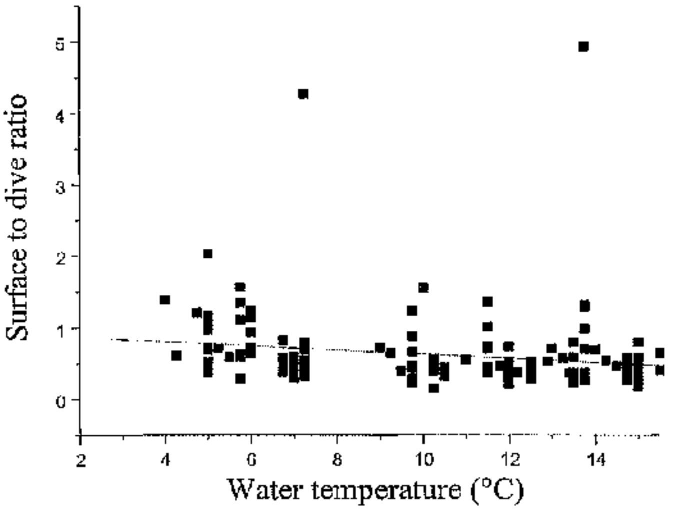


Figure 8.11. The relationship between water temperature and surface pause to dive ratio for unsuccessful dives

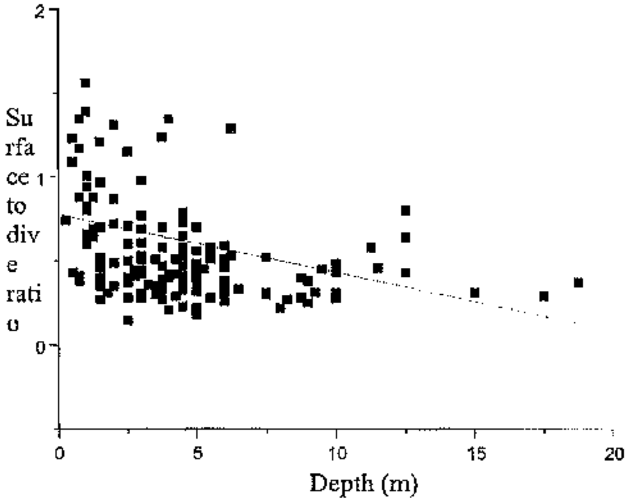


Figure 8.12. the relationship between dive depth and surface pause to dive ratio, for unsuccessful dives.

(b) Foraging intake and success

The relationship between water temperature and the mean rate of food intake can be described by the equation:

$$y = 0.01x + 0.001x^2 + 0.01x^3 - 0.15$$

(non-linear regression analysis, $r^2 = 0.31$, d.f. = 34, $p < 0.01$). Generally, as water temperature rose, so did the rate of food intake., (see figure 8.13.). The relationship between the proportion of dives that were successful in each bout and water temperature was also positive, although this was a weak correlation, (Pearson's Product Moment Correlation Coefficient, with proportion of dives Arcsine transformed, $r = 0.23$, $n = 174$, $p < 0.01$), see figure 8.14.

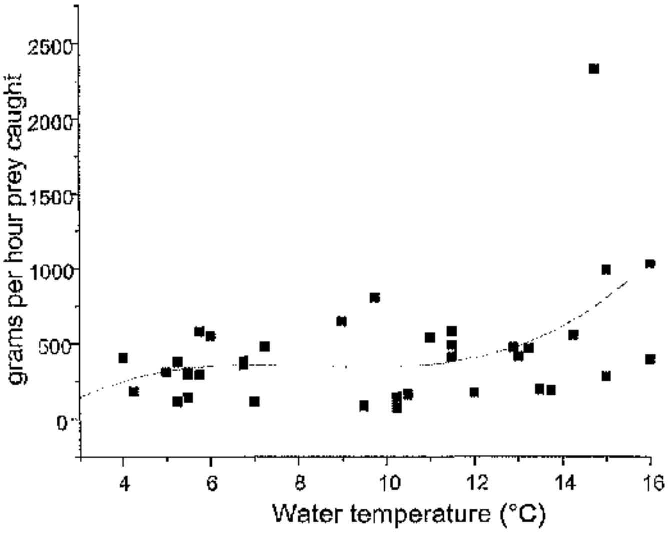


Figure 8.13. The relationship between water temperature and the rate of food intake of foraging otters

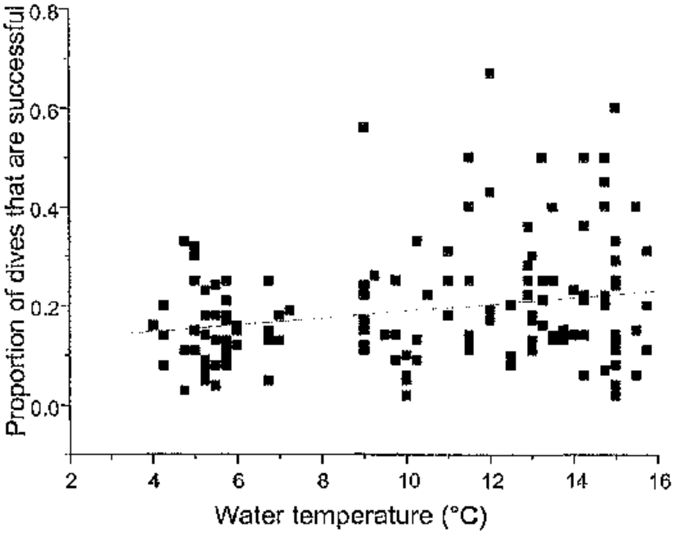


Figure 8.14. The relationship between the proportion of dives that are successful and the water temperature.

(c) Recovery period on land

Due to the difficulties of obtaining continuous observations of otters, without losing sight of them even briefly, only 35 complete continuous bout and resting periods were observed. There was a highly significant relationship between the proportion of the foraging bout that took place in the water, and the water temperature, which is described by the equation: $\frac{\tau_W}{\tau_W + \tau_L}$ ($r^2 = 0.48$, d.f. = 33, $p < 0.001$), see figure 8.15. There is an overall decrease in the proportion of the activity that is spent in the water, relative to the time recovering on land.

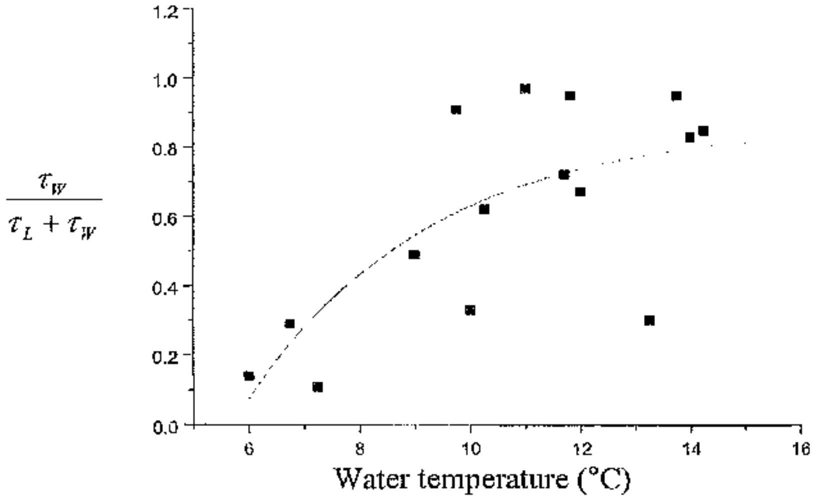


Figure 8.15. The relationship between water temperature and the proportion of time an otter spends in the water.

8.4. DISCUSSION

In this section we have examined the possible behavioural responses to the physiological demand of foraging in cold water temperatures. Kruuk *et al* (1994) demonstrated an elevated metabolic rate with decreased water temperatures, and we examined a number of the parameters of foraging by otters to look for variation in them related to these increased metabolic costs

9.4.1. The dive parameters

Observation of the duration of dives gave us a slightly lower value than other workers. For example Kruuk and Hewson (1978) recorded mean dive durations of 23.1 seconds at the Ardnish peninsula, near Arisaig on the west coast of Scotland, Conroy and Jenkins (1986) recorded dives of 20.1 seconds in Shetland, Watt (1991) recorded 22.7 seconds on Mull, and Nolet *et al.* recorded 23.3 seconds, again at Shetland. All of these figures are lower than any estimates of the aerobic dive limit of otters, which may be greater than 96 seconds (Kruuk 1995).

The linearity of the relationship between dive duration and the subsequent surface recovery period is similar to that described by Nolet *et al.* (1993) and Kruuk *et al.* (1997). While the relationship is strongly linear, the correlation breaks down above 40 second dives, see figure 8.5, with a seemingly random relationship from this point upward. Nolet *et al.* (*Ibid.*) did not present their data graphically, but the same data is displayed by Kruuk (1995), however only dives lasting less than 40 seconds are shown, so the comparison cannot be made with our data. Kruuk *et al.* (1997) also did not display their data. The reason for the seeming randomness of the relationship between the dive duration and recovery time of these longer dives may be caused by observer error. There exists the possibility that during observations of diving that a surfacing, recovery and subsequent dive was not seen, and so what was recorded as a single dive was in fact more than one, and therefore the recovery period was not a reflection of the actual cost. However since there were relatively few longer dives, (65 dives out of a total of 5495 were recorded that were over 50 seconds in duration), we can be confident that this did not affect our analyses to any appreciable extent.

Nolet *et al.* (1993) used their described linear relationship between underwater and recovery time to conclude that the energetic costs per unit time underwater were constant, regardless of activity, that is actively foraging as opposed to travelling to the foraging patch, or any other variables. However Houston and Carbone (1992) modelled a situation where an approximately linear relationship between surface and underwater time is created, despite the relationship between surface time and underwater oxygen consumption being non-linear. This situation was created as a consequence of varying the travel time, and thereby the proportion of underwater time devoted to foraging, in order to maximise the proportion of time spent foraging. In this light the conclusion by Nolet *et al.* must be viewed as tentative.

Mean feeding success of the otters in this study, measured as the proportion of dives that were successful in obtaining prey, was lower than that described in Shetland. While locally the homogeneity in success rates recorded has been striking, (Kruuk *et* *al.* 1990), overall it is common to see large fluctuations related to season, depth, level of exposure, and year. Success rates have been recorded as low as 12 per cent in the sea (Kruuk and Moorhouse 1990), 7 per cent in freshwater (Conroy and Jenkins 1986) and as high as 38 per cent in the sea (Nolet *et al.* 1993). This is consistent with variations in success rates of other species of otter, such as Sea otters whose success rates can vary between 35 and 90 percent (Estes *et al* . 1981 and Ostfield 1982, respectively) and Marine otters (*Lutra felina*) where variations between 38 and 16 per cent have been recorded. Kruuk *et al.* (1990) suggest that success rate is not a suitable measure of prey catching effort, however in some situations it can be of use, see for example Ostfield 1991, and chapter 9.

8.4.3. Fluctuations in the foraging parameters with water temperature

The first parameter of foraging examined was the otters use of depth, and this was seen to increase significantly with water temperature. We shall deal with this phenomenon at some length in chapter 9.

We examined two components of the dive cycle, underwater time and the subsequent recovery time on the surface, and the ratio between them, in relation to water temperature, and depth. Both of the variables had a positive linear relationship with depth, but only the surface time had any relationship with water temperature. This relationship though, despite its significance is very weak ($r^2 = 0.039$), and the significance of it is likely to be a function of the large sample size, rather than of any genuine relationship. If this is the case then our data is in accord with Kruuk *et al.*

(1997), who while they demonstrated larger dive and recovery times in colder water, the relationships were weak and were explained as an effect of depth, (though this was not recorded directly in their study), rather than one related to physiological costs. This is consistent with our prediction that there would be little direct effect of water temperature on these diving parameters. This prediction was made in the context of the study by de Leeuw (1996), that suggested that the metabolic costs of thermoregulation are met after the foraging bout, rather than during it. The temperature of the water foraged in by coastal otters in Scotland is always going to be lower than the body temperature of the animals themselves, (we recorded no sea temperatures higher than 16.5°C) so there will always be a degree of heat loss to the water. As such we would expect a otter to minimise its time in the water, whether the water is warm or cold, and so we would expect there to be little change in these parameters. We did however predict that there would be longer recovery periods on land, and this prediction will be dealt with subsequently.

The other measures of otter foraging behaviour showed significant relationships with water temperature. Both the success rate of dives and the mass of prey caught per minute increased in warmer water. It is of course likely that these two measures were linked. This result would not have been expected for two reasons

1. our data on fish behaviour and water temperature suggested that fish would be easier to catch in cold water
2. The otters catch larger prey in the winter

In chapters 6 and 7 we discussed how temperature mediated changes in prey behaviour would influence predator behaviour, and concluded that it did not influence the dive durations needed to capture different prey types, rather it affected the timing of foraging activity, and these results are consistent with that conclusion. That the otters catch larger prey, particularly gadoids, (see chapter 4) in winter does not mean they have a greater food intake rate. With the success rate of dives lower it means that while their prey is bigger, there is less of it. The increase in mass per minute food intake is also consistent with our estimates of prey availability, chapters 2 and 5, where we demonstrated a higher available biomass in warmer water. Furthermore the results confirm that the traps give a genuine measure of prey abundance since they are correlated with the actual rates of capture by otters, and reinforce the conclusion that water temperature affecting the catchability of prey in the traps is not the main determinant of the catches we obtained.

These results also add further dimensions to the model described by Kruuk and Carss (1996) which predicted that otters would have to spend more time foraging in colder water temperatures to compensate for the increased metabolic costs. The model assumed a constant intake of food in all temperatures. With the decrease in both the success of dives, and the mass of prey taken per unit time described by our data, the otters would need to further increase the time spent foraging during the colder months of the year. In chapter 7 we hypothesised that otters may forage during the night in the winter. In the circumstances predicted by Kruuk and Carss model (1996) and reinforced by our data, where an otter is having to spend the larger part of its day searching for food, it seems even more likely that foraging will occur during the night as well as during the day.

8.4.4. The recovery period on land

De Leeuw (1996) hypothesised from a study of the diving behaviour of tufted ducks, that during diving the main energetic costs are derived from overcoming hydrodynamic forces, and the costs of thermoregulation are met after the diving bout is completed. We developed the implications of this hypothesis by describing a simple model that examined the relationship between the water temperature in which an animal is foraging, and the subsequent recovery period after a foraging bout. A linear relationship was predicted between water temperature and the proportion of time an animal spends actively foraging, as opposed to recovering on land.

The data collected from Taynish was analysed to examine the extent to which the predictions of the model were met. While there was an overall decline in the proportion described by: $\frac{\tau_W}{\tau_W + \tau_L}$, at lower temperatures, the relationship deviated from linearity, as the proportion of time allocated to recovery increased (see figure 8.15). As such our overall prediction was met, that is that the metabolic costs of thermoregulation during foraging in water would be met after the foraging bout is completed, and that this would be reflected in proportionately larger recovery periods after bouts. However the data did not fit that of the model in that the relationship was non-linear, falling sharply after the initial decrease. This may be due to one or both of the following:

1. The model is a simplification of a complex situation. In particular we estimated our constants, α and β from observations made of a single individual otter,

therefore there may be errors both in the estimation and in the possibility that the data itself is atypical.

2. A key assumption of the model is that the constants, α and β are indeed constant. This assumption is likely to be contradicted in reality. These constants are in the equations as a means of describing heat loss and gain over time, and in assuming that they are constant we are assuming that the rate of heat loss and gain will also be constant, under the influence of the other variables described. It is however probable that other factors may influence the rate of heat loss. While there is no direct evidence of the influence of such variables on rates of thermal change in the otter, a large body of theoretical and empirical data exists that suggests such is the case. For example Hind and Gurney (1996) have described a model which incorporates heat loss by free and forced convection, as created by swim speed, into its parameters and the model suggests a strong relationship between swimming speed and thermoregulatory costs. This model could also be extended to the speed at which the water a predator is foraging in travels due to tidal currents. The temperature of the surrounding water may also have an effect on the rate of heat loss. MacArthur (1984) has demonstrated this for aquatic muskrats and in the model described here there may also be a similar effect on the rate that heat is recovered on land, caused by the temperature of the air. Furthermore these effects of water and air temperature would not be independent of each other. While the model described here did not include such parameters, we can hypothesise to some extent how changes in them would affect the overall predictions. If the rate of heat loss from otters foraging in water is increased by depressed water temperatures, in a manner similar to that described by MacArthur (1984) then we would predict the

necessity of longer recovery period on land. Similarly when the air temperature, which is likely to be positively correlated with water temperature, is low, the rate of recovery would be slower, so again we would predict longer recovery periods on land, relative to the length of the preceding foraging bout.

Kruuk *et al* (1997) suggested that otters actively increase their body temperature before a foraging bout, for example by vigorous activity, and then cease the bout when their temperature falls below a certain level. Unfortunately due to the difficulties of catching otters and implanting them with transmitters, their sample sizes were small and so their results were somewhat tentative. During data collection for this study otters have been observed commencing foraging directly from rest, which would not give them the opportunity to raise their temperature, so this hypothesis may not be true for all foraging bouts, if any. Moreover since the model described in this study defines T_B as a maximum body temperature, were the hypothesis of Kruuk *et al* (*Ibid.*) true it would not affect the predictions of the model.

In conclusion, overall, the data we collected from observations of otters foraging in the wild were consistent with the predictions made from the model, that is,

1. Water temperature has no strong effect on the individual components of the dive cycle

2. Otters spent a greater proportion of their time recovering on land when foraging in colder water

We therefore conclude that otters postpone the metabolic costs of recovering from heat loss during foraging until after the foraging bout is completed.

CHAPTER 9.

TEMPERATURE-MEDIATED FLUCTUATIONS IN THE USE OF DEPTH BY FORAGING OTTERS

CHAPTER 9

9.1. INTRODUCTION

Orians and Pearson (1979) introduced the term "central place forager" for animals that regularly return to the same place with food. Diving animals can be considered to be central place foragers since they always return to the same place, the surface, (Houston and MacNamara 1985), and as such optimality analysis has been applied to a number of diving foragers, particularly avian and pinniped. The role of depth in influencing a variety of the parameters of dive behaviour has been examined, and the role it plays in the energetic costs and benefits of aquatic foraging discussed to some degree for a number of species. In general many animals do not dive as deep as they are physiologically capable of (Burger 1991), and in particular the Eurasian otter has been shown to forage almost entirely in shallow water (Kruuk *et al.* 1984, Kruuk and Moorhouse 1991, Nolet *et al.* 1993, chapter 8) despite being capable of attaining greater depths (Twelves 1983) and there being better quality food available at these depths (Kruuk *et al.* 1984, Kruuk *et al.* 1988). Nolet *et al.* (1993) suggested that this was due to increased heat loss with depth, and presented data to support this. However Houston and McNamara (1994) argued that other possible explanations were not eliminated, particularly the optimal breathing model of Kramer (1988). Although Houston and McNamara (1994) did not reject the heat loss hypothesis, they criticised it for not making explicit predictions about how the pattern of diving depends on depth.

The tendency for otters to show a preference for foraging in relatively shallow water was first described by Kruuk *et al.* (1985) for otters feeding in coastal waters in Shetland; 64% of the dives (n = 1008) observed in this study were of depths less than three metres deep, and subsequent observations confirmed this (Kruuk and Moorhouse 1990). Otters were observed diving as deep as 14m during this study (Kruuk 1995) and an otter has been found in a lobster creel set at 15m depth (Twelves 1983). Also described by Kruuk *et al.* (1985) was an increase in productivity, in terms of the mass of prey caught, in deeper water, and an increase in the success rate of dives with depth. Fish trapping in the same area confirmed that there were larger prey in deeper water (Kruuk *et al.*1988). The occurrence of these deeper dives was not tested in relation to any other variables.

Otters rely upon a layer of air trapped within their pelt for insulation against heat loss (Tarasoff 1974), and this thermo-insulatory function can be compromised by pollution (in sea otters, Costa and Kooyman 1982) and also by the formation of salt crystals after foraging in salt water (Kruuk and Balharry 1990). Associated with the maintenance of the pelts, otters spend large amounts of time grooming and the amount of time spent grooming has been significantly correlated with the depth of foraging prior to it (Nolet and Kruuk 1989). Many of these observations however were of radio-collared animals and the grooming and rolling behaviours seen are likely to have been related, at least in part, to the presence of the transmitters (Kruuk 1995).

Following Boyle's law, which states that volume of gas is inversely proportional to pressure, depth will compromise the thermo-insulatory capacity of any trapped air layer, leading to increased heat loss. Thermo-insulation via a trapped air layer is also common to virtually all diving birds (Wilson *et al.* 1992) and birds have been shown to compensate for the increased heat loss metabolically (Culik *et al.* 1989) and via muscular heat genesis (Paladino and King 1984). Vigorous grooming, such as described by Nolet and Kruuk (1989) after deep dives, may act as non-shivering thermogenesis, and compensate for the increased heat loss.

Depth is only one of a number of factors that could affect heat loss. For example McArthur (1984) described faster rates of heat loss in colder water temperatures in muskrats (*Ondatra zibethicus*) implanted peritoneally and subcutaneously with thermal radio-transmitters. Conversely Croll and McLaren (1993) found no change in the thermal conductance of common (*Uria aalge*) and thick - billed murres (*U. lomvia*) with water temperature, although they assumed a constant body temperature for their calculations, an assumption likely to be contradicted in reality (see for example the fluctuations in otter body temperature described by Kruuk *et al.* 1994). It would therefore seem probable that environmental factors, such as water temperature could influence the occurrence of deeper water dives

Nolet *et al.* tested their heat loss hypothesis against data obtained in Shetland between 1983 and 1985, largely during the summer months. Observations in 1984 were of a single otter which was radio-collared and this may have affected its use of depth when foraging. Their data supported the hypothesis that rate of heat loss influenced the use of depths, in that they demonstrated a negative correlation between the duration of a hunting bout with the weighted average of the maximum pressure encountered.

During their observations measurements of water temperature were not made, so any influence it may have had upon heat loss and the occurrence of deeper dives was not measured. However the tentative support given by their data to the hypothesis that otters limit their foraging to shallow water in order to limit heat loss due to the effect of hydrostatic pressure on the insulatory air-layer in their pelt implies a further hypothesis. That is, in warmer water temperatures, the otters would take advantage of the reduced costs due to heat loss and forage in the more productive deeper water, thereby maximising their rate of energy gain.

In this part of the study, we therefore set out to examine the factors influencing the otters use of depth. To do so, we;

1. examined the potential benefits of foraging at greater depths, in relation to available biomass and the success of dives
2. examined the potential costs of foraging at greater depth, that is in terms of length of dives and prey handling time, and whether the rate of heat loss is greater at increased depth
3. tested the prediction that if heat loss limits the otters use of depth then in higher water temperatures they will dive deeper
4. constructed a post-hoc optimality model to account for these features.

9.2. METHODS

We set out to test the optimality of foraging at different depths by otters, and so we firstly examined the benefits of feeding in different depths, then the costs, and finally we examined what relationship there was, if any, between water temperature and the depth of otter dives

9.2.1. Benefits of Foraging in Deeper Water

1. Prey availability

In order to determine the relative availability of prey species at different depths we set double-funnelled creels, as described in chapter 2, (see also Kruuk *et al.* 1988). The traps were placed in a straight line going out from a point on the Loch Sween side of the Taynish peninsula. Two traps were placed at each of the following depths, 2m, 4m, 6m, 8m and 10m. Depths were measured with a plumb line from a boat, at low tide. The traps were emptied and checked every 24 hours, and all the contents were weighed to the nearest 0.1 grams and the length from tail fork to the end of the head measured to the nearest mm. Crab length was measured as the widest part of the carapace. This was carried out for 5 days in July 1996. Due to adverse weather conditions it was only possible to do this during the summer.

Available biomass was measured as the weight of the food available to the otter. For the piscine prey, available was taken as being the whole fish, while for the crustacean prey, this was only the carapace flesh, which is the only part of a crustacean that an otter will eat, (Watt 1991).

2. Dive behaviour

Observations were made of otters feeding along the Loch Sween side of the Taynish peninsula, where a range of depths was available. Using a Psion 2 organiser, the lengths of dives were recorded. A complete dive was scored as from the point of submersion of the head, to the point of the emersion. Dives were recorded as either successful or unsuccessful, and whenever possible prey was identified, and an estimate of its size made, using the width of the otters head as a guide. For crustacean prey, which was eaten on the land, an exact measure of size was made by the recovery and measurement of the carapace, which was discarded by the otter after removal of the crab flesh. The position of the otter in the water was recorded onto maps using terrestrial markers as guides, and depth was obtained from Admiralty depth sounding charts, corrected for state of tide. A feeding bout was taken as the whole of a period that the otter was in the water, without coming on to land, and success rate during that bout was measured as the proportion of dives that were successful. The success rates of bouts were examined with respect to the mean dive depth of the bout to identify any relationship between them.

9.2.2. Costs of Foraging in Deeper Water

1. Dive parameters

From the observations described above, the durations of both successful and unsuccessful dives were correlated with the depth in which they occurred by non-linear regression analysis, and the slopes of the two lines were compared.

2. Prey capture costs

Handling time of prey items was measured as the time from the beginning of the successful dive to the moment when the prey item was completely consumed, and these were compared to each other by means of a Kruskall-Wallis one -way ANOVA. This non-parametric test was used due to heteroscedasticity of the groups

3. Heat loss

To assess the rate of heat loss from an otter four "artificial otters" were constructed. The pelt from an otter that had died in a road accident was removed, and this was used to line the exterior of four tins of length 15cm and diameter 8cm. The pelt was attached to the metal by "Superglue" and any seams were sewn using 0.69mm-diameter "Prolene" monofilament suture thread. The lid of the tin was pierced and a thermal probe inserted, attached by a length of wire to a digital thermometer, then the lid was lined with a thermo-insulator. The four fur-covered tins were attached to a dexian metal frame.

During experiments the tins were filled with boiling water and the lids sealed on. The frame was then put into water of fixed depths of 2m, 4m, 6m, 8m and 10m. For each depth, and for each tin, the temperature of the water inside the tin was measured every five seconds. The rate of heat loss was subsequently recorded as the no. of seconds it took for the temperature of the water to drop from 38° to 28°C.

The experiment was carried out twice, to prevent decay of the skins, once in freshwater at Loch Lomond, and once in salt water at Hunterston quay, on the firth of Clyde. Both times the experiment was carried out on still days to minimise water currents, and at Hunterston the experiment was carried out at slack tide.

The data was analysed in the form of an ANOVA general linear model. The dependent variable was rate of heat loss, as above, the covariant was depth, and the factors were tin, that is the tin in which the recordings were made, and type of water, that is fresh or salt.

9.2.3. Water Temperature and the Use of Depth

During the observations of otters described above the temperature of the water at 2m was measured using a Conductivity Salinity and Temperature (S,C.T.) meter. Clark (1987) described the temperature in temperate shallow water as being constant throughout the water column, so this figure was assumed to be correct for all dives. The temperature was measured after the observations had taken place to avoid any disturbance. The mean depth of dives occurring at each temperature was calculated and this was examined in relation to temperature, using non-linear regression analysis. Since otters feed on demersal prey (for example Kruuk 1995) it was assumed that they always dived to the bottom of the water column. This and all the above statistics were carried out using SPSS 7. statistical computing package.

9.2.4. Post-Hoc Optimality Model

In order to explain any relationship observed between water temperature and the use of depth in otters, in 9.2.3. we combined the data from the costs and benefits of foraging in the form of a post-hoc model, describing the optimal depth in which an otter should forage throughout a range of water temperatures.

9.3. RESULTS

9.3.1. Benefits

9.3.1.1. Prey availability.

Figure 9.1. shows the proportion of the catch of the important otter prey items caught in the traps over the 5 days. The majority of prey were caught in water under 5m depth. However of note is the numbers of edible crabs in increasingly deeper water. If this data is described in terms of relative biomass available, in grams, (see methods) there is a marked increase in available biomass above six metres in depth., (figure 9.2.).

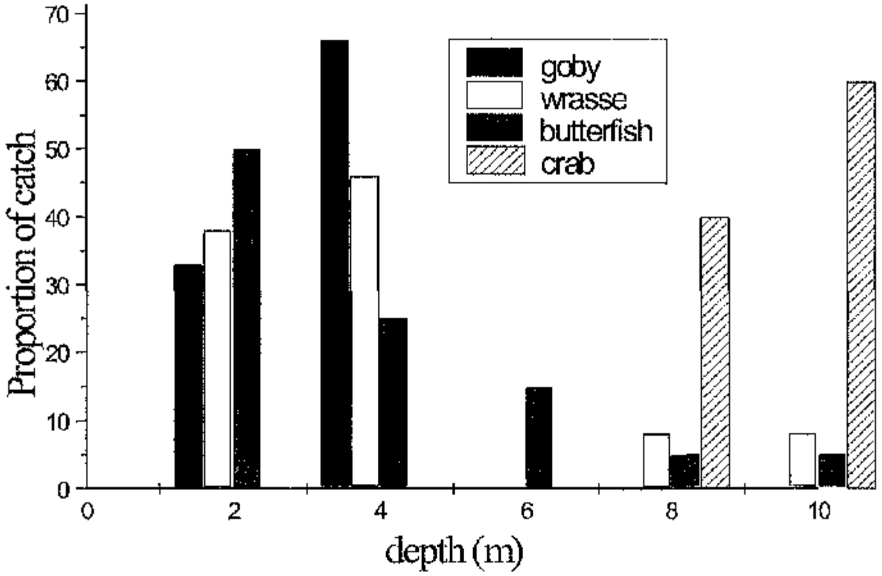


Figure 9.1. The proportion of the catch of some important otter prey species that were obtained at different depths

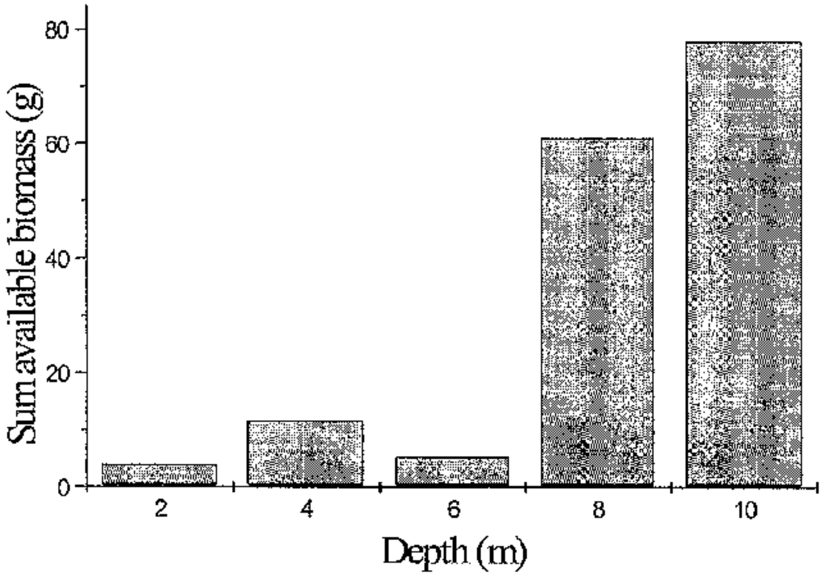


Figure 9.2. The total available biomass, as determined by trapping, at different depths

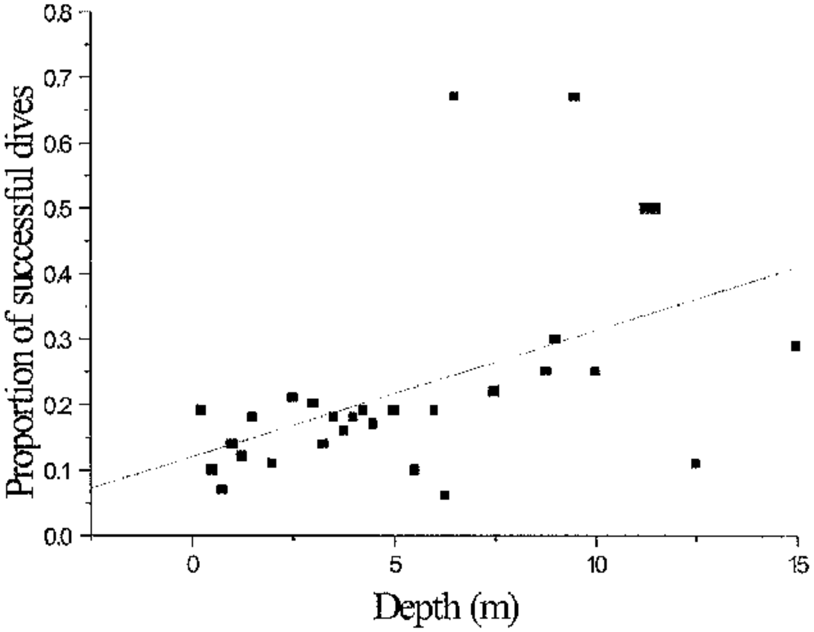


Figure 9.3. The proportion of dives observed at different depths that are successful

9.3.1.2.Dive success

The proportion of dives that were successful at different depths is positively correlated with depth, (Figure 9.3.) and this relationship was highly significant, (Spearmans rank correlation coefficient, $n = 30$, $r = 0.60$, $p < 0.001$). That is the deeper the dive was, the greater the probability that it would be successful.

9.3.3. Costs

9.3.3.1. Dive duration

Both the mean duration of successful dives and unsuccessful dives had highly significant relationships with depth, but these relationships were different, (figure 9.4. and 9.5.). The relationship between the length of unsuccessful dives corresponded to the equation:

$$y = 10.98\,x^{0.37},$$

($r^2 = 0.67$, $p < 0.001$), while that of successful dives corresponded to:

$$y = 7.78 + 0.88\,x - 0.01\,x^2,$$

($r^2 = 0.58$, $p < 0.001$). The unsuccessful curve increases initially but levels off, so the dive times increase sharply with depth, but begin to level off at a depth of roughly 10m. Successful dives also initially increase with depth then level out, but then they begin to decrease with depth, although this decrease is only caused by one popint on the graph.

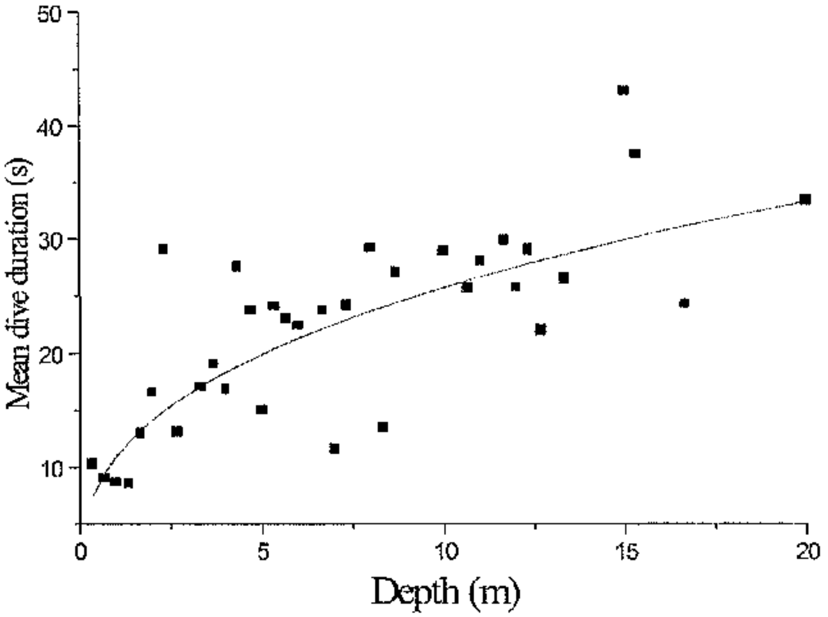


Figure 9.4. The relationship between the mean duration of unsuccessful dives and depth

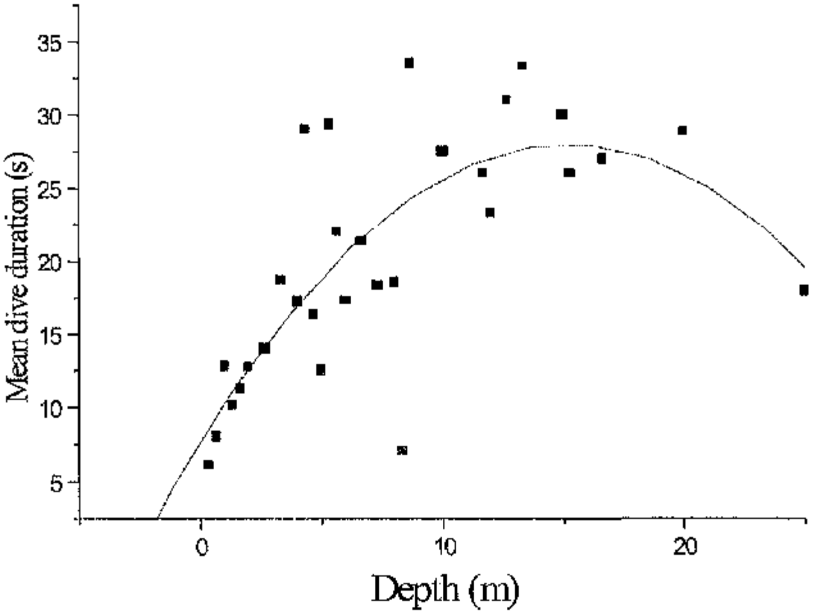


Figure 9.5. The relationship between the mean duration of successful dives and depth.

9.3.3.2. Prey capture

When the handling time of the nine most important prey types was examined, that is the time from initiating the capture dive until the prey is completely eaten, there were highly significant differences between the eight most important prey types, (Kruskall-Wallis one-way ANOVA, $\chi^2 = 27.47$, df = 7, $p < 0.001$). As shown in figure 9.6. the largest handling time was associated with crustacean prey. Crustacean prey, which was almost entirely edible crabs, were always taken onto land to be eaten, (see also Watt 1991 and Kruuk 1995), and so this increased handling time greatly, and the prey type with the second largest handling time, sea-scorpions, were also always eaten on land. On the whole, if we compare these data with those from chapter 4 of prey depths, and the data above, the prey with the longest handling times were on the whole those that were captured at the greatest depth, suggesting another cost of foraging in deeper water.

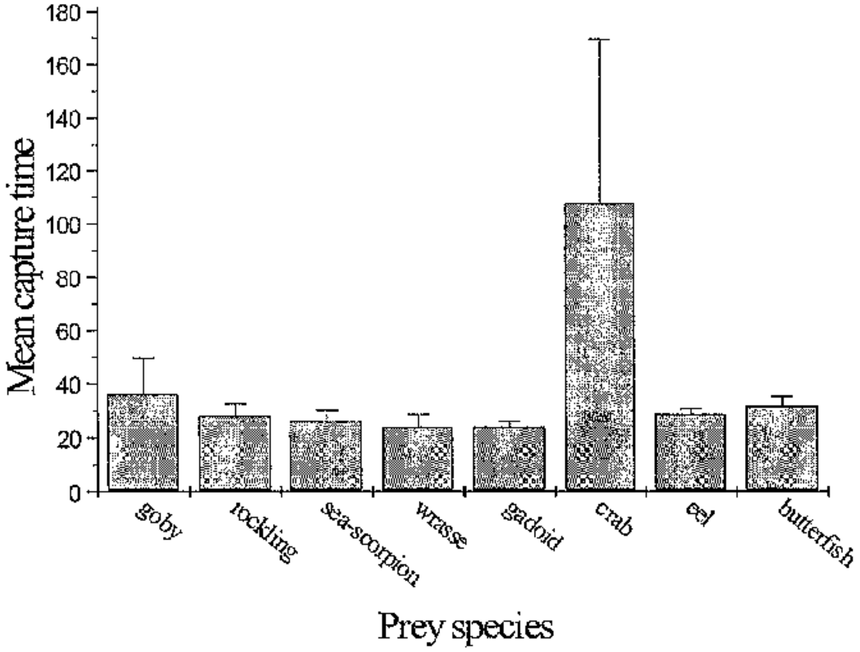


Figure 9.6. The mean capture times, ± standard errors, of the prey species of otters.

9.3.3.3. Heat loss

The results of the ANOVA general linear model examining the effects of depth on rate of heat loss are summarised in table 9.2. There was a very significant positive correlation between water depth and rate of heat loss, (figure 9.7.) and the type of water, (salt or fresh) and the individual tin being used did not have an effect, neither were there any significant interaction terms.

Factor / covariant	d.f.	F	Sig.
Depth	1,30	12.45	<0.01
Skin	2,30	1.69	N.S.
Water	1,30	5.74	N.S.
Skin*depth interaction	2,30	0.69	N.S.
Water*depth interacion	1,30	0.412	N.S.

Table 9.2. Results of the ANOVA general linear model examining the influence of the rate of heat loss from three vessels covered in otter fur, in both sea water and fresh water.

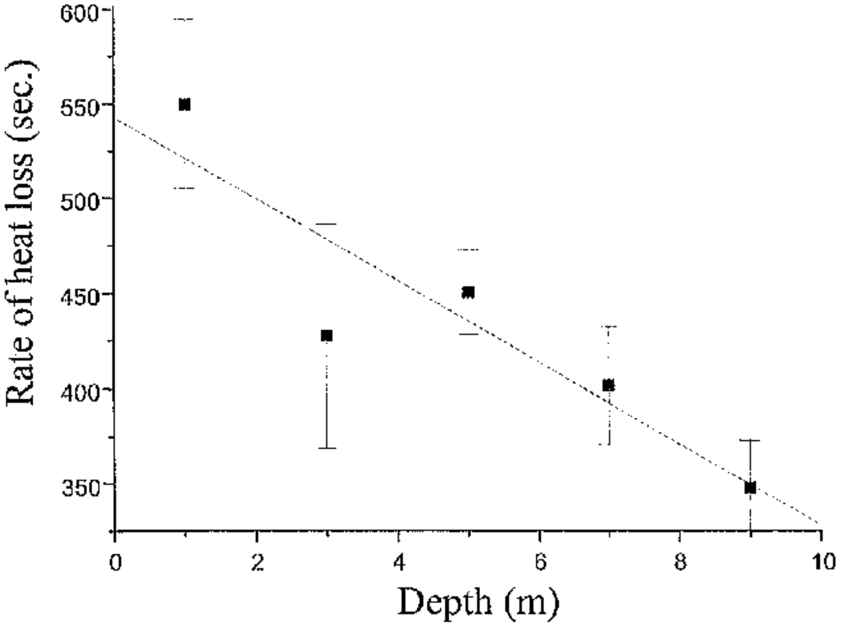


Figure 9.7. The rate of heat loss in relation to depth

9.3.4. Use of Depth in Relation to Water Temperature

There was a highly significant positive relationship between mean dive depth and water temperature, which can be described by the equation:

$$y = 26.62.x - 3.06.x^2 + 0.11.x^3 - 63.63,$$

($r^2 = 0.79$, df = 15, $p < 0.001$). This relationship is shown in figure 9.7. The relationship increases sharply from zero, stays level from 6°C to 12°C and then rises rapidly.

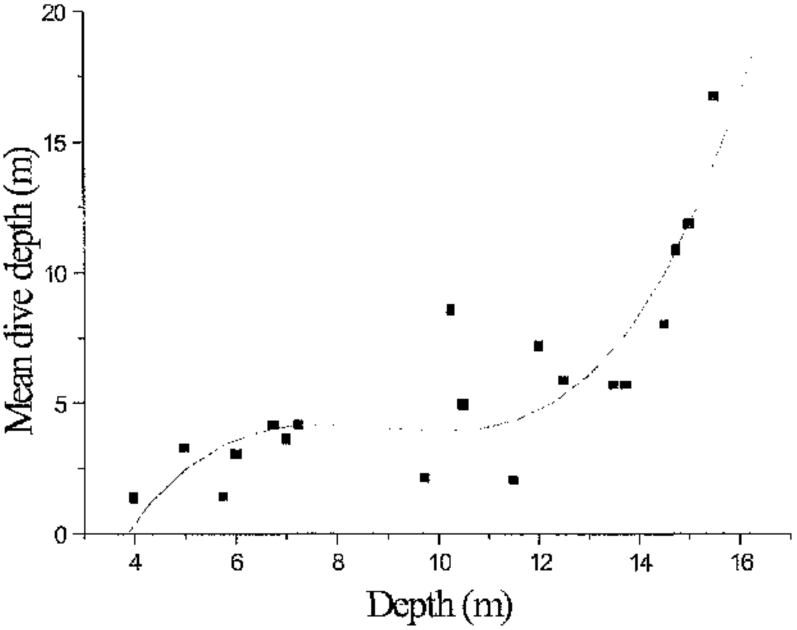


Figure 9.8. The relationship between depth and the mean depth of otter dives.

9.4. OPTIMALITY MODEL

Examination of an animals decision where and when to forage can be approached from simple Darwinian logic, that selection will favour a phenotype that minimises energetic costs, and maximises energetic gains, (Krebs and Kaclnik, 1991). Optimality models allow us to examine such energetic decisions, and from this to explain or predict an animals behaviour. Here we have constructed an optimality model to explain the foraging behaviour of otters in relation to depth.

If we examine the data obtained from fish trapping at various depth and plot it as a graph of available energy against depth, assuming a starting point of zero, we can express the relationship between energetic gains and depth as shown in figure 9.9.

Figure 9.9. Modelled relationship between available biomass, expressed as energy, and depth.

This graph shows that from the initial stating point of zero available biomass at a depth of 0m, that is, on land, there is an initial sharp increase in biomass in shallow water. As demonstrated by the trapping experiment, the available biomass then is constant for a range of depth, until around eight metres, when edible crabs become available, and so the available biomass increases sharply (see also figure 9.2) and then levels off again.

From the data of heat loss, as well as dive duration and prey handling times, we can reasonably assume that the costs in terms of energetic loss steadily increase with depth. Increases in water temperature will decrease these costs of foraging, though the starting point of the relationship at zero depth, that is, when the animal is out of the water, will be the same. We can picture this graphically as shown in figure 9.10.

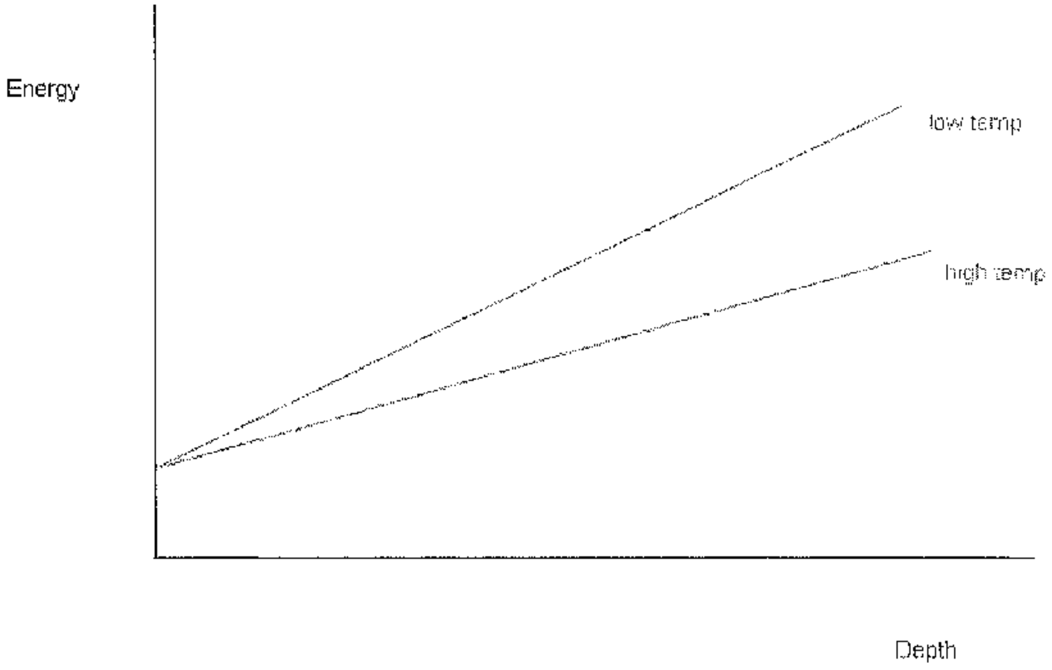


Figure 9.10. The modelled relationship between the costs of foraging and depth, at two hypothetical water temperatures

This graph demonstrates that difference in energetic costs of an otter foraging between two water temperatures. At zero depth it is assumed that the only energetic costs are those required to maintain the basal metabolic rate, and that these will be the same irrespective of water temperature. Once in water the energetic costs will increase linearly with the depth of water foraged in, due to increased heat loss due in part to the effect of pressure on the insulating air layer of the pelt, and also to greater exposure to the water, hence longer periods of heat loss, because of increased dive times. The difference between the rate of heat loss and hence the energetic costs of foraging will increase as the depth of foraging increases.

Finally, we can combine the two graphs, as shown in Figure 9.11. This figure shows that at low water temperature the optimal dive depth for an otter to forage will be shallow, but as the temperature increases there will be a switch and it will become more profitable to dive at greater depth. This depth will then remain the optimal depth as the temperature increases, so most foraging will occur at this depth. From the model we therefore would predict that at low water temperatures most otter activity will occur in shallow water, and this remains the same as temperature increases, until at a given point at which the otters will switch to deeper water and concentrate most foraging at that depth. This will then remain the most commonly used depth as water temperature increases.

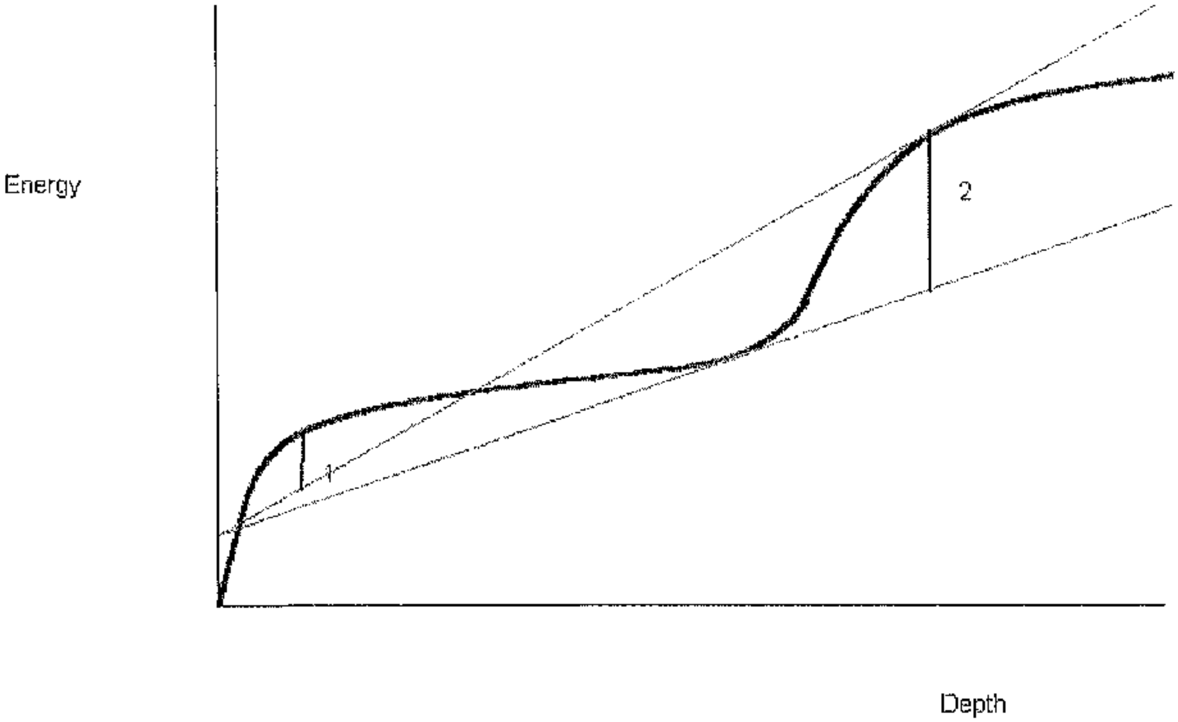


Figure 9.11. Completed modelled relationship describing the costs and benefits of foraging at different depths. The currency used is energy. The vertical lines represent the maximum net energy gain at the two temperatures; 1. *Low temperature,* 2. *High temperature.*

These predictions fit the data from the observations of the use of depth in relation to water temperature reasonably well; the use of depth increases then levels out until warmer water temperatures when it rises sharply. It is only in the final levelling out of the model that the observed data does not fit.

9.5. DISCUSSION

The overall aim of this section was to account for the observation that otters forage in relatively shallow water despite there being better prey in the deeper water in which they are physiologically capable of diving. Following Nolet *et al.* (1993) we set out to test whether heat loss was a key determinant of this behaviour, and then to try and understand the manner in which this relationship worked by providing a basic model. To do so firstly it was necessary for us to confirm that the results from Shetland, from which these ideas were developed, matched the situation at Taynish. These results were that otters foraged chiefly in shallow water, that there was better prey in deeper water, that dive durations were longer in deeper water and that otters foraged with a higher success rate in deeper water. Secondly we experimentally determined whether the hypothesis that otters would lose heat faster in deeper water, due to the effect of increased pressure compromising the thermo-insulatory function of the pelt by compression of the air layer, was true. Thirdly we tested the hypothesis that depth of foraging in otters was limited by heat loss, by assuming that if it were true then otters would forage deeper in warmer water, by field observations. Finally we attempted to explain the observations of foraging, by means of an optimality model. Each of these aspects of this study will now be discussed.

9.5.1 The Use of Depths

As described in chapter 8, in common with the results of other workers, we found that otters tended to forage in shallow water. What is immediately interesting about the relationship however is that there are a number of deeper dives, and it was the point of this chapter to determine why this is so. It is also worth re-examining the methods from which we obtained this data, to eliminate any potential sources of error. Firstly, we assumed that otters always dive to the bottom. This assumption is borne out by the choice of prey that otters eat, and our results in chapter 4, have confirmed those of every other worker, (see reviews in Mason And Macdonald 1986, and Kruuk 1995) that otters feed almost entirely on bottom dwelling prey. From this knowledge that otters are diving to the bottom, by accurately pinpointing the position of a foraging otter on the map, and correcting for tide states, we were able to quantify with a high degree of accuracy the depth that an otter was diving to. Therefore it is likely that there are only minimal errors in our dive depth data.

9.5.2. Prey Availability

We have already discussed at some length in chapter 2 some of the possible problems with the use of stationary traps to assess prey populations, and concluded that overall they gave a reasonably accurate picture of overall abundance. The results of chapter 5, which demonstrated that to a large extent otters followed the trends in overall biomass that were described by these traps, further confirmed their value as a means of gaining a snapshot of overall prey availability to a foraging otter.

A key trend that the placing of these traps at different depths demonstrated was the occurrence of edible crabs in deeper water. Our analysis of the meat within these crabs showed that they were an excellent food source, despite the longer handling time associated with them. Crustaceans have previously been thought of as a poor prey item (for example Watt 1991 and 1993), and eaten largely in times of poor food conditions or during the development of hunting behaviour in young otters (*Ibid.*). However such observations were of shore and velvet crabs, which have very low food values and long handling times (Watt 1991). These are also found in shallower water than edible crabs (Matheson and Berry 1997). While edible crabs also have long handling times, a large period of this is on land, and this may not entirely be an energetic cost, since heat will be no longer lost at the same rate. It may, therefore, be an opportunity for the otter to recover some of the heat lost whilst in the water.

The relationship between available biomass and depth was not a linear one. There is an initial period, up to about 6m were the available biomass is level. However after this, with the occurrence of edible crabs, there is a sharp increase. It also should be pointed out that there may have been more edible crabs available, but they tended to block the entrance to the traps being unable to get through fully. While fish would have been able to get past no other edible crab would. Furthermore, the trap catches in the deeper water, 8 and 10 m, were usually one crab per trap per night, suggesting that this was only a small amount of the available prey but that others simply could not enter the traps.

It has been assumed, however, that this relationship will be the same in all water temperatures, and therefore it does not take into account any season migrations of prey species, although the evidence for such migrations has been called into question

(Sayer *et al.* 1994). A trap regime throughout the year would be required to fully test this assumption.

Overall therefore we have confirmed the findings of the Shetland study, that there is an increase in biomass with depth, but we have also been able to go further and demonstrate the shape of that relationship, which reinforces the question, why are the otters not feeding in deeper water.

9.5.3 Dive Success

Again in agreement with the findings from Shetland, the deeper a dive was, the greater were its chances of success. If we consider dive success as a measure of prey encounter rate, this would suggest to us that the prey is more abundant, or easier to catch in deeper water. Fluctuations in success rate have been related to switches in diet in the sea otter, *Enhydra lutris*, (Estes *et al.* 1981), associated switch was from vertebrate to invertebrate prey, with higher success rates for the latter. Our above description (9.4.2) of a decrease in piscine prey and increase in crustacean prey with depth, could therefore result in the observed increase in diving success.

While Kruuk et al. (1990) advise caution in using diving success as a measure of individual ability or habitat quality, basing their assertion on the homogeneity of success rates among otters observed foraging in different habitats in Shetland. However other studies, (see review in Ostfield 1991) have usefully used comparisons of diving success to determine information on prey type, dietary switching and prey community organisation. Our data demonstrates very significant differences in success rate with depth, and we also see a switch in diet that was not seen in Shetland, therefore there is no reason to view the increase in success rate as anything other than a benefit of feeding at greater depth.

9.5.4. Dive Durations

It is not surprising to note an overall increase in dive time with depth, since the travel time to get to the bottom will be longer. A similar pattern has been found in foraging otters elsewhere, (for example Nolet *et al.* 1993) and is also commonly found in diving birds, (for example Wanless *et al.* 1993, Carbone *et al.* 1996). Such increased dive durations may be associated with greater foraging time (for example Wilson and Wilson 1988) or decreased foraging time (for example Wanless *et al.* 1993). Of particular interest in our data are the differences between successful and unsuccessful dives. On the whole successful dives are shorter than unsuccessful dives, suggesting that otters capturing a prey will surface immediately, if not they will continue foraging for longer and then terminate the dive. The differences between dives are not related just to depth but the shape of the relationship between dive duration and depth is different. The duration of unsuccessful dives increases with depth and then begins to level out, in a power function, suggesting that a limit, such as an aerobic limit (although most dives much shorter than estimates of aerobic dive limits), has been reached. This is consistent with predictions from Houston and MacNamara (1994), provided that we assume that travel time increases with depth. As such, as depth and therefore travel times increase it would be necessary to decrease the actual foraging time. The relationship between depth and foraging time is polynomial; that is after an initial increase then levelling out the times begin to drop again, suggesting that prey in deeper water are in fact easier to catch. This idea fits with the concept of a prey switch, from fishes to crabs, which are easier to catch (Watt 1993). A possible implication from this would be that medium length dives are the least profitable, rather than shallow or deep ones. Nonetheless unsuccessful dives will be decreasingly efficient with depth because of the reduced foraging times and the increased costs. It would, however, be wrong to attach too much importance to the decline in this curve, as it is caused by only one data point. However the data used were means, and so the curve is likely to be evidence of a genuine trend.

9.5.5. Prey handling times

There were very significant differences in the handling times of the different prey items with by far the longest time being for crustaceans. Otters will always climb onto land to eat crustaceans, and it is this, along with the transit time of getting to and from land, that makes their consumption so time consuming. However, as stated above, it is not necessarily correct that this period on land is a cost. In chapter 8 we showed that there was a longer recovery time on land associated both with feeding in colder water and feeding at depth. As such, eating prey on land while costly in terms of time, is not necessarily so in terms of energetics, since heat is not lost as rapidly, and presumably the body begins returning to its resting body temperature and metabolic state.

9.5.6. Heat loss

Our experiments on differential rates of heat loss through the pelt in different water depth were to a large extent preliminary, and a more detailed study would be required, with a number of variables accounted for, in order to accurately determine the precise relationship between heat loss and depth. On the other hand our results are in agreement with one of the basic tenets of physics, Boyle's Law, and we can therefore say with some confidence that there is an increase in the rate of heat loss with depth. However what we cannot do is put this in the context of other variables that affect will heat loss without carrying out more detailed experiments. Such variables include

1. the temperature of the surrounding water, which has been shown to both have an effect on rate of heat loss (for example MacArthur (1984) described increased rates of heat loss in muskrats with depressed water temperatures) and to have no effect (for example Croll and McLaren (1993) describing thermal conductivity of the pelage of murres)
2. the speed of the water current and the swimming speed of the animal will have a positive relationship with heat loss due to an increase in the rate of forced convection, (Hind and Gurney 1996).
3. the salinity, and levels of other solutes, of the surrounding water with affect heat loss due to an increase in thermal conductivity with increased solutes.

Finally some discussion should be given to the relationship between the air layer and buoyancy. While the air layer in the otters pelt confers a thermo-insulatory benefit, there is also a cost in terms of an increase in buoyancy (Wilson *et al.* 1992). Stephenson *et al* (1989) demonstrated that buoyancy is the most important force to be overcome by diving ducks, (the lesser scaup, *Aythya affinis*). While diving at depth will compromise the thermo-insulatory function of the pelt, it will also decrease the buoyancy by the same mechanism, the compression of the air layer, (Wilson et al. 1992), hence actually conferring an energetic benefit to the diver. To further complicate this relationship, during a dive air escapes from the otters pelt, and is visible as a stream of bubbles (Kruuk 1995, *pers. obs.*). Therefore the interacting relationship between heat loss, buoyancy and depth has a further variable to consider, time, with the effect of heat loss increasing with time and that of buoyancy decreasing.

9.5.7. The Use of Depth

From the Nolet *et al.* (1994) hypothesis that increased heat loss prevented otters from foraging at greater depth, we predicted that in warmer waters, otters would forage deeper. Our data confirmed the prediction, but the relationship was more complicated than a simple linear one, and could be summed up by the formula:

$$y = 26.62.x - 3.06.x^2 + 0.11\, x^3 - 63.63$$

This curve showed an initial increase, then a levelling out, and then a sharp increase again. In others words at very low water temperatures, under 4°C, otters are foraging in very shallow water, though in the water at Taynish the temperature never fell below this level, so this is purely hypothetical. The mean foraging depth remains at a fairly constant level through a range of water temperatures and then rises again sharply at the upper range of the temperatures we encountered, above about 14°C. This pattern is consistent with the other data we obtained, and to explain this we must first make reference to our model.

9.5.8 Optimality Model

In the model two general assumptions were made, and these should be dealt with in turn.

1. That the benefits of foraging at greater depth were accurately represented by figure 9.6. While the data we obtained from fish trapping gave a result that matched this figure, our trapping was only carried out during the summer, and so we have no evidence that this is the same pattern throughout the year. The pattern could change in several ways. Migration of prey species could occur, and hence change the overall pattern, for example by moving inshore in the winter. This does occur with gadoids, though these species were not included in our data. Other authors have said that there may be better food in deeper water in the winter, but this was said before the pattern of a winter retreat into crevices was described by Sayer *et al.* (1994), and it was thought that many prey species migrated offshore in the winter. A further change may occur if there are physiological changes to the prey species, such as those due to breeding or starvation. The only way to eliminate these potential sources of error from our data would be to carry out a complete trapping programme through a range of water temperatures

2. That there is a linear relationship between costs of foraging and depth. We have followed the hypothesis that the main cost to foraging otters is the metabolic costs due to loss of heat. Kruuk *et al.* (1994) examined the metabolic costs, as determined by oxygen consumption, of otters in different water temperatures, and described a linear relationship, and similar relationships have been shown in other species, (for example the beaver, MacArthur and Dyck 1990). The rate of heat loss we measured in the experiments with otter pelts also showed a linear relationship between heat loss and depth. Taken together these strongly suggest that we are correct in this assumption.

If the assumptions are reasonable we must examine why the predictions of the model do not entirely fit the data. It is only in the final flattening of the model curve, at the highest temperatures, that the observed data do not fit. It is likely therefore, that the reason why the fit is incomplete is that we were not able to record the full range of temperatures needed, simply because the temperatures in Scottish waters do not get warm enough. We can therefore predict that if otters were foraging in warmer waters, and that such waters had a similar distribution of available biomass, that there would be an optimal depth reached, as in the model, and the otter would not forage deeper than this.

CHAPTER 10

FINAL DISCUSSION AND CONCLUSIONS

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Fluctuations in environmental variables will, to a large extent, define the parameters of foraging behaviour. Such external variables can be considered as components of the animals state (Houston 1993) and the fluctuations in these variables result in a relationship between the animals state and it's behaviour (Mangel and Clark 1988). This relationship will manifest itself by shifts in what can be perceived as the optimal behaviour, as environmental conditions fluctuate. For example, it has been demonstrated that the optimal foraging strategy for three desert seed harvester ant species, *Pogonomyrmex barbatus*, *P. desertorum*, and *P. occidentalis* is to minimise the amount of travel time when loaded with a food item (Morehead and Feener 1998). This travel time is strongly affected by environmental temperature, since it influences running speed, and therefore this can be viewed in terms of a relationship between state, as influenced by environmental temperature, and optimal foraging strategy.

Such environmentally-driven changes in state may have profound effects on foraging strategies, such as prey choice, site selection and the temporal pattern of foraging. Aquatic foragers in particular are influenced by the specific demands imposed upon them by the medium in which they forage. These demands have provided strong selection pressures upon aquatic animals physiological capabilities, such as aerobic tolerance (for example Kooyman and Ponganis 1998) and thermoregulation (e.g. Croll and MacLaren 1993). Therefore most aquatic animals are highly adapted in this regard. However it has been suggested that the Eurasian otter is not highly adapted for the aquatic environment (Kruuk 1995) and as such provides us with an opportunity to examine how the influence of habitat variables on an animals state influence its behavioural parameters.

In this study these parameters were examined for the foraging of the otter, in particular in the context of changes in water temperature. Previous studies have demonstrated that this is a major determinant the metabolic costs of foraging (Kruuk *et al.* 1994). The overall aim here was to determine what, if any behavioural shifts occurred in order to satisfy the increased physiological demands of foraging at low water temperatures. Within this, it was important to separate any possible indirect effects of water temperature, such as those on prey behaviour and habitat quality, which were likely to influence the predator behaviour, from direct effects on the otters physiological demands. We therefore firstly established a prey-monitoring regime around the peninsula, as discussed in chapter 2.

As a tool for measuring the relative abundance of the prey species of the Eurasian otter, stationary fish trapping has, since its initiation by Kruuk *et al.* (1988), been used widely in studies of predator prey relations of this species when it is foraging in salt water (there are other more reliable methods of monitoring fresh water prey such as electro-fishing, see for example Kruuk *et al.* 1993). In many ways it can be considered an imperfect but useful tool, and our results in chapter 2 confirm this. They do this in particular with regard to catches of butterfish, one of the most important prey species at Taynish (chapter 4), and elsewhere (for example Watt

1995). Previously, there had been doubts cast on the reliability of stationary trapping as a means of monitoring populations of this species by the results of Gibson *et al,* (1993), who compared the catches of butterfish from such traps with those from trawling, and found profound differences. Our catches of this species were minimal, despite there being a seeming abundance available to the foraging otters (chapter 4). As such we concluded that we could not derive reliable information on this prey species from fish trapping data.

In terms of the other prey species of the otters at Taynish the trapping provided us with fairly clear information of seasonal and spatial trends in prey abundance and distribution. The species present at Taynish showed some similarities with other studies, (for example Watt 1995), although there were unusually large numbers of both wrasse and gobies, and such differences implied a degree of local inter-habitat heterogeneity. Indeed within the three adjacent habitats of the study site we demonstrated fairly profound differences in species composition and in most of the species that did not show a statistically significant difference this was in all probability due to small sample sizes of these species. There were also marked seasonal differences in prey abundance, notably with eels and some of the gadoids. These are high quality prey items and therefore such variation would be expected to strongly influence patterns of otter predation.

Due to interspecies variation in the behavioural responses to the traps, and therefore catchability, it was not possible to draw direct comparisons of the relative abundance of the prey species. It was however possible to use the data to obtain a snapshot of the overall habitat quality by using biomass as a measure. By doing so it was clear that habitat quality varied seasonally, and it could be predicted that such changes may influence otter predation and use of habitats.

Having determined to some extent the seasonal and spatial fluctuations in prey populations, it was now important to examine the influences this would have on the otter foraging behaviour, and to so it was necessary to examine the actual prey consumed. There were two possible methods of doing so, spraint analysis and direct observation. Both methods have advantages and disadvantages that are discussed in chapters 3 and 4 (see also Kruuk 1995, Carss and Parkinson 1996 and Carss and Elston 1996), but no actual comparison of the two had hitherto been made in the wild. Therefore as well as the overall aim of describing predation patterns of the otters, this study offered the opportunity to make such a comparison for the first time.

Initially however the process of spraint analysis had to be clarified to examine sources of potential error. Recent work by Carss and Parkinson (1996) had demonstrated potential errors in the current methodology, and proposed the use of key bones from the prey skeleton as a more accurate means of assessing diet. Carss and Elston (1996) carried out feeding trials on captive otters to define this for freshwater prey, and in the present study this was attempted for marine prey. It was shown by these feeding trials that while the current method of quantifying diet from spraint analysis (frequency of occurrence) gave a correct rank order of prey numbers, it did not do so for the relative biomass contributed to the diet by each prey type. It was therefore necessary to describe a more accurate method of assessing diet from spraint analysis. This was done with the use of key bones to some extent but further trials are necessary to extend and solidify this work.

While there had already been numerous studies of the diet of the otter, it was necessary to describe it at our study site in order to identify all the influences on foraging behaviour that were acting upon the otters, as part of the overall objective of determining the effects of water temperature. Also, as stated above, it provided us with an opportunity to compare the two methods of diet assessment. Our results by both methods confirmed those of other studies, in that the otters fed almost entirely on bottom-dwelling fish. The two methods were significantly different, and the differences between them were those that one would expect intuitively, for example smaller prey such as gobies, were not detected as commonly as by spraint analysis, and occasional prey items, such as amphibians were not detected at all by observation. Conversely, observational data show the importance of large prey items such as lumpsuckers, which are not detected by spraint analysis. It was therefore concluded that the best way of assessing the otters diet was by a combination of both direct observation and spraint analysis.

It was also demonstrated from these data that there was a degree of dietary preference shown by the otters in that there were large differences in the relative importance of all the prey groups in comparison with the data from fish trapping. In general this preference was shown in the selection of heavier prey items. Seasonal and spatial variation in dietary patterns was also demonstrated. These variations can be explained by in part by prey abundance, for example the sandy habitat has the lowest available biomass, and also is the least used by the otters. Conversely catches in the traps are lowest in the winter but this is when the otters eat the greatest numbers of prey, possibly due to the increased metabolic costs of foraging in the lower water temperatures (Kruuk *et al.* 1994). Therefore, it was demonstrated that one aspect of foraging behaviour, prey choice, was influenced both by prey distribution and by physiological demands. A final trend worth mentioning in these data was the peak in crustacean predation during the autumn, associated with foraging in deeper water. This point will be returned to.

A further aspect of foraging behaviour that may be influenced by fluctuating temperature is the choice of foraging site. The study site was divided into three discreet habitats, and the data from fish trapping (chapter 2) and descriptions of the diet of otters revealed that there were differences between habitats both in the suite of prey available and in the prey items eaten by otters. An investigation into the relative usage of these habitats as foraging sites was then carried out, with the underlying prediction that the otters would choose the habitat with the highest biomass. In each habitat there was a different relationship between water temperature and the total available biomass, in such a way that at 10.7°C there was a switch from which of two habitats (rocky and tidal) had the greatest biomass. If the choice of foraging site was governed by biomass, then it would be predicted that the otters would change their choice as the temperature-mediated shift in which habitat had the highest biomass took effect. In fact these predictions were not met by the data. Although there was an overall preference for the habitat with the highest biomass (the tidal habitat), shifts in usage of the habitats predicted by the fluctuations in biomass were not observed. It was concluded that other factors are involved in the choice of foraging site by otters, such as differences in aspects of the prey other than biomass, in the amount and composition of algal cover, in the species diversity and in the availability of depth.

The foraging behaviour of any predator will be influenced by the behaviour of its prey (Sih 1993), and in an investigation into the effect of an environmental variable on a predator, it is necessary to have some information regarding the effect on the behaviour of the prey. We investigated the effect that water temperature had on the general activity levels and escape responses of some of the piscine prey species of the otter, and consequently whether this caused variation in the capture time of these animals with water temperature. Our results showed that while there was an overall decrease in the activity and escape response of three of the prey species of the otter with depressed water temperatures, there was no evidence of a reduction in the capture times of these species. It is likely that this is can be explained the fact that otters predate on their prey during the point in the prey's activity cycle when the prey are inactive anyway, therefore there is no effect caused by the amount of activity at other times. Implicit in this hypothesis is that the timing of the predators foraging would change as the overall activity of the prey decreased, since the timing is based around the activity of the prey.

Descriptions of the partition of the otters time into an activity cycle had been made previously (Kruuk and Moorhouse 1990), but was only completely carried out in the summer. The conclusions of these authors were that the otters feed when their prey are inactive, during low tide and early morning or late evening. In the present study, we made observations throughout the year in order to determine the effect that the temperature mediated decline in activity of the prey species had on the activity cycle of the otter. It was found that there was no effect of tide on otter activity at any time of year. This effect can be explained by the fact of a small tidal range at Taynish, so there is not a strong enough tidal *zeitgeber* to entrain tidal behaviours in the prey, therefore there is no effect on the otter. However there was a pattern of foraging evident in a daily cycle, similarly to Kruuk and Moorhouse (1990) Shetland study, there was a preference for foraging during the morning, followed by evening and midday was used the least for foraging activity. This pattern changed in winter, when most foraging occurred in the evening. To some extent this matches the prediction that with the decline in the prey's activity associated with winter water temperatures the otters no longer follow the prey activity cycle. This also raises the possibility that coastal otters may forage nocturnally to some extent in the winter.

Much of the study of physiological effects of foraging in water have concentrated on the components of the diving cycle, travel time, foraging time and surface recovery time (for example Walton *et al.* 1998), despite evidence that most of the metabolic costs of such behaviour are met after the foraging bout is completed (de Leeuw 1996). Since the metabolic costs of foraging otters increase with decreasing water temperatures, we would predict from this that greater recovery times would be required after foraging in depressed water temperatures, and this was quantified mathematically in the present study. The results confirmed the predictions, in that recovery periods on land, associated with vigorous grooming, increased relative to the time spent in the water when water temperature was depressed. It was also confirmed that none of the components of the dive cycle showed a strong relationship with water temperature. Therefore it is clear that otters postpone the metabolic costs of heat loss during foraging until after the foraging bout is completed.

Finally, it was noted that the depth of water in which foraging was carried out increased with the water temperature that the foraging occurred at. Particularly associated with this was predation on edible crabs. An examination of this phenomenon by cost benefit analysis was made. It was determined that there was better quality prey in deeper water and that the success of dives was higher. Conversely there was an increase in travel time, prey-handling times were greater and the rate of heat loss was higher in deeper water. Since one of the key costs of foraging to an otter is the metabolic recovery of heat, it would be predicted that they would only forage in deeper water, as indeed was demonstrated by the data. An optimality model derived from the cost benefit analysis suggested that rather than there being a linear relationship between water temperature and depth of foraging, as the temperature of the water increased, there would be a switch between foraging in shallow water to doing so in deeper water. Such a relationship did exist in the data, however there was not the final levelling of the graphical relationship between water temperature and depth predicted by the model. This could be explained by the fact that the water at the study site never reaching the temperatures required for this to be seen.

It can therefore be concluded that water temperature does have a strong influence on the foraging behaviour of the Eurasian otter, and this manifests itself in the following ways:

1. An increase in the numbers of prey consumed in the winter is required in order to compensate for the increased metabolic demands of foraging in colder water.
2. There is a change in the timing of foraging in the winter due to decreased activity of the prey
3. Post foraging recovery times are longer in relation to the length of foraging bout after swimming in colder water, again to compensate for the increased metabolic costs of foraging in colder water
4. In colder water, the otters are restricted in their use of depth, despite better prey being available in deeper water.

The fact that the otter is so affected by cod water temperature raises the possibility that it is temperature limited. An examination of its range (Foster-Turley *et al.* 1990) shows that it does stop short of the arctic circle, so this may well be the case. Furthermore our results are in general agreement with Kruuk's (1995) assertion that otters are not particularly well adapted to an aquatic mode of life.

Our conclusions also indicate that the costs and benefits of foraging are complex for any animal and cannot be looked at in terms of simple handling time and the energetic content of the prey, rather the effects of other variables on the animals state must be taken into account

Implications for otter conservation

The IUCN action plan for otter conservation (Foster-Turley *et al.* 1990) proposed that among the priorities for the conservation of the Eurasian otter was the need to identify the otters ecological needs in order to instigate management programs. In this study we have shown that there is a complex relationship between the otters behaviour and its habitat, particularly with regard to water temperature. There is a degree of variability in the ecological requirements of the otters as its habitat fluctuates, and this must be taken into account when formulating management programs. A key relationship to be incorporated into such a program is that between the otter and its prey, due largely to the evidence that the otter is prey limited (Kruuk 1995). This relationship changes seasonally, with otters having the opportunity to select quality prey items at certain times of year (for example edible crabs when the water temperature is relatively high, chapter 9) and having to exploit poor prey items at others (for example 15-spine sticklebacks in February, chapter 4 and 5). Furthermore, the times of the exploitation of poorest food occurs at the time when the otters metabolic demands due to heat loss are the highest; when the water is the coldest (Kruuk *et al.* 1994). A survey of the causes of mortality of otters in Shetland (Kruuk and Conroy 1991) suggested that the major cause of death was gastro-intestinal haemorrhaging, caused in all probability by starvation. This mortality is highly seasonal (Kruuk *et al.* 1987, Kruuk and Conroy 1991) occurring simultaneously with low food availability (Kruuk *et al.* 1988, chapter 2) and depressed water temperatures (Kruuk 1995). A comprehensive management plan would need to take such fluctuations in habitat quality into account in order to fully protect the animal.

Further research

In order to clarify and reinforce the conclusions of this study, I would recommend that the following further research is carried out:

1. An investigation into the effect of fish behaviour on the success of the stationary traps used in chapter 2.
2. Further feeding trials to extend the data on key bones of marine prey recoverable in spraints (chapter 3).
3. Radio tracking of marine otters to extend our knowledge of habitat use (chapter 5) and activity patterns (chapter 7). The use of thermo-sensitive transmitters would permit further information on the thermal recovery costs of foraging (chapter 8).
4. Refining of the mathematical model of recovery time and water temperature (chapter 8) to include stochasticity in the equation parameters.
5. A trapping regime to investigate seasonal changes in the depth distribution of prey, and the energetic value of the prey.

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